Assessing nest attentiveness of Common Terns via video cameras and temperature loggers

Jeffery D. Sullivan[1] , Paul R. Marbán[2], Jennifer M. Mullinax[3], David F. Brinker[4], Peter C. McGowan[5], Carl R. Callahan[5] and Diann J. Prosser[6*]

Abstract

Background: While nest attentiveness plays a critical role in the reproductive success of avian species, nest attentiveness data with high temporal resolution is not available for many species. However, improvements in both video monitoring and temperature logging devices present an opportunity to increase our understanding of this aspect of avian behavior.

Methods: To investigate nest attentiveness behaviors and evaluate these technologies, we monitored 13 nests across two Common Tern (*Sterna hirundo*) breeding colonies with a paired video camera - temperature logger approach, while monitoring 63 additional nests with temperature loggers alone. Observations occurred from May to August of 2017 on Poplar (Chesapeake Bay, Maryland, USA) and Skimmer Islands (Isle of Wight Bay, Maryland, USA). We examined data respective to four times of day: Morning (civil dawn–11:59), Peak (12:00–16:00), Cooling (16:01–civil dusk), and Night (civil dusk–civil dawn).

Results: While successful nests had mostly short duration off-bouts and maintained consistent nest attentiveness throughout the day, failed nests had dramatic reductions in nest attentiveness during the Cooling and Night periods ($p < 0.05$) with one colony experiencing repeated nocturnal abandonment due to predation pressure from a Great Horned Owl (*Bubo virginianus*). Incubation appeared to ameliorate ambient temperatures during Night, as nests were significantly warmer during Night when birds were on versus off the nest ($p < 0.05$). Meanwhile, off-bouts during the Peak period occurred during higher ambient temperatures, perhaps due to adults leaving the nest during the hottest periods to perform belly soaking. Unfortunately, temperature logger data alone had limited ability to predict nest attentiveness status during shorter bouts, with results highly dependent on time of day and bout duration. While our methods did not affect hatching success ($p > 0.05$), video-monitored nests did have significantly lower clutch sizes ($p < 0.05$).

Conclusions: The paired use of iButtons and video cameras enabled a detailed description of the incubation behavior of COTE. However, while promising for future research, the logistical and potential biological complications involved in the use of these methods suggest that careful planning is needed before these devices are utilized to ensure data is collected in a safe and successful manner.

Keywords: Common Tern, iButton, Nest attentiveness, *Sterna hirundo*, Temperature logger, Video monitoring

*Correspondence: dprosser@usgs.gov
[6] U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708, USA
Full list of author information is available at the end of the article

Background

Although avian reproductive success is tied to many factors, nest attentiveness, defined as the time at least one

adult is present on the nest (Nisbet 2017), plays a large role in determining if a nest will successfully hatch (Martin 2002). The effect of nest attentiveness on nest success appears intuitive, at least for surface-nesting species, as eggs are protected from a variety of threats during on-bouts, when an adult is on the nest, and vulnerable during off-bouts, when the nest is unattended (Martin 2002). However, natural systems are rarely this simple, and the incubation process is no exception as birds are constantly presented with situations that require leaving their nest. While the exact challenges and subsequent responses vary by species and respective habitat use and nesting practices, this concept is best illustrated by focusing on a family such as Laridae, which generally nest colonially in open habitat where these challenges are exacerbated.

One factor that impacts nest attentiveness is extreme weather. For species that nest in open habitat there is little to buffer eggs from challenging conditions such as temperature extremes or precipitation. Thus, Larids will often remain on the nest during especially challenging periods, exposing themselves to ameliorate conditions for their eggs (AlRashidi 2016; Hart et al. 2016). For instance, Common Terns (*Sterna hirundo*; hereafter COTE) have their highest nest attendance during cold precipitation events or midday heat (Nisbet 2017). However, during extended periods of high temperatures, adult COTE may leave the nest and soak their bellies and feet in water before quickly returning to the nest. This soaking can have several functions including cooling the adult, cooling the eggs, and increasing nest humidity (Grant 1981; Nisbet 1983) and has been observed in numerous terns (e.g. Grant 1982; AlRashidi 2016; Kar and Debata 2019) and other Larids (Grant 1978; Hand et al. 1981). Unfortunately, even short exposure to high temperatures can impede development or kill embryos (Webb and King 1983) presenting adults with a tradeoff between cooling themselves and maintaining nest humidity versus limiting the exposure of their clutch to dangerous conditions. This tradeoff is reduced by the fact that COTE engage in biparental care (Nisbet 1983), allowing individual parents to leave the nest without risking nest exposure, but this still does not result in continuous nest attentiveness.

A second factor known to dramatically impact nest attentiveness is the presence of predators. As colonial nesters, Larids have two main responses to predators. First, birds may aggressively mob a predator in an effort to drive it away from the colony (Gotmark and Andersson 1984; Palestis 2005; Mallory 2016), though the level of aggression towards the predator is likely a function of adult size and experience with the predator (Clode et al. 2000; Nordstrom et al. 2004). The second response to predator presence is the forming of large evasive flocks composed of numerous adults (Burger and Gochfeld 1991; Meehan and Nisbet 2002), which can occur as generally short duration upflights (normally diurnal) or longer duration desertions (generally nocturnal). While there have been multiple reports of entire colonies flocking at once to evade a predator (Wendeln and Becker 1999; Meehan and Nisbet 2002), this may not always be the case (Arnold et al. 2006). Interestingly some species, such as Little Terns (*Sternula albifrons*) have been found to decrease the duration of their evasion when ambient temperatures are particularly high (Amat et al. 2017). While mobbing generally removes the threat presented by the initial predator, it leaves eggs vulnerable to other predators that are normally forced away (Nisbet and Welton 1984), increases the risk to the adults, and leaves eggs exposed to the elements. Similarly, while evasion increases the adult's odds of survival, it leaves the nest completely unattended. As would be expected, nest attentiveness and nest success are both reduced in colonies that experience heavy predator presence (Morris et al. 1976).

Finally, proximity to food sources and prey availability can also affect nest attentiveness rates. The availability of food leads to a tradeoff between incubation and foraging in which adults must balance foraging for themselves with incubating their eggs (Martin 1987; Deeming and Reynolds 2015) though biparental care does help lessen these divergent demands. Still, the more time adults spend incubating eggs, the shorter overall time required before the eggs hatch and the less time they are vulnerable to predation or adverse weather conditions (Morris and Hunter 1976; Vedder et al. 2017). Conversely, if adults must expend more time foraging, the incubation period is extended, and the period of risk is prolonged (Morris and Hunter 1976; Vedder et al. 2017) or nests can be completely abandoned (Neumann et al. 2018). Additionally, adults may not be able to access prey items evenly throughout all periods of the day. For instance, Saunders's Gulls (*Chroicocephalus saundersi*), which feed on mudflats, have been found to increase incubation with higher sea levels regardless of time of day suggesting a tradeoff between incubation and temporal food availability (Yoon et al. 2014).

While previous work has revealed a good deal about nest attentiveness in colonially nesting Larids such as COTE, there is still much to be learned regarding fine-scale behaviors that may have been missed by early work that was limited to either human observation (Wiggins and Morris 1987; Shealer and Kress 1991) or reported data at low temporal resolution (i.e. day vs night; Morris and Hunter 1976). Fortunately, recent work with techniques such as camera traps (Norwood 2011; Hart et al. 2016), RFID loggers (Bonter and Bridge 2011; Riechert and Becker 2017), temperature loggers (Arnold et al.

Sullivan *et al. Avian Res*   (2020) 11:22

Page 3 of 18

2006; Norwood 2011) and egg loggers (Shaffer et al. 2014; Taylor et al. 2018) appears to provide a promising means to resolve the dearth of high temporal resolution nest attentiveness data. For example, Arnold et al. (2006) used temperature loggers to quantify the period of time COTE deserted their nests when evading owl predation pressure. Similarly, during their study of COTE Riechert and Becker (2017) used a data-logging system to identify if parents were at the nest site at ~ 10 s intervals, allowing them to report how long nests were left unattended during both day and night periods and the influence of prior breeding experience on parental nest attentiveness. However, despite their sound methodology and multiple contributions, previous works have not answered all relevant questions concerning COTE nest attentiveness patterns that require fine-scale temporal data. For instance, insight into differences in behavior across time of day and how this relates to nest and ambient temperature has yet to be quantified for COTE (Nisbet 2017). Answering these questions could shed light on how observed nest attentiveness impacts nest success and could allow managers to better recognize and respond to factors impacting colonies of concern.

The recent advancements in monitoring technologies provide a unique opportunity to improve our knowledge of the fine scale details of nest attentiveness across times of day and their impact on the nest. The objective of this study was to characterize nest attentiveness in COTE while also exploring the ability of both remote video monitoring and temperature-logging devices to be used to gather such data independently and as part of a paired system. The specific objectives were to: (1) quantify COTE nest attentiveness rates by frequency and duration of attendance, and determine how these may relate to the reproductive success of the observed colonies, (2) examine the practicality of remote video data collection on COTE nests for reproductive monitoring, and (3) evaluate the ability of data collected via temperature loggers to determine nest attentiveness by comparing these data to paired video evidence.

Methods
Study area
We conducted this project at the two known long-term active breeding sites of COTE in Maryland, USA during the 2017 nesting season (May–August). The first of our two sites was the Paul S. Sarbanes Ecosystem Restoration Project at Poplar Island (38.762° N, 76.384° W; hereafter Poplar). The restoration of Poplar is the product of a partnership between the U.S. Army Corps of Engineers and the Maryland Department of Transportation Maryland Port Administration (Maryland Environmental Service 2017) focused on the beneficial use of clean dredged

material to restore remote island habitat. The breeding population of COTE on Poplar has been the highest, on average, in the state for the past several years. While terns bred at various locations on Poplar, our work (2017) focused on the largest breeding site located in the northwest corner. This colony encompassed ~ 0.45 ha, with 227 marked nests from an estimated 182 breeding pairs. While the colony was long and narrow, it was a clearly defined colony with no nests located in outcroppings away from the main colony.

