Colony attendance patterns by mated Forster's Terns *Sterna forsteri* using an automated data-logging receiver system

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In order to examine 24-hour colony attendance patterns by mated Forster's Terns *Sterna forsteri* in South San Francisco Bay, California, during incubation and chick-rearing stages, we radio-marked 10 individuals consisting of five pairs and recorded colony attendance using an automated data-logging receiver system. We calculated and analyzed five variables: the total attendance time by pairs and individuals, the duration of individual attendance bouts, and the duration both members of a pair either overlapped in colony attendance or were both absent from the colony. The percentage of time spent on the colony by at least one individual of a pair was highest during incubation and declined during chick rearing. Overall, male terns spent a greater proportion of time diurnally attending the colony than females. Females spent a greater proportion of time on colony at night, and without these nocturnal records, we would have reported overall female colony attendance rates as being much lower. Despite sex-specific differences in attendance rates, the length of attendance bouts did not differ between the sexes. Simultaneous colony attendance by both members of a pair was high at night, but during the day, pairs infrequently overlapped in their colony attendance and both members were frequently absent. Our data-logging system functioned well, and our data illustrates the importance of collecting 24-hour records when considering attendance rates.

Key words: colony attendance, data-logging receiver, Forster's Tern, nocturnal attendance, *Sterna forsteri*, San Francisco Bay

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Patterns of colony attendance can provide an estimate of the time individuals allot to parental care of their young (Nelson 1987, Harding *et al.* 2007), although these studies are often observational and limited by daylight. Consequently, our understanding of colony attendance patterns can be distorted if attendance rates differ between diurnal and nocturnal periods. This may be especially true in studies examining colony attendance patterns between male and female seabirds. For example, diurnal studies of terns indicate that females spend more time than males incubating eggs and brooding chicks at the colony site (Nisbet 1973, Morris 1986, Wiggins & Morris 1987, Quinn 1990), leading to the conclusion that females invest more time to on-colony parental care duties than male terns. However, data presented by van der Winden (2005) indicate that male Black Terns *Chlidonias niger* nocturnally attend the colony to incubate eggs, whereas females roost at off-colony sites during this period. Although direct observations did not occur during complete darkness, these data suggest that male terns invest more in the incubation of eggs than females when a 24-h period is considered (van der Winden 2005). However, without direct evidence of attendance during nocturnal hours, disturbance or predation events that can cause terns to temporarily abandon the colony (Nisbet 1975, Shealer & Kress 1991, Wendeln & Becker 1999, Arnold *et al.* 2006) are not considered.

Nocturnal colony attendance data is difficult to obtain by direct visual observations, often due to low visibility. Devices such as electronic weighing platforms placed under the nest (Frank & Becker 1992) or temperature sensors placed in nests (Arnold *et al.* 2006) have been used to acquire nocturnal attendance data. However, these methods cannot identify individuals; reliably collect data diurnally when ambient temperatures approach the temperature of the incubated nest; or, for species with precocial chicks, be used dependably during the chick-rearing stage. Also, these sensors only detect presence on the nest rather than on the colony, which excludes colony attendance by individuals not incubating the nest.

Therefore, to examine sex-specific differences in colony attendance rate over a 24-h period, we designed a system to sample presence and absence of individual Forster's Terns *Sterna forsteri* at a remote colony site in the San Francisco Bay, California. Here, we describe our novel field methods, which included radio-marking both individuals of several pairs and using an automated data-logging receiver system stationed at the colony. We also present methods of analyzing the data collected from the system, assess the reliability of this method, and compare 24-h colony attendance records of Forster's Terns to colony attendance patterns of other tern species.

METHODS

Study area

We conducted our study within the Newark salt pond complex of the Don Edwards San Francisco Bay National Wildlife Refuge in South San Francisco Bay, California (37.32°N, 122.06°W). The levee system and dredge spoil islands associated with salt pond construction provide nesting habitat for Forster's Terns (Harvey *et al.* 1990, Strong *et al.* 2004, U.S. Geological Survey, unpubl. data). In 2006, approximately 600 pairs of Forster's Terns nested on levees within Pond N7, an artificial salt evaporation pond (U.S. Geological Survey, unpubl. data). During the study period, the average time between sunrise and sunset was 14.7 h.