Our second study location was Skimmer Island (38.336° N, 75.094° W; hereafter Skimmer), a small uninhabited island in the Isle of Wight Bay along the Maryland portion of the Atlantic seaboard. The island has been an important nesting site for COTE in recent decades but has a history of colony collapse due to extensive predation by Great Horned Owls (GHOW) (*Bubo virginianus*). Additionally, Skimmer has been slowly eroded by waves and boat wake action (Maryland Department of Natural Resources 2016). During our study (2017) the colony encompassed ~ 0.04 ha, with 151 marked nests from an estimated 123 breeding pairs. Terns occupied the southern portion of this island in a circular colony containing all nests on the island, though the colony occupied only ~ 1/3 of the available sand habitat.

Nest success
As part of routine colony monitoring, we marked and monitored all nests within the COTE colonies associated with this project during the incubation/hatching period. Colony monitoring consisted of researchers walking through the colony (2–3 times weekly for Poplar; once weekly for Skimmer) in a line abreast formation identifying and marking new nests, recording the number of eggs and their condition by nest, and capturing chicks for banding with plastic field readable bands and metal U.S. Geological Survey bands. Unfortunately, due to the low sampling interval at Skimmer, we were not able to estimate the hatching success of each nest within the colony, instead determining fate only for camera-monitored nests. However, determining hatching success of monitored nests was possible on Poplar. We considered a nest on Poplar to have likely hatched if eggs were no longer found in the nest within 19–31 days after the clutch initiation date, unless (1) sign of failure was present (i.e., sign of predation, nest wash out, etc.) in which case it was considered confirmed failed, or (2) a chick was captured or observed in which case it was considered confirmed hatched. Eggs gone from the nest prior to 19 days or remaining after 31 days of clutch initiation were considered likely to have failed. While incubation length has been reported to vary between approximately 21–29 days (Hays and LeCroy 1971; Burger and Gochfeld

Sullivan *et al. Avian Res*   (2020) 11:22

Page 4 of 18

1991; Arnold et al. 2006), we used a slightly wider range as nests were not monitored daily. Since hatching and fledging success is known to be lower for nests established later in the season when less experienced nesters generally breed and environmental conditions are harshest (Arnold et al. 2008), we differentiated between original and re-nesting attempts based upon the date at which a large number of individuals were documented arriving at the colony following the collapse of a nearby colony (a separate sub-colony on Poplar Island, ~3 km from focal colony) due to predator pressure. Additionally, we examined the maximum number of eggs in completed clutches on Poplar, though a comparison with nests on Skimmer was not performed due to the longer interval between nest monitoring. Only nests where eggs were present and appeared viable to observers during two consecutive observations were included to avoid including nests where egg laying may have been interrupted by predation or weather events and thus may show an artificially low number of eggs. Hatching success and number of eggs were separately examined based on the type of equipment at the nest (camera + iButton, iButton only, or no equipment) via linear regression in R 3.3.3 (R Core Team 2018). A Tukey test was used to make comparisons within groups of all nests or original nests only, with no between group comparisons. Though the location of nests within a colony is known to impact nest survival (Hunt and Hunt 1975; Antolos et al. 2006), it is not accounted for in this analysis as the colony is long and narrow making differentiation between nests on the interior versus edge of the colony difficult and likely arbitrary.

Video data collection

In order to continuously monitor both nest attentiveness and colony behavior without regular disruption, six cameras were placed in each colony, and each camera was connected to the same eight channel DVR. On Poplar, the wireless receivers for these cameras were secured to the wall of a waterproof container housing the DVR using duct tape. On Skimmer, receivers were secured to 3 m tall PVC pipes to provide a clear line of sight between the receivers and cameras over tall vegetation. At each site, five of the cameras were placed at individual nests and one camera was placed on an elevated post at the edge of the colony facing the length of the colony for overall predator detection. Cameras were scattered as much as possible to limit spatial correlation but kept to a confined portion of the colony to minimize the amount of wire running through the colony to power cameras. To ensure that cameras would not be used as a perch by potential predators, bird spikes were secured to cameras and the posts on which they were mounted. Video was recorded continuously from a 78° field of view in 720 p resolution

at a frame rate of 25 fps. The camera's built-in IR light was able to record video at a minimum illumination of 0 lx. All cameras within a colony recorded their data to a single 1 to 4 TB hard drive, capable of storing ~1.5 weeks of video data, within the DVR. These hard drives were replaced during colony surveys to avoid reaching storage capacity. Video-surveillance systems were installed at colonies on both Poplar and Skimmer once a majority of nests in the colony contained at least two eggs in an effort to provide birds the opportunity to acclimate prior to the start of incubation (Nisbet and Cohen 1975; Nisbet et al. 2017). Cameras were relocated to other nearby nests entering the incubation stage when nest failure or hatching was apparent to colony observers. A full description of the video-monitoring system design and installation can be found in Wall et al. (2018).

To review video, the hard drive from the field DVR needed to be removed and placed into an in-lab DVR for processing. Video was reviewed one channel at a time in 24-h segments at four times normal speed. Video reviewers documented each time an adult left and returned to the nest to the nearest minute resulting in a data file that listed the status of the nest (adult on or off the nest) at every one-minute interval for which video existed. Any change in status that lasted less than 1 min (i.e. nest left exposed during mate switching or upflights) was not included as we sought to view attentiveness as a status of the nest and not the individual parents. While behaviors at the nest such as mate switching were also documented during review, they were not further analyzed (see "Results" section). Finally, when reviewing colony camera video, reviewers noted the number of times adults flocked and, when determinable, the cause for the flocking. The limited range of IR lights (only a few meters in front of the camera were visible) prevented review of colony camera video between 22:00 and 04:00 nightly. It should be noted that this limitation on the review of nocturnal footage was present only for the colony camera, as nest cameras were close enough to nests to overcome this limitation.

iButton data collection

Similar to our placement of cameras, we placed Thermochron® iButtons (model Nos. DS1921G, DS1921H, DS1922L; Maxim Integrated, San Jose, CA; hereafter iButtons) throughout both colonies in a sub-sample of active nests containing two or more eggs (37 on Poplar and 39 on Skimmer; Nisbet and Cohen 1975; Nisbet 2017). All nests monitored by video cameras had iButtons, ensuring comparability of datasets. While video-monitored nests, and thus the iButtons within them, were spatially clustered to facilitate powering of the cameras, the remaining iButtons were dispersed

Sullivan *et al. Avian Res* (2020) 11:22

Page 5 of 18

throughout both colonies. We placed iButtons into a ring of craft foam to prevent the iButtons from damaging eggs as they were rotated by the incubating adult. To maximize likelihood of the iButton remaining within the nest we attached them to 15 cm plastic tent stakes using Velcro® and then placed them in the center of nests flush with the nesting substrate at the bottom of the nest cup. These methods are a modification of those described by Hartman and Oring (2006). Since iButtons cannot detect changes in temperature sooner than 3 min (Maxim Integrated, San Jose, CA) we set this as our sampling interval and interpolated between recorded temperatures through use of the "na.interpolation" function within R to reach the same minute by minute precision as video data. In instances when data was not recorded for > 5 min, due to an internal error causing a missed recording cycle or lost data, interpolation was not performed. It is critical to recognize that this approach is intended to monitor the temperature of the nest bowl in an effort to determine attentiveness, and will not provide exact egg temperatures.

Data manipulation and supplementation
Climatological data
While efforts were made to collect local climatological data directly at the study sites, complications with in-colony weather stations resulted in unusable data and required the use of external data sources. Thus, we gathered temperature and barometric pressure data for 1 June to 31 July 2017 from National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information stations WBAN:00124 (38.976° N, 76.333° W) and WBAN:93786 (38.308° N, 75.124° W) to approximate weather conditions on Poplar and Skimmer Islands, respectively (NOAA 2018). These stations were chosen as they were within ~ 10 km of their respective colonies. Since temperature and barometric pressure were recorded approximately every 20 and 60 min, respectively, these data were then interpolated for each 1 min interval between recorded observations of less than 59 min in length using the same method as described above and paired with corresponding video and iButton data.

Time-of-day bins
We assigned each minute increment of paired video and iButton data to a distinct time-of-day bin. The Morning bin ranged from civil dawn through 11:59 EDT, Peak from 12:00 through 16:00 EDT, Cooling from 16:01 EDT until civil dusk, and Night from civil dusk until civil dawn. Civil dusk and dawn were based on the times reported by the United States Naval Observatory weather stations in Cambridge, MD (38.561° N, 76° 76.079° W)

and Ocean City, MD (38.406° N, 75.060° W) for Poplar and Skimmer, respectively (U.S. Navy Observatory 2016). The Peak bin was set based upon manual review of the data, with the time (s) of peak daily temperature per day recorded across the study period per site. We then found the nearest hours (noon to 16:00) that would contain > 95% of these peak times.

Analysis
Natural bout characteristics
After all data supplementation and manipulation was complete we identified all bouts, or consecutive periods of time in which an adult was present (on-bout) or absent (off-bout) from the nest, based on the on/off statuses generated during video review. The minimum consecutive length of time required to be labelled a bout was 1 min, as this was the precision with which video data was recorded. Bouts before or after periods when video was not recorded or was not viable due to interference providing an "out-of-range" error, were discarded since one could not accurately confirm the actual duration of the bout. Similarly, bouts at the beginning or end of the entire sampling period, and bouts during or immediately surrounding in-colony researcher presence were discarded. This approach was designed to provide a basic understanding of nest attentiveness rates while also providing researchers with a general description of how adults behaved naturally. Since attentiveness and related behaviors are known to differ among egg laying, incubation, and hatching (Courtney 1979), we only included data from the date of clutch completion (when nest was observed to have all eggs eventually deposited) until the date of first chick hatch (successful nests; Courtney 1979) or 31 days after clutch completion (failed nests). For nests that had no new eggs deposited after cameras were in place (suggesting the clutch was already complete) the first 2 days of footage were discarded to allow for the birds to acclimate to the presence of the equipment.

We used three metrics to summarize nest attentiveness and the impact on the nest during natural bouts: bout duration, mean bout temperature, and overall nest attentiveness. Bout duration, or the time from beginning to end of a bout, was calculated for each natural bout documented in our study period without respect for time-of-day as there is no biological reason to expect these behaviors to fall smoothly within the artificially created bins. Instead, this metric was grouped by bin during which the bout originated. Since both data and residuals were non-normally distributed we calculated the mean, median inter-quartile range, and standard deviation of bout duration by time-of-day, nest success, and attentiveness status and compared these distributions via a pairwise Wilcoxon rank sum test using the Benjamini

and Hochberg correction via the "pairwise.wilcox.test" function in R. Mean bout temperature, or the average of all iButton temperature data during natural bouts, was calculated by attentiveness status (on or off nest) and nest success for each time-of-day bin. Differences between mean bout temperatures were examined via linear mixed effects models using the 'nlme' package in program R (temp ~ time-of-day bin + nest attentiveness status + nest success + time-of-day bin: nest attentiveness status + time-of-day bin: nest success + nest attentiveness status: nest success, random = ~ 1|Nest ID). Least squares means and pairwise comparisons were calculated via the "emmeans" function in R.

Finally, to evaluate nest attentiveness, we calculated the percentage of time an adult was on the nest during natural bouts per bin by day and nest. Percent attentiveness was only generated for bins with at least half of their durations composed of natural bouts to avoid skewing data with short duration samples. We then used a Beta regression to evaluate differences in nest attentiveness (percent nest attentiveness ~ time-of-day bin + nest success + time-of-day bin:nest) success via the "betareg" function in R. Since beta regression requires data bounded between zero and one, bins with values of zero or one were transformed via the formula $x' = \frac{x(n-1)+s}{n}$ (Smithson and Verkuilen 2006) where n is sample size and s is a numerical constant set to 0.5. Least squares means and pairwise comparisons were then calculated via the "emmeans" function in R.

Bout status comparative modeling

We identified comparison bouts (bouts to use for comparing status assigned via video review and via iButton modeling) in the same fashion as natural bouts with the following exceptions: (1) bouts which occurred when researchers were within the colony were similarly discarded but bouts before or following research presence were not discarded and (2) bouts before video data went out of range were retained. Since comparison bouts were only for use in modeling the ability of iButton data, when paired with other covariates, to determine if an adult was on or off of the nest and not the description of bouts characteristics, the full restrictions set for natural bouts were not necessary here. Only footage determined to be within the incubation period was included in comparison bouts as thermal properties of the nest may change as chicks hatch and eventually leave the nest cup.

We tested a suite of six a priori logistic regression models against a subset of the comparison bouts dataset to determine the best-fit model for determining nest attentiveness based on iButton and climatological data. The subset of the comparison bout dataset was created such that it contained only records that had a value for

all covariates used in the most complex model. This was completed to ensure that sample size would not change between models and invalidate AIC comparison (Konishi and Kitagawa 2008). We ran all models by time-of-day bin and compared them based on AIC score (Konishi and Kitagawa 2008). After best-fit models were selected for each time-of-day bin, we further split data into training (25%) and testing (75%) subsets via a stratified random sampling of the on vs off comparison bouts. The training subsets were then used to inform the previously determined best-fit models. Following model fitting, we used the "predict" function in R to determine the predicted probability of each record in the testing dataset being part of an on-bout. All points with a predicted probability of an adult being on the nest < 0.5 were considered off while the remainder was classified as on. We then compared outcomes to the status assigned via video classification (assumed as truth since status could be visually confirmed) and the percentage of data correctly predicted was calculated by probability bins and by the duration of the bout with which each record was associated.

Results

We placed cameras at a total of 14 nests (9 on Poplar and 5 on Skimmer). However, one Poplar nest failed within 3 days of deployment causing the camera to be relocated and the data discarded for all analyses except nest success rates leaving us with 13 camera-monitored nests. In total, cameras captured more than 5000 h of video. An additional several thousand hours of video were lost due to various technological problems (see "Discussion" section). Once inviable (out-of-range) footage and video from outside of the incubation period was removed, approximately 3300 h of usable video data remained. When considering only the data classified as 'natural bouts' (periods when birds were on/off of the nest that were fully observed and without researchers in the colony; see "Methods") our dataset consisted of approximately 313, 146, 190 and 262 h of data on Poplar and 303, 211, 297, 375 h of data on Skimmer during Morning, Peak, Cooling, and Night periods, respectively. We monitored a total of 76 nests with iButtons (37 on Poplar and 39 on Skimmer), of which nine (Poplar: 4, Skimmer: 5) were lost due to nest wash-out, removal by parent, or other unknown reasons. During colony surveys, 18 iButtons (8 on Poplar and 10 on Skimmer) were discovered buried under an average of 3.18 and 1.39 cm of nesting substrate on Poplar and Skimmer, respectively. However, none of the iButtons paired with cameras were buried. Foam rings surrounding iButtons were removed by unknown means from nests on five occasions (four on Poplar and one on Skimmer). The largest issue with iButtons was the loss of data due to reaching storage capacity

when access to our island field site was preempted by weather. More than half (51.35%) of Poplar iButtons had > 10 d of lost data whereas only a single iButton on Skimmer lost this much data (14 d).

During video review, several disturbances were noted, all of which occurred on Skimmer. In every instance, nests were temporarily abandoned while the disturbance was present in the colony. Domestic Dogs (*Canis lupus familiaris*) were observed walking among nests on 11 June and 23 June 2017 and fishermen were observed walking along the edge of the colony twice on 6 June 2017. Additionally, GHOW, a key nocturnal predator of COTE, were detected at individual nests on nine separate instances. In one instance, we observed a GHOW depredation of a chick near the nest. While some behaviors such as flocking and mate switching were observed, these behaviors appeared sporadic and were not analyzed further.

Nest success

Hatching success on Poplar did not differ for all nests in the colony or the subset of only original nests (those in the first wave of nesting) based upon the equipment at the nest site ($p > 0.05$; Table 1). It should be noted that the original nest with a camera that failed on Poplar was the result of the nest washing out and that the nest had not been abandoned following camera placement. However, all nests with cameras on Skimmer failed and, though we did not evaluate nest success on Skimmer due to the infrequent sampling intervals, the colony at large seems to have had minimal hatching success, with only five out of 149 nests confirmed to have hatched a chick. The low nest success is likely due to predation from GHOW as several adults (> 3, though

detailed records of adult mortality were not kept) were found depredated during colony surveys, and nightly colony abandonment while the GHOW entered the colony was observed via both nest cameras and the colony camera. Additionally, 25 nests showed clear signs of egg predation, likely from a Black-crowned Night Heron (*Nycticorax nycticorax*) observed near the colony, but this cannot be confirmed. However, the actual number of nests predated could be much higher as eggs that were wholly consumed would be difficult to assign to predation.

While cameras were not observed as having caused direct damage to the eggs or nest structures of any nests (i.e., via equipment dislodging and hitting nests), suspected egg damage from iButtons was documented once on Poplar and 11 times on Skimmer. Of these damaged eggs, only the Poplar egg hatched while all damaged Skimmer eggs are assumed to have been depredated. Interestingly, while most COTE nests on Poplar without any monitoring equipment consisted of three egg clutches ($n = 176$, $\bar{x} = 2.61$ eggs), all but one camera-monitored nest contained only two eggs ($n = 9$, $\bar{x} = 2.11$; Tukey HSD: $q_{3,210} = 3.338$, $p = 0.033$; Table 2). Similarly, all camera-monitored nests on Skimmer contained only two egg clutches, but infrequent monitoring and consistent predator pressure precluded analysis of these data as it was not possible to determine complete versus incomplete clutches.

Natural bout characteristics

While on and off-bout durations varied widely between and within nests at Poplar and Skimmer, most off-bouts were relatively short with median bout duration of successful nests on Poplar ranging from 2 min during the Cooling period to 4 min during the Morning period

Table 1 Impact of cameras and iButtons on the hatching success of Common Tern nests

	Equipment at nest	Confirmed hatched	Likely hatched	Confirmed failed	Likely failed	Total nests	% Success[b]
All nests	No equipment	98	28	53	11	190	66.3
	With iButtons	17	7	4	0	28	85.7
	With iButton + camera	5	0	3	1[a]	9	55.6
Original nests	No equipment	90	16	23	9	138	76.8
	With iButtons	14	5	0	0	19	100
	With iButton + camera	5	0	0	1[a]	6	83.3

[a] The camera was removed from the nest site before a definitive status could be determined, though all signs point to nest failure

[b] Hatching success (%) was determined by equipment class using the following formula: (Confirmed hatched + Likely hatched)/Total nests × 100

The impact of cameras and iButtons on the hatching success of all Common Tern nests in the focal colony at Poplar Island based upon colony survey data. We differentiated between original and re-nesting attempts based upon the date at which a large number of individuals were documented arriving at the colony following the collapse of a nearby colony. We considered a nest to have likely hatched if eggs were no longer found in the nest within 19–31 days after the clutch initiation date, unless (1) sign of failure was present (i.e., sign of predation, nest wash out, non-pipping related holes, etc.) in which case it was considered confirmed failed, or (2) a chick was captured or observed in which case it was considered confirmed hatched. Eggs gone from the nest prior to 19 days or remaining after 31 days of clutch initiation were considered likely to have failed

Sullivan *et al. Avian Res*   (2020) 11:22

Page 8 of 18

Table 2 The impact of cameras and iButtons on the number of eggs in Common Tern nests

	Equipment at nest	Number of eggs					Significance[a]
		1	2	3	4	$\bar{x}$	
All nests	No equipment	8	54	113	1	2.61	A
	With iButtons	1	11	16	0	2.54	AB
	With iButton + camera	0	8	1	0	2.11	B
Original nests	No equipment	3	26	94	1	2.75	A
	With iButtons	0	8	11	0	2.58	A
	With iButton + camera	0	6	0	0	2.00	B

[a] Different letters signify statistically significant ($p < 0.05$) differences as determined via linear regression between groups within a nest classification (All nests or Original nests). A Tukey honestly significant difference test was used to make comparisons within groups of all nests or original nests only, with no between-group comparisons