Radio-marking and data-logging system

We used treadle-activated bow nets to capture both individuals in a pair of Forster's Terns on their nest. All nests had 3 eggs and had been incubated for 16 to 23 days (determined by egg flotation; Hays & LeCroy 1971). From these nests, we randomly removed one egg from each nest as part of a study examining contaminant concentrations in San Francisco Bay birds (Ackerman & Eagles-Smith 2009). To minimize disturbance and avoid recapture, we held the first captured individual of a pair in a partitioned, shaded, and screen-lined poultry cage (model 5KTC, Murray McMurray Hatchery, Webster City, Iowa) until we captured the mate. Including processing, we held terns for no longer than 2.5 h. We measured morphological features (Bluso *et al.* 2006), collected a drop of blood to determine sex via DNA genotyping (Zoogen Services, Inc, Davis, California), and attached radio-transmitters (Model A2440, 2.2 g, Advanced Telemetry Systems, Inc., Isanti, Minnesota) fastened to an aluminium band (U.S. Geological Survey, size 3) to the right tarsometatarsus of each tern. Radio-transmitter packages weighed ≤ 2.3 g (<3% of body weight).

In order to continuously monitor radio-marked terns, we used a data-logging telemetry receiver (model R4500S, Advanced Telemetry Systems Inc., Isanti, Minnesota) linked to an omni-directional dipole antenna (Advanced Telemetry Systems Inc., Isanti, Minnesota) and powered by a 12-volt marine battery and solar panel. We tested the reception range of the data-logging system by placing transmitters at the outer edges of the colony and adjusting the sensitivity of the data-logging system until only transmitters placed within 150 m of the system were detected. To ensure correct function, we also placed a reference transmitter at the colony and programmed four false frequencies not deployed on any tern into the data-logging system. We visited the logger system least once every two weeks to ensure the system was functioning correctly. The data-logging system continuously scanned for marked terns and scanned each individual radio frequency approximately once every 15 min. When the data-logging system detected a radio-marked tern, the system stored the radio frequency, date, time of day, and number and strength of pulses detected. We interpreted the lack of detection as an absence from the colony within range of the data-logging system (150 m radius). All nests of radio-marked terns were located less than 150 m from the data-logging system.

Data processing and analysis

We first categorized the breeding season for each tern into an incubation and chick-rearing stage. We used egg flotation (Hays & LeCroy 1971) to determine nest age and estimated the hatch date based on a 24-day incubation period for Forster's Terns (McNicholl *et al.* 2001). We then used nest age to assign breeding stage since we were not conducting observations at the nest.

We defined the incubation stage as the period between capture and the projected hatch date of the first chick. We defined the chick-rearing stage as the period beginning on the projected hatch date of the first chick and concluding when either chicks reached 28 days of age (approximate age of fledging; U.S. Geological Survey, unpubl data); nests failed due to depredation, flooding, or disturbance; or when one member of the pair was permanently missing from the study area (e.g. not found during daily searched conducted using logger, truck, or aircraft telemetry systems; see Bluso-Demers *et al.* 2008 for details).

In order to describe and analyze patterns of colony attendance by Forster's Terns at the N7 colony, we established time intervals for analysis based on colony attendance bouts. We determined the duration of colony attendance bouts by calculating the number of logging cycles that a tern was continuously present and averaged colony attendance bout duration among all terns. We only considered data collected beginning four hours (equivalent to two average attendance bouts [120 ± 24 min]) after a tern's release to allow terns to adjust to the transmitters. Additionally, we calculated the duration of attendance bouts of radio-marked terns and selected the 90% value of the data (180 min) to divide each 24-h period into eight 3-h intervals.

We then created and statistically analyzed five variables for analysis. We calculated the total attendance time by pairs as the proportion of time that at least one member of the pair attended the colony, determined by dividing the number of logging cycles within each 3-h interval when at least one member of a pair was detected by the total number of logging cycles completed during each interval. Similarly, we calculated the attendance time of individual terns as the proportion of time that each tern attended the colony by dividing the number of logging cycles that a tern was detected by the number of logging cycles completed. For both analyses, we pooled all days within each breeding stage and used repeated measures ANOVA (PROC MIXED; SAS Institute Inc. 1999) to test for difference among groups and Tukey–Kramer multiple comparison tests to test for difference within groups. We tested for differences in attendance by pairs between breeding stage, time of day (3-h intervals), and the interaction between breeding stage and time of day. We tested for differences in individual attendance between sex, breeding stage, time of day, and the interactions between sex and breeding stage and sex and time of day. We arcsine square-root transformed all proportional data prior to analysis, however, we present untransformed proportions throughout to facilitate interpretation.

We calculated attendance bout duration for each tern by calculating the number of logging cycles that a tern was continuously present. Each logging cycle was approximately 15 min, therefore we considered each cycle a tern was present as 15 min of attendance. We pooled all days within each breeding stage and assigned each bout to the 3-h interval in which it began. We log10-transformed data for normality and tested for differences between sex, breeding stage, time of day, and the interactions between sex and breeding stage and sex and time of day using a repeated measures ANOVA (PROC MIXED; SAS Institute Inc. 1999) and Tukey–Kramer multiple comparison tests, while controlling for the effect of pairs.