The impact of cameras and iButtons on the number of eggs in all Common Tern nests with completed clutches within the focal colony on Poplar Island based upon colony survey data. We differentiated between original and re-nesting attempts based upon the date at which a large number of individuals were documented arriving at the colony following the collapse of a nearby colony
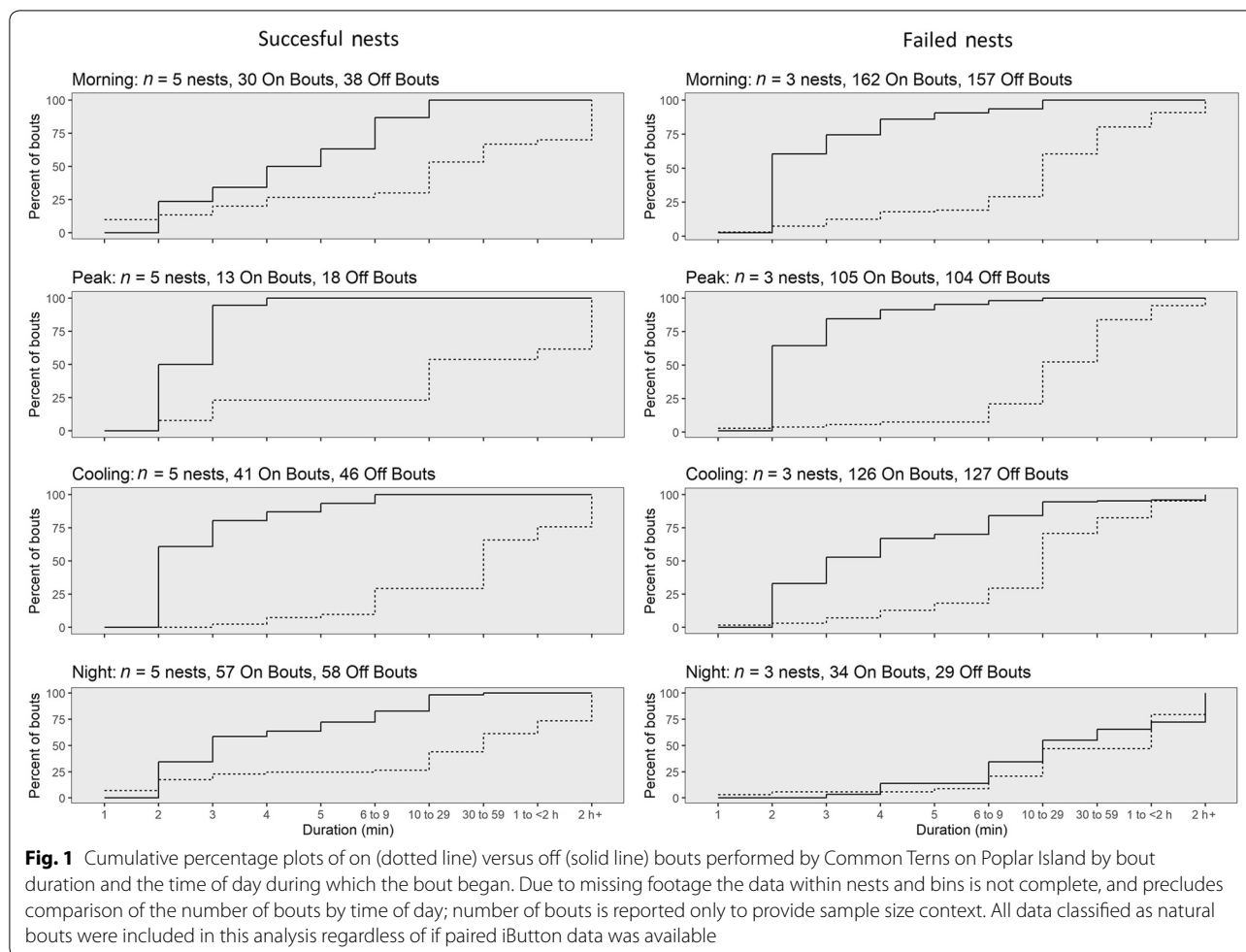
(Table 3; Figs. 1 and 2). On-bouts were generally longer than off-bouts across all times of day. For instance, successful nests on Poplar had median on-bout durations of 23, 22, 36, and 44 min versus off-bout durations of 4.5, 2.5, 2, and 3 min during the Morning, Peak, Cooling, and Night periods, respectively. The exception to this trend was the disproportionately large percentage of on-bouts during the Night period on Skimmer (all of which were

Table 3 The numeric summary of Common Terns on and off-bout durations

Site	Time of day	Status	Nest successful	n	$\bar{x}$	SD	Median	IQR	Significance[1]
Poplar	Morning	On	Y	30	214.83	372.07	23	204	DEF
		Off	Y	38	5.97	4.87	4.5	4	A
	Peak	On	Y	13	161.62	284.19	22	146	DEF
		Off	Y	18	2.56	0.62	2.5	1	B
	Cooling	On	Y	41	128.56	333.39	36	111	DEF
		Off	Y	46	2.83	1.37	2	1	B
	Night	On	Y	57	137.35	238.38	44	118	C
		Off	Y	58	5.41	5.42	3	4	A
	Morning	On	N	162	47.90	85.00	20	34.25	DE
		Off	N	157	3.71	4.43	2	2	B
	Peak	On	N	105	36.80	39.15	28	35	DEF
		Off	N	104	2.83	1.92	2	1	B
	Cooling	On	N	126	31.71	40.77	17.5	27.75	D
		Off	N	127	31.55	129.06	3	5	A
	Night	On	N	34	64.29	75.09	31.5	70.75	EF
		Off	N	29	126.07	179.98	19	243	DEF
Skimmer	Morning	On	N	133	162.74	536.74	42	126	A
		Off	N	142	2.55	3.29	2	1	B
	Peak	On	N	103	69.50	82.26	37	108.5	A
		Off	N	109	3.75	6.45	2	1	C
	Cooling	On	N	373	27.87	37.06	13	29	D
		Off	N	410	32.03	117.18	2	2	E
	Night	On	N	48	242.21	253.61	147	280.25	F
		Off	N	30	214.50	267.27	74	413	ADFE

[a] Different letters signify statistically significant differences ($p < 0.05$) in distributions based upon a pairwise Wilcoxon test with a Benjamini & Hochberg correction

The numeric summary of the duration (minutes) of on and off-bouts by Common Terns at nests on Poplar and Skimmer Islands as a function of the time of day during which the bout began and whether or not the nest is thought to have hatched at least one chick

Fig. 1 Cumulative percentage plots of on (dotted line) versus off (solid line) bouts performed by Common Terns on Poplar Island by bout duration and the time of day during which the bout began. Due to missing footage the data within nests and bins is not complete, and precludes comparison of the number of bouts by time of day; number of bouts is reported only to provide sample size context. All data classified as natural bouts were included in this analysis regardless of if paired iButton data was available

failed nests) that lasted two or more hours (58.3%). Off-bout duration fluctuated more than on-bout duration across time-of-day bin, with off-bouts being shortest during the Peak period and longest during the Night period across study sites. As with on-bouts, off-bouts during the Night period at Skimmer were particularly long, often encompassing the entire night (50% were ≥ 2 h). The largest difference between successful and failed nests on Poplar was at Night when failed nests had longer off-bouts than successful nests (median durations of 19 versus 3 min, respectively).

At both Poplar and Skimmer, mean nest temperature followed expected daily trends, with temperatures lowest at Night and rising during the Morning before reaching their highest levels during the Peak bin and steadily declining during the Cooling bin. For instance, on Poplar successful nests had mean temperatures of 27.4, 31.8, 30.8, and 26.6 °C during Morning, Peak, Cooling, and Night, respectively when birds were on the nest (Fig. 3). On Poplar, while failed nests had generally higher temperatures at all times of day than

successful nests, failed nests for which we had usable data all occurred later in the season when ambient temperatures were higher. The greatest differences in nest temperature between on and off-bouts, across locations and regardless of nest success, occurred during the Peak period, when temperatures were higher with birds off the nest (Poplar Successful: $\bar{x} = 31.8$ (On) vs 33.8 °C (Off), $t_5 = 9.322$, $p \leq 0.001$; Poplar Failed: $\bar{x} = 36.3$ (On) vs 37.1 °C (Off), $t_6 = 5.018$, $p \leq 0.001$; Skimmer Failed: $\bar{x} = 30.5$ (On) vs 31.8 °C (Off), $t_3 = 6.450$, $p \leq 0.001$), and Night period which expressed the opposite trend with higher temperatures when birds were on the nest (Poplar Successful: $\bar{x} = 26.6$ (On) vs 24.4 °C (Off), $t_5 = -11.125$, $p \leq 0.001$; Poplar Failed: $\bar{x} = 31.6$ (On) vs 28.2 °C (Off), $t_6 = -57.206$, $p \leq 0.001$; Skimmer Failed: $\bar{x} = 24.6$ (On) vs 21.7 °C (Off), $t_3 = -30.284$, $p \leq 0.001$; Fig. 3).
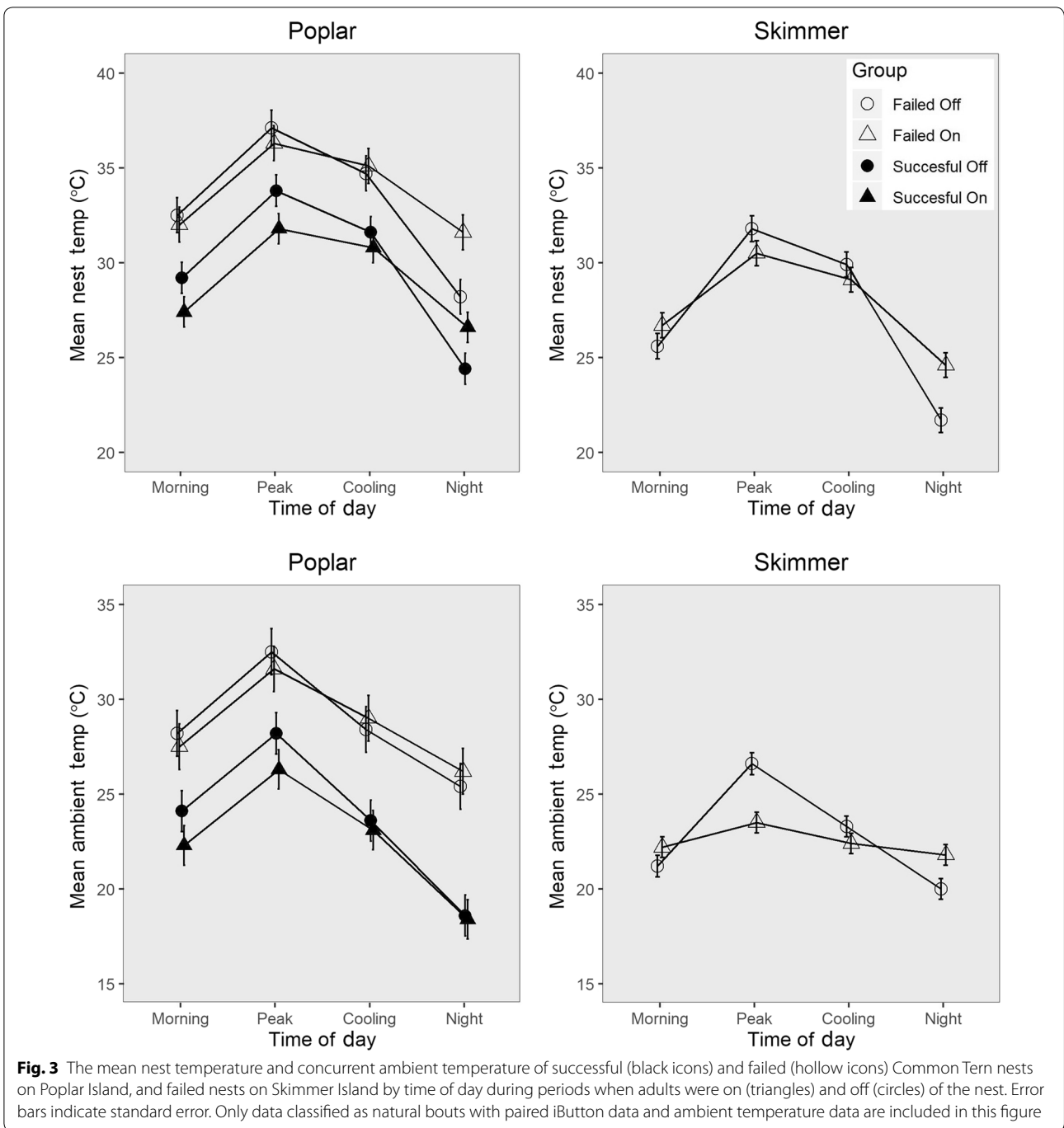
Nest attentiveness also showed similar trends between study sites, with failed nests having dramatically lower attentiveness rates during the Night bin (Poplar: $\bar{x} = 0.153$, Skimmer: $\bar{x} = 0.334$) than during

Sullivan *et al. Avian Res*   (2020) 11:22

Page 10 of 18
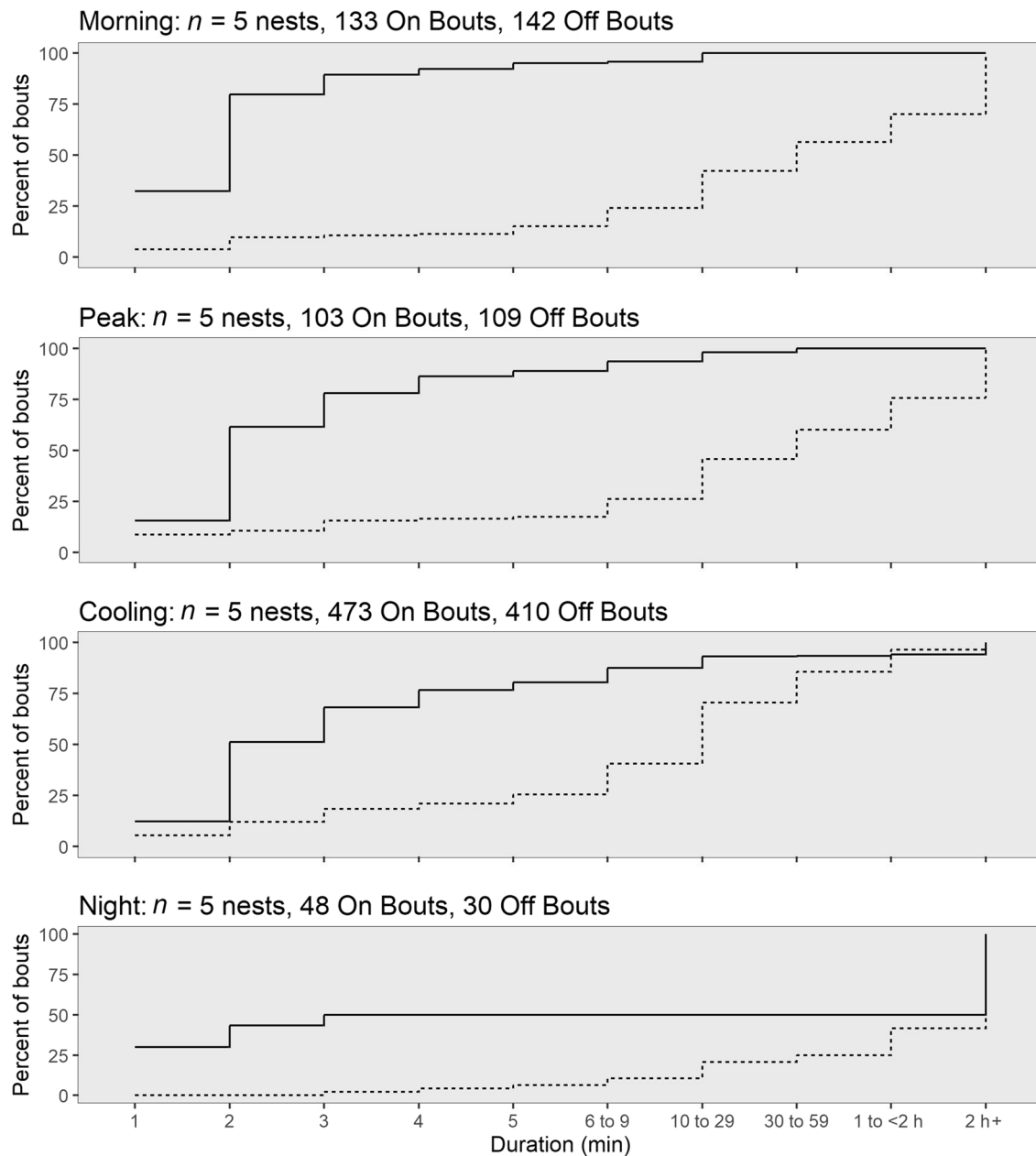
Fig. 2 Cumulative percentage plots of on (dotted line) versus off (solid line) bouts performed by Common Terns on Skimmer Island by bout duration and the time of day during which the bout began. Due to missing footage the data within nests and bins is not complete, and precludes comparison of the number of bouts by time of day; number of bouts is reported only to provide sample size context. All data classified as natural bouts were included in this analysis regardless of if paired iButton data was available

Morning (Poplar: $\bar{x}=0.882$, $z=--17.965$, $p\leq0.001$; Skimmer: $\bar{x}=0.834$, $z=-12.190$, $p\leq0.001$), Peak (Poplar: $\bar{x}=0.909$, $z=-20.326$, $p\leq0.001$; Skimmer: $\bar{x}=0.843$, $z=-12.784$, $p\leq0.001$), or Cooling periods (Poplar: $\bar{x}=0.754$, $z=-12.161$, $p\leq0.001$; Skimmer: $\bar{x}=0.733$, $z=-9.178$, $p\leq0.001$; Fig. 4). Interestingly, nest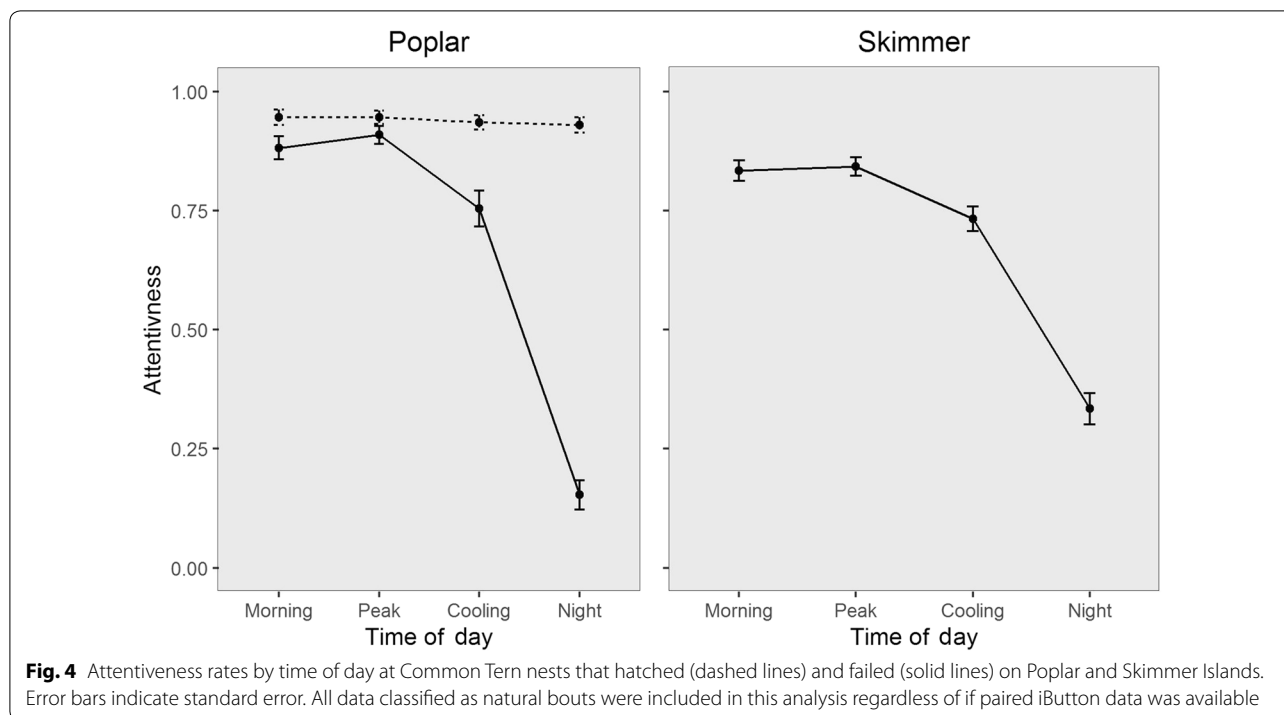 attentiveness at successful nests (Poplar only, no successful nests monitored on Skimmer) was relatively consistent throughout the day (Morning: $\bar{x}=0.946$, Peak: $\bar{x}=0.946$, Cooling: $\bar{x}=0.935$, Night: $\bar{x}=0.930$) with no significant differences between bins ($p>0.05$).