Finally, we calculated the duration that both members of a pair overlapped in colony attendance and the duration of time when both members of a pair were absent from the colony. We determined the duration of pair overlap by calculating the number of logging cycles that both members of pairs were continuously present, only considering overlaps of pairs occurring during two or more logging cycles. Data-logging system detections were not simultaneous and detection of both members of a pair during one cycle may not represent true overlap. We calculated the duration of time absent from the colony by calculating the number of logging cycles that both members of pairs were continuously not detected. We considered each cycle that both members of a pair were present or absent as 15 min of overlap, and we pooled all days by breeding stage and assigned each overlap to the 3-h interval in which it began. For both analyses, we tested for differences between breeding stage, time of day, and the interactions between breeding stage and time of day using a repeated measures ANOVA (PROC MIXED; SAS Institute Inc. 1999) and Tukey–Kramer multiple comparison tests. We $\log_{10}$ transformed data for normality, however, we present untransformed data throughout to facilitate interpretation. In all models, insignificant interaction terms were dropped. Means are reported ± 1SD.

RESULTS

From 10–19 June 2006, we captured and radio-tagged 10 individuals consisting of five pairs of Forster's Terns. We obtained presence/absence data on five pairs during the incubation stage, and obtained data on four pairs during the chick-rearing stage as one pair lost their entire clutch during incubation. The data-logging system recorded 11975 locations, detected the reference transmitter 99.7% of the time, and detected false

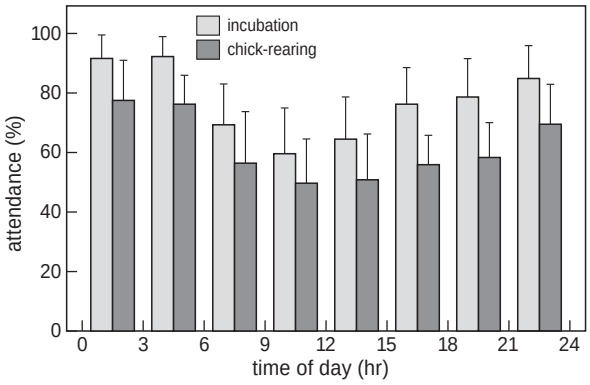

Figure 1. The total attendance time at the colony (%) by Forster's Tern pairs during incubation (n = 5) and chick-rearing stages (n = 4). On average, the sun rose at 5:48 and set at 20:29.

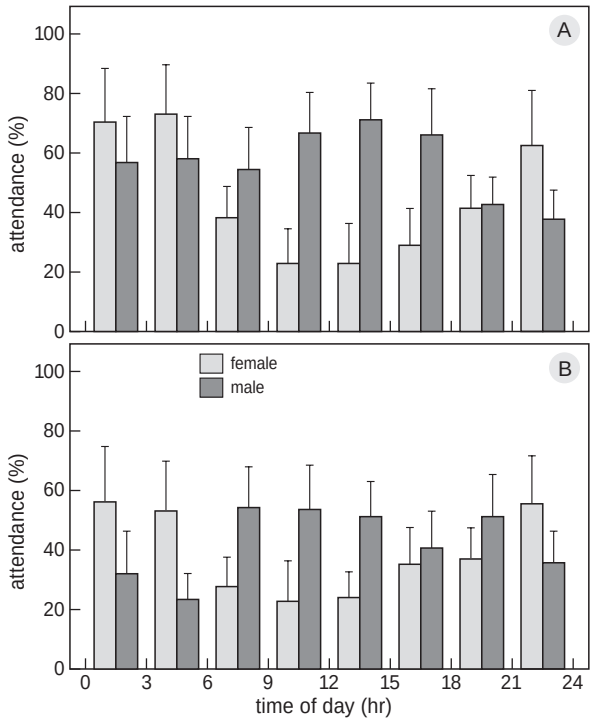

Figure 2. The attendance time (%) by paired female and male Forster's Terns during (A) incubation (n = 5) and (B) chick-rearing stages (n = 4). On average, the sun rose at 5:48 and set at 20:29.

frequencies only three times during the study period. In total, we obtained continuous colony attendance data for each pair ranging from 30 to 223 hrs during incubation and 96 to 360 hrs during chick-rearing.

Attendance by pairs varied significantly by breeding stage ($F_{1,59}$ = 28.10, P < 0.001) and time of day ($F_{7,59}$ = 5.53, P < 0.001; Fig. 1), after the non-significant interaction between time of day and breeding stage was dropped ($F_{7,52}$ = 0.19, P = 0.99). At least one individual of a pair attended the colony 78.1% of the time during incubation and 61.9% of the time during chick-rearing. Attendance by pairs was highest during the two 3-h intervals 0:00–5:59 (85.0%) and lowest during the two 3-h intervals 9:00–14:59 (57.0%; all t_{59} ≥ 3.32, P ≤ 0.01; Fig. 1).