Sullivan *et al. Avian Res*   (2020) 11:22

Page 11 of 18

Fig. 3 The mean nest temperature and concurrent ambient temperature of successful (black icons) and failed (hollow icons) Common Tern nests on Poplar Island, and failed nests on Skimmer Island by time of day during periods when adults were on (triangles) and off (circles) of the nest. Error bars indicate standard error. Only data classified as natural bouts with paired iButton data and ambient temperature data are included in this figure

Bout status comparative modeling

At both Poplar and Skimmer, the best-fit model for the Peak, Cooling, and Night bins was the most complex model. However, the Morning bin on Skimmer was best fit by the model without the interaction between iButton and ambient temperature readings, though there was minimal difference between this and the most complex model (ΔAIC = 1.5; Tables 4 and 5). At both colonies,

modeling was only effective at determining bout status when a bout occurred during the Night bin (Tables 6 and 7). While all time-of-day bins had strong cumulative success (Poplar: Morning = 99.90%, Peak = 97.92%, Cooling = 92.92%, Night = 85.21%; Skimmer: Morning = 94.05%, Peak = 97.20%, Cooling = 85.77%, Night = 84.62%), all periods except Night resulted in points almost exclusively being classified as all on

Fig. 4 Attentiveness rates by time of day at Common Tern nests that hatched (dashed lines) and failed (solid lines) on Poplar and Skimmer Islands. Error bars indicate standard error. All data classified as natural bouts were included in this analysis regardless of if paired iButton data was available

(Poplar) or off (Skimmer) the nest. Accuracy tended to increase as bout duration increased.

Discussion
Natural bout characteristics
As would be expected, video monitoring of successful nests revealed that off-bouts were shortest during the period of the greatest thermal stress (Peak; Nisbet et al. 2017), and median on-bout length was greatest during the Night period when the attending parent, likely the mother (Nisbet et al. 2017; Riechert and Becker 2017), would be sleeping for extended periods. Though one would expect on-bouts to be especially long during the Peak period, this may have been interrupted by belly-soaking behavior or influenced by our small sample size during this particular time of the day. Similarly, data from iButtons demonstrated that nest attentiveness had the largest thermal impact during Peak and Night periods. During the Night period there was no difference in ambient temperature between on and off-bouts but nest temperature was significantly warmer when nests were attended, supporting the findings of Arnold et al. (2006) and Norwood (2011) that adults ameliorate low temperatures during Night via incubation. Conversely, during the Peak period lower nest temperatures were observed during on-bouts, but off-bouts occurred at higher ambient temperatures suggesting that adults may have left the nest for activities such as belly soaking (Grant 1981; Nisbet 1983). It should be noted that the temperatures

reported here are well below the known incubation ranges for terns (e.g. Taylor et al. 2018), providing further evidence that iButtons would not be sufficient for measuring exact egg temperatures but provide a sufficient proxy for the purposes of our work.

Perhaps the most dramatic finding from our examination of natural bout characteristics is the difference in nest attentiveness rates between successful and failed nests. Nest attentiveness remained constant throughout the day for successful nests, suggesting that parents balanced longer trips with the need to ensure the nest was never unattended for too long (Courtney 1979; Webb and King 1983). Though attentiveness rates for successful nests were higher than those reported in Riechert and Becker (2017), this may be due to higher ambient temperatures at our study site, given the ~15° difference in latitude, necessitating increased parental care in line with values observed in other studies (Courtney 1979; Bollinger et al. 1990). However, failed nests showed precipitous declines in nest attentiveness during Cooling and Night hours at both sites, a finding that matches our observation that off-bouts were longer for failed nests than successful nests at Night. While the decline in nocturnal nest attentiveness for failed nests contradicts the findings of Riechert and Becker (2017), this may be in part due to site differences such as local weather, temperatures, and the absence of predators.

On Skimmer, the observed nocturnal abandonment was likely due to predation from GHOW as confirmed by

Table 4 Candidate models for the prediction of Common Tern nest attentiveness status on Poplar Island

Time of day	Model[a]	AIC	ΔAIC	w_i	K	n
Morning	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure + RectifiedTemp:AmbientTemp	4250.2		0.611	4	10,134
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure	4251.1	0.9	0.389	3	10,134
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + RectifiedTemp:AmbientTemp	4285	34.8	0	3	10,134
	BoutStatus_logistic ~ RectifiedTemp	4283.9	33.7	0	1	10,134
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp	4283.7	33.5	0	2	10,134
	BoutStatus_logistic ~ 1	4418.4	168.2	0	1	10,134
Peak	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure + RectifiedTemp:AmbientTemp	3151.3		0.995	4	6745
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + RectifiedTemp:AmbientTemp	3161.9	10.6	0.005	3	6745
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure	3210.1	58.8	0	3	6745
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp	3249.2	97.9	0	2	6745
	BoutStatus_logistic ~ RectifiedTemp	3248.4	97.1	0	1	6745
	BoutStatus_logistic ~ 1	3318.4	167.1	0	1	6745
Cooling	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure + RectifiedTemp:AmbientTemp	6389.9		1	4	8999
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + RectifiedTemp:AmbientTemp	6480.8	90.9	0	3	8999
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure	6690.6	300.7	0	3	8999
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp	6697.6	307.7	0	2	8999
	BoutStatus_logistic ~ RectifiedTemp	6802.4	412.5	0	1	8999
	BoutStatus_logistic ~ 1	6956.7	566.8	0	1	8999
Night	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure + RectifiedTemp:AmbientTemp	9143.6		1	4	11,998
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure	9195.3	51.7	0	3	11,998
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + RectifiedTemp:AmbientTemp	9444.8	301.2	0	3	11,998
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp	9585.4	441.8	0	2	11,998
	BoutStatus_logistic ~ RectifiedTemp	16,148	7004.4	0	1	11,998
	BoutStatus_logistic ~ 1	16,163	7019.4	0	1	11,998

[a] Model terms are defined as follows: BoutStatus_logistic = whether the bird was on (1) or off (0) the nest; RectifiedTemp = the temperature of the nest (in °C) after imputation; AmbientTemperature = the air temperature after imputation; AmbientPressure = barometric pressure after imputation

A priori candidate models, number of model parameters (*K*), Akaike's Information Criterion (AIC), and associated model ranks (ΔAIC), and weights (*w_i*) for the prediction of Common Tern nest attentiveness status on Poplar Island by time of day

both colony-camera and nest-camera footage. Colonial nighttime desertion has been well documented (Nisbet and Welton 1984; Hébert 1985; Arnold et al. 2006) for colonies where GHOW predation is prevalent. Interestingly, our data suggested that desertion events were much longer than those reported in Arnold et al. (2006) and were more in keeping with the multi-hour desertion events reported by Norwood (2011), likely due to the multiyear history of GHOW predation at this site. Unfortunately, it is unclear why nest attentiveness declined for failed nests on Poplar as similar predator threats to those on Skimmer were not documented within this colony. While the location of the nests within colony could influence nest attentiveness, we do not think that was the case in this study as date of nest initiation seemed to play the dominant role in nest success. For instance, all original (initial nesting wave) camera-monitored nests on Poplar were successful (excluding one washed-out nest) despite

all but one being located near the colony edge, but late nesting attempts were unsuccessful in the same locations. One potential explanation is that late season nests were those of birds that relocated from a heavily predated sub-colony on Poplar (see "Methods" section), and their behaviors were impacted by this previous within-season experience; though we are unable to differentiate these birds and test this possibility. Regardless of cause, we think that the longer duration off-bouts and reduced nest attentiveness observed during Night caused these nests to fail, an assumption also made by researchers in similar previous scenarios (Marshall 1942; Norwood 2011). While it is possible that these behaviors were merely due to the adults recognizing their eggs were inviable, this is unlikely as visual examination shows these trends were consistent throughout the incubation period (i.e. attentiveness did not drop suddenly near the end of the

Table 5 Candidate models for the determination of Common Tern nest attentiveness status on Skimmer Island

Time of day	Model[a]	AIC	ΔAIC	w_i	K	n
Morning	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure	3869.4		0.679	3	9412
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure + RectifiedTemp:AmbientTemp	3870.9	1.5	0.321	4	9412
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp	4428.1	558.7	0	2	9412
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + RectifiedTemp:AmbientTemp	4428.8	559.4	0	3	9412
	BoutStatus_logistic ~ RectifiedTemp	4447.5	578.1	0	1	9412
	BoutStatus_logistic ~ 1	4464.3	594.9	0	1	9412
Peak	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure + RectifiedTemp:AmbientTemp	2186.7		1	4	5884
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure	2308.3	121.6	0	3	5884
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + RectifiedTemp:AmbientTemp	2360	173.3	0	3	5884
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp	2407.5	220.8	0	2	5884
	BoutStatus_logistic ~ RectifiedTemp	2497.9	311.2	0	1	5884
	BoutStatus_logistic ~ 1	2521.9	335.2	0	1	5884
Cooling	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure	8928		0.721	3	9814
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure + RectifiedTemp:AmbientTemp	8929.9	1.9	0.279	4	9814
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp	8959.7	31.7	0	2	9814
	BoutStatus_logistic ~ RectifiedTemp	8960.4	32.4	0	1	9814
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + RectifiedTemp:AmbientTemp	8961.3	33.3	0	3	9814
	BoutStatus_logistic ~ 1	9040.3	112.3	0	1	9814
Night	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure + RectifiedTemp:AmbientTemp	13,035		1	4	14,439
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + RectifiedTemp:AmbientTemp	13,051	16	0	3	14,439
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp + AmbientPressure	13,486	451	0	3	14,439
	BoutStatus_logistic ~ RectifiedTemp + AmbientTemp	13,492	457	0	2	14,439
	BoutStatus_logistic ~ RectifiedTemp	13,492	457	0	1	14,439
	BoutStatus_logistic ~ 1	13,777	742	0	1	14,439

[a] Model terms are defined as follows: BoutStatus_logistic = whether the bird was on (1) or off (0) the nest; RectifiedTemp = the temperature of the nest (in °C) after imputation; AmbientTemperature = the air temperature after imputation; AmbientPressure = barometric pressure after imputation

Candidate models, number of model parameters (*K*), Akaike's Information Criterion (AIC), and associated model ranks (ΔAIC), and weights (w_i) for the determination of Common Tern nest attentiveness status on Skimmer Island by time of day

incubation period), and birds were still regularly tending to the nest during other periods of the day.

Bout status comparative modeling

Though the paired use of video monitoring and temperature loggers successfully provided a unique look into the behavior of incubating COTE, the results from our comparative modeling exercise were less promising. Although cumulative success was high across times of day at both study sites, this was generally due to the oversaturation of the data with either on or off-bouts. It was only during the Night periods that attentiveness statuses determined via modeling were relatively reliable, and even then, success was low for short-duration bouts. Unfortunately, it cannot be confirmed if the deficiencies in our approach are the result of limited sample size (most periods of day are dominated by one nest attentiveness status), some unidentified covariate not incorporated into our suite of

candidate models, or that differences between the relevant variables were too minute to allow for accurate bout status prediction. However, the low overall success does not mean that iButtons cannot gather useful data unless paired with video systems. Instead, like others who have examined the use of iButtons, we think the precision of data required to answer questions of interest should inform what technologies should be utilized (Schneider and McWilliams 2007; Norwood 2011). For instance, our approach was able to successfully identify long-duration bouts during the Night period at both locations. Thus, if managers are interested in identifying nest abandonment or heavy overnight predator disturbance then an iButton-only approach may work, but if researchers are interested in fine-scale detail then video monitoring or other high precision data collection techniques would likely be required.

Sullivan *et al. Avian Res*   (2020) 11:22

Page 15 of 18

Table 6 Success of the best-fit model for determining nest attentiveness of Common Terns on Poplar Island

Time of day	Duration bin (min)	True On	False On	True Off	False Off	Correct On (%)[a]	Correct Off (%)[b]	Correct Cumulative (%)[c]
Morning	< 4	24	143	0	0	14.37	NA	14.37
	4–9	75	115	0	0	39.47	NA	39.47
	10–29	461	167	0	0	73.41	NA	73.41
	30–59	635	0	0	0	100.00	NA	100.00
	60+	5974	6	0	0	99.90	NA	99.90
Peak	< 4	12	136	0	0	8.11	NA	8.11
	4–9	35	24	0	0	59.32	NA	59.32
	10–29	316	44	0	0	87.78	NA	87.78
	30–59	541	55	0	0	90.77	NA	90.77
	60+	3814	81	0	0	97.92	NA	97.92
Cooling	< 4	16	103	0	0	13.45	NA	13.45
	4–9	130	176	0	0	42.48	NA	42.48
	10–29	535	149	0	0	78.22	NA	78.22
	30–59	427	69	0	0	86.09	NA	86.09
	60+	4780	364	0	0	92.92	NA	92.92
Night	< 4	0	14	2	0	0.00	100.00	12.50
	4–9	4	23	2	4	14.81	33.33	18.18
	10–29	44	49	28	68	47.31	29.17	38.10
	30–59	65	6	19	28	91.55	40.43	71.19
	60+	4139	259	3225	1019	94.11	75.99	85.21

[a] Correct On (%) = True On/(True On + False On) × 100

[b] Correct Off (%) = True Off/(True Off + False Off) × 100

[c] Correct Cumulative (%) = (True On + True Off)/(True On + False On + True Off + False Off) × 100

The success of the best-fit model for determining nest attentiveness status of adult Common Terns during the breeding season on Poplar Island by time of day. Nest attentiveness status was compared against paired video data to determine accuracy, allowing classifications of True On (bird was correctly assigned as on the nest), False On (bird was assigned as on the nest but was actually off the nest), True Off (bird was correctly assigned as off the nest), and False Off (bird was assigned as off the nest but was actually on the nest). Status determinations occurred at randomly selected minute(s) during a bout

Nest success

While it is necessary for researchers and managers to understand the type of questions they can expect to answer via the use of video monitoring and temperature logging devices, it is also important to understand the impact these approaches may have on the colonies in which they are deployed. The placement of iButtons and paired cameras on Poplar did not have a significant impact on hatching success, especially once re-nesting attempts were separated out. Though all nests monitored with cameras on Skimmer failed, this was likely the result of GHOW predation on the colony at large and not due to our study equipment. While there was some damage to eggs we assume to have been caused by iButtons, careful installation should limit or eliminate such instances (Schneider and McWilliams 2007). Perhaps the greatest concern with the implementation of this technology was that nearly all clutches with cameras had only two eggs while most other nests had three. While this is still within a normal range for COTE nests (Nisbet 2017), we question whether these reductions are coincidental. This issue warrants additional research before this technique is widely adopted or recommended for endangered or threatened species, though such a result has not been reported for other video monitoring studies (Richardson et al. 2009; Weathers and Zaun 2010).

Methodological considerations

The detailed data obtained in this study demonstrates the promise of using remote data collection techniques to answer a broad array of ecological questions regarding breeding colonial waterbirds. However, there are some technological limitations that must be accounted for when considering this approach. For instance, camera placement is restricted by limited cable length, allowing a single system to monitor only nests which are relatively nearby. While wireless cameras remove the DVR-to-camera cabling, they still require their own power source and may only be placed a set distance from the DVR without picture loss (< 152 m). The use of small battery-powered game cameras could provide an alternative to our approach as they can be set

Table 7 Success of the best-fit model for determining nest attentiveness of Common Terns on Skimmer Island

Time of day	Duration bin (min)	True On	False On	True Off	False Off	Correct On (%)[a]	Correct Off (%)[b]	Correct Cumulative (%)[c]
Morning	< 4	3	66	0	0	4.35	NA	4.35
	4–9	17	5	0	0	77.27	NA	77.27
	10–29	94	39	0	0	70.68	NA	70.68
	30–59	201	27	0	0	88.16	NA	88.16
	60+	6214	317	0	76	95.15	100	94.05
Peak	< 4	10	51	0	0	16.39	NA	16.39
	4–9	27	24	0	0	52.94	NA	52.94
	10–29	68	16	0	0	80.95	NA	80.95
	30–59	165	45	0	0	78.57	NA	78.57
	60+	3895	109	0	3	97.28	100	97.20
Cooling	< 4	70	255	0	0	21.54	NA	21.54
	4–9	250	187	0	0	57.21	NA	57.21
	10–29	321	162	0	0	66.46	NA	66.46
	30–59	974	20	0	0	97.99	NA	97.99
	60+	4038	670	0	0	85.77	NA	85.77
Night	< 4	0	0	7	0	NA	100	100.00
	4–9	0	0	6	6	NA	50	50.00
	10–29	0	0	0	86	NA	0	0.00
	30–59	0	0	0	88	NA	0	0.00
	60+	175	18	8825	1618	90.67	85	84.62

[a] Correct On (%) = True On/(True On + False On) × 100

[b] Correct Off (%) = True Off/(True Off + False Off) × 100

[c] Correct Cumulative (%) = (True On + True Off)/(True On + False On + True Off + False Off) × 100

The success of the best-fit model for determining nest attentiveness status of adult Common Terns during the breeding season on Skimmer Island by time of day. Nest attentiveness status was compared against paired video data to determine accuracy, allowing classifications of True On (bird was correctly assigned as on the nest), False On (bird was assigned as on the nest but was actually off the nest), True Off (bird was correctly assigned as off the nest), and False Off (bird was assigned as off the nest but was actually on the nest). Status determinations occurred at randomly selected minute(s) during a bout

to record images or video when motion is detected or at set time intervals, and have proven useful in other studies (Norwood 2011; Seefelt and Farrell 2018). However, due to limited storage, they would not be viable in studies which seek continuous surveillance of the nest. Signal interruptions between the wireless cameras and their respective receivers were another common issue throughout this study. If a receiver did not have a completely clear line of sight to the camera (generally due to growth in vegetation or equipment shifting from weather events), picture quality decreased or no video was collected. A complete list of potential concerns and remedies associated with our video monitoring approach can be found in Wall et al. (2018).

There are also several constraints to consider prior to using iButtons. The primary limitation with iButtons is the inability to collect new data once the limited memory space is full, an issue we encountered regularly during this study. Researchers can reduce their sampling interval to allow for prolonged sampling period, but this reduces the temporal resolution of your data.

The nest characteristics of COTE also proved to be a challenge, as the simple scrape nest structure allowed iButtons in unattended nests to be easily covered with windblown sand and invalidate subsequent data. Researchers should carefully consider their objectives and the use of other logger techniques (i.e., Arnold et al. 2006; Taylor et al. 2018) if windblown substrate is likely to present a challenge.

Conclusions

This study was the first to quantify nest attentiveness rates across all times of day for COTE, demonstrating that despite complications leading to lapses in data collection the combined use of temperature logging and video monitoring technologies can provide a detailed description of avian nesting behavior. While these approaches both have several limiting factors, the singular and paired use of iButtons and video cameras seems practical so long as studies are carefully designed to address technological limitations and collect data of an appropriate resolution to meet research goals. We hope

Sullivan *et al. Avian Res*   (2020) 11:22

Page 17 of 18

that our study will help to promote the consideration of novel approaches to help better understand not only nest behavior during the incubation period such as sleep rates and mate switching behavior, but also allow examination into adult and chick behaviors post-hatching such as food provisioning and chick care.

Authors' contributions
JDS, PRM, JMM, DFB, and DJP conceived and designed the study; PRM, PCM, and CRC collected data; JDS, PRM, and DJP analyzed the data; and JDS, PRM, JMM, and DJP wrote the paper. All authors read and approved the final manuscript.

Availability of data and materials
The datasets analyzed during the current study are available in the USGS ScienceBase repository: https://doi.org/10.5066/P9M7S70D (Sullivan 2019).

Ethics approval and consent to participate
All data reported in this study were collected in accordance with protocol approved by the Patuxent Wildlife Research Center Animal Care and Use Committee (2013-05).

Consent for publication
Not Applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1] Natural Systems Analysts, Winter Park, FL 32789, USA. [2] Marine, Estuarine, and Environmental Sciences Program, University of Maryland, College Park, MD 20742, USA. [3] Department of Environmental Science and Technology, University of Maryland, 1443 Animal Sciences Bldg, College Park, MD 20742, USA. [4] Department of Natural Resources, Maryland Natural Heritage Program, Annapolis, MD 21401, USA. [5] Chesapeake Bay Field Office, U.S. Fish and Wildlife Service, Annapolis, MD 21401, USA. [6] U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708, USA.

References
AlRashidi M. The challenge of coping in an extremely hot environment: a case study of the incubation of Lesser Crested Terns (*Thalasseus bengalensis*). Waterbirds. 2016;39:215–21.

Amat JA, Gomez J, Linan-Cembrano G, Rendon MA, Ramo C. Incubating terns modify risk-taking according to diurnal variations in egg camouflage and ambient temperature. Behav Ecol Sociobiol. 2017;71:72.

Antolos M, Roby DD, Lyons DE, Anderson SK, Collis K. Effects of nest density, location, and timing on breeding success of Caspian Terns. Waterbirds. 2006;29:465–72.

Arnold JM, Saboom D, Nisbet ICT, Hatch JJ. Use of temperature sensors to monitor patterns of nocturnal desertion by incubating Common Terns. J Field Ornithol. 2006;77:384–91.

Arnold JM, Hatch JJ, Nisbet ITC. Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? J Avian Biol. 2008;35:33–45.

Bollinger PB, Bollinger EK, Malecki RA. Tests of three hypotheses of hatching asynchrony in the Common Tern. Auk. 1990;107:696–706.

Bonter DN, Bridge ES. Applications of radio frequency identification (RFID) in ornithological research: a review. J Field Ornithol. 2011;82:1–10.

Burger J, Gochfeld M. The Common Tern: Its breeding biology and social behavior. New York: Columbia University Press; 1991.

Clode D, Birks JDS, Macdonald DW. The influence of risk and vulnerability on predator mobbing by terns (*Sterna* spp.) and gulls (*Larus* spp.). J Zool. 2000;252:53–9.

Courtney P. Seasonal variation in intra-clutch hatching intervals among Common Terns *Sterna hirundo*. Ibis. 1979;121:207–11.

Deeming DC, Reynolds SJ. Nests, eggs, and incubation: new ideas about avian reproduction. Oxford: Oxford University Press; 2015.

Gotmark F, Andersson M. Colonial breeding reduces nest predation in the Common Gull (*Larus canus*). Anim Behav. 1984;32:485–92.

Grant GS. Foot-wetting and belly-soaking by incubating Gull-billed Terns and Black Skimmers. J Bombay Nat Hist Soc. 1978;75:148–52.

Grant GS. Belly-soaking by incubating common, sandwich, and royal terns. J Field Ornithol. 1981;52:244.

Grant GS. Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. Ornithol Monogr. 1982;30:iii.

Hand JL, Hunt GL Jr, Warner M. Thermal stress and predation: influences on the colony structure of a gull colony and possibly breeding distributions. Condor. 1981;83:193–203.

Hart LA, Downs CT, Brown M. Sitting in the sun: nest microhabitat affects incubation temperatures in seabirds. J Therm Biol. 2016;60:149–54.

Hartman CA, Oring LW. An inexpensive method for remotely monitoring nest activity. J Field Ornithol. 2006;77:418–24.

Hays H, LeCroy M. Field Criteria for determining incubation stage in eggs of the Common Tern. Wilson Bull. 1971;83:425–9.

Hébert PN. Breeding failure and decline of a Common Tern colony in southern Manitoba. Col Waterbirds. 1985;8:183–5.

Hunt GL Jr, Hunt MW. Reproductive ecology of the Western Gull: the importance of nest spacing. Auk. 1975;92:270–9.

Kar T, Debata S. Breeding ecology of the endangered Black-Bellied Tern (*Sterna acuticauda*) in eastern India and implications for conservation. Waterbirds. 2019;42:314–20.

Konishi S, Kitagawa G. Information criteria and statistical modeling. New York: Springer; 2008.

Mallory ML. Reactions of ground-nesting marine birds to human disturbance in the Canadian Arctic. Arct Sci. 2016;2:67–77.

Marshall N. Night desertion by nesting Common Terns. Wilson Bull. 1942;54:25–31.

Martin TE. Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst. 1987;18:453–87.

Martin TE. A new view of avian life-history evolution tested on an incubation paradox. Proc R Soc Lond B. 2002;269:309–16.

Maryland Department of Natural Resources. Maryland's Natural Areas: Skimmer Island, Worchester County. 2016. http://dnr2.maryland.gov/wildlife/Pages/NaturalAreas/Eastern/Skimmer- Island.aspx.

Maryland Environmental Service. About Poplar Island. 2017. http://www.poplarislandrestoration.com/Home/About.

Meehan TD, Nisbet ICT. Nest attentiveness in Common Terns threatened by a model predator. Waterbirds. 2002;25:278–84.

Morris RD, Hunter RA. Monitoring incubation attentiveness of ground-nesting colonial seabirds. J Wildl Manage. 1976;40:354–7.

Morris RD, Hunter RA, McElman JF. Factors affecting the reproductive success of Common Tern (*Sterna hirundo*) colonies on the lower Great Lakes during the summer of 1972. Can J Zool. 1976;54:1850–62.

Sullivan *et al. Avian Res*   (2020) 11:22

Page 18 of 18

Neumann JL, Larose CS, Brodin G, Feare CJ. Foraging ranges of incubating Sooty Terns *Onychoprion fuscatus* on Bird Island, Seychelles, during a transition from food plenty to scarcity, as revealed by GPS loggers. Mar Ornithol. 2018;46:11–8.

Nisbet ICT. Belly-soaking by incubating and brooding Common Terns. J Field Ornithol. 1983;54:190–2.

Nisbet ICT, Cohen ME. Asynchronous hatching in Common and Roseate Terns *Sterna hirundo* and *S. dougallii*. Ibis. 1975;117:374–9.

Nisbet ICT, Arnold JM, Oswald SA, Pyle P, Patten MA. Common Tern (*Sterna hirundo*). In: The Birds of North America. Cornell Lab of Ornithology. 2017. https://birdsna.org/Species-Account/bna/species/comter/introduction.

Nisbet ICT, Welton MJ. Seasonal variation in breeding success of Common Terns: consequences of predation. Condor. 1984;86:53–60.

NOAA National Centers for Environmental Information. 2018. Climate Data Online. https://www.ncdc.noaa.gov/cdo-web/.

Nordstrom M, Laine J, Ahola M, Korpimaki E. Reduced nest defence intensity and improved breeding success in terns as responses to removal of non-native American mink. Behav Ecol Sociobiol. 2004;55:454–60.

Norwood GJ. Nest-site selection, nocturnal nest desertion, and productivity in a Common Tern (*Sterna hirundo*) colony at Detroit River, Michigan. Master's Thesis. Ypsilanti, MI: Eastern Michigan University. 2011.

Palestis BG. Nesting stage and nest defense by Common Terns. Waterbirds. 2005;28:87–94.

R Core Team. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2018. https://www.r-project.org/.

Richardson TW, Gardali T, Jenkins SH. Review and meta-analysis of camera effects on avian nest success. J Wildl Manage. 2009;73:287–93.

Riechert J, Becker PH. What makes a good parent? Sex-specific relationships between nest attendance, hormone levels, and breeding success in a long-lived seabird. Auk. 2017;134:644–58.

Schneider EG, McWilliams SR. Using nest temperature to estimate nest attendance of Piping Plovers. J Wildl Manage. 2007;71:1998–2006.

Seefelt NE, Farrell PD. Indirect negative impacts of Double-crested Cormorant (*Palacrocorax auritus*) management on co-nesting Caspain Terns (*Hydroprogne caspia*) in Northern Lake, Michigan, USA. Waterbirds. 2018;41:417–23.

Shaffer SA, Clatterbuck CA, Kelsey EC, Naiman AD, Young LC, VanderWerf EA, et al. As the egg turns: monitoring egg attendance behavior in wild birds using novel data logging technology. PLoS ONE. 2014;9:e97898.

Shealer DA, Kress SW. Nocturnal abandonment response to Black-Crowned Night-Heron disturbance in a Common Tern colony. Col Waterbirds. 1991;14:51–6.

Smithson M, Verkuilen J. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol Methods. 2006;11:54–71.

Sullivan JD, Marban PR, Mullinax JM, Brinker DF, McGowan PC, Callahan CR, et al. Assessing nest attentiveness of Common Terns (*Sterna hirundo*) via video cameras and temperature loggers. 2019. U.S. Geological Survey data release, https://doi.org/10.5066/P9M7S70D.

Taylor GT, Ackerman JT, Shaffer SA. Egg turning behavior and incubation temperature in Forester's terns in relation to mercury contamination. PLoS ONE. 2018;13:e0191390.

U.S. Navy Observatory. Sun or Moon Rise/Set Table for One Year. 2016. http://aa.usno.navy.mil/data/docs/RS_OneYear.php.

Vedder O, Kurten N, Bouwhuis S. Interspecific variation in and environment-dependent resource allocation to embryonic development time in Common Terns. Physiol Biochem Zool. 2017;4:453–60.

Wall JW, Marban PR, Brinker DF, Sullivan JD, Zimnik M, Murrow JL, et al. A video surveillance system to monitor breeding colonies of Common Terns (*Sterna hirundo*). J Vis Exp. 2018;137:e57928.

Weathers WW, Zaun BJ. Egg-turning behavior and nest attentiveness of the endangered Hawaiian Goose on Kauai. West Birds. 2010;41:2–9.

Webb DR, King JR. An analysis of the heat budgets of the eggs and nest of the White-Crowned Sparrow, *Zonotrichia leucophrys*, in relation to parental attentiveness. Physiol Zool. 1983;56:493–505.

Wendeln H, Becker PH. Does distrubance by nocturnal predators affect body mass of adult Common Terns? Waterbirds. 1999;22:401–10.

Wiggins DA, Morris RD. Parental care of the Common Tern *Sterna hirundo*. Ibis. 1987;129:533–40.

Yoon J, Yoon H, Go B, Joo E, Park S. Tide associated incubation and foraging behavior of Saunders's Gulls *Larus saundersi*. Ardea. 2014;101:99–104.