We used separate ANOVAs for each sex to test the effects of breeding stage and time of day on individual attendance as the interaction between sex and time of day was significant ($F_{7,122}$ = 5.50, P < 0.001; Fig. 2). Interactions between time of day and breeding stage were not significant for females ($F_{7,52}$ = 0.76, P = 0.62) or males ($F_{7,52}$ = 1.10, P = 0.38). Female terns attended the colony for 45.1% of the day during incubation and 39.1% of the day during chick-rearing, but this difference was not significant ($F_{1,59}$ = 1.71, P = 0.20). Instead, attendance of female terns varied by time of day ($F_{7,59}$ = 8.85, P < 0.001). Female terns spent more time attending the colony during the night (21:00–5:59; 54.5% of the time) than during the day (9:00–17:59; 25.9% of the time; all t_{60} ≥ 3.36, P ≤ 0.03; Fig. 2). Unlike female terns, colony attendance of male terns differed between breeding stages ($F_{1,59}$ = 12.02, P = 0.001), but not by time of day ($F_{7,59}$ = 1.59, P = 0.16; Fig. 2). Males attended the colony for 56.9% of the day during incubation and 43.0% of the day during chick-rearing.

Next, we ran separate ANOVAs for each 3-h time interval to test effects of sex and breeding stage on individual colony attendance. The interaction between sex and breeding stage was not significant during any 3-h interval (all $F_{1,10}$ ≤ 1.91, P ≥ 0.20). Attendance did not differ between breeding stages during any 3-h intervals (all $F_{1,11}$ ≤ 4.53, P ≥ 0.06). However, in the two 3-h intervals 9:00–14:59, attendance varied by sex (all $F_{1,11}$ ≥ 10.08, P ≤ 0.01), and male attendance (61.8%) was higher than female attendance (23.0%; Fig. 2). Attendance did not differ between the sexes during any other 3-h intervals (all $F_{1,11}$ ≤ 3.44, P ≥ 0.09; Fig. 2).

Attendance bout lengths of Forster's Terns averaged 120 ± 24 min. The interaction between breeding stage and time of day on bout length was significant ($F_{7,674}$ = 2.18, P = 0.034), therefore we used separate ANOVAs for each breeding stage to test the effects of sex and time of day on bout length. During incubation, the interaction between sex and time of day was not significant ($F_{7,259}$ = 0.72, P = 0.65). Incubation attendance bouts averaged 220.3 ± 60.7 min. Bout lengths differed

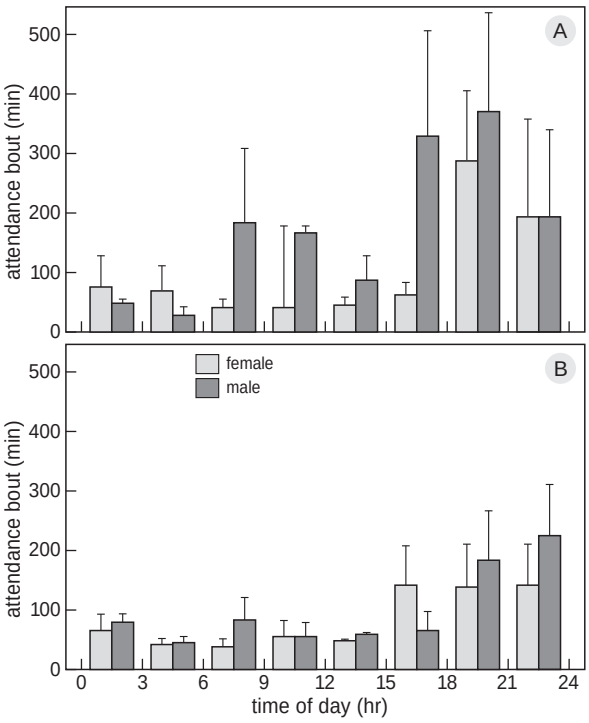

Figure 3. The mean duration (± SE) of attendance bouts by paired female and male Forster's Terns during (A) incubation (n = 5) and (B) chick-rearing (n = 4) stages.

between the sexes ($F_{1,259}$ = 4.34, P = 0.038) with male bouts (272.3 ± 107.1 min) longer than female bouts (168.3 ± 61.5 min). Incubation bout lengths also differed by time of day ($F_{7,259}$ = 2.37, P = 0.023). Attendance bouts begun between 6:00 and 8:59 (47.8 ± 9.7 min) were significantly shorter than those begun between 15:00 and 17:59 (216.0 ± 110.1 min; t_{259} = 3.04, P = 0.023).

During chick-rearing, the interaction between sex and time of day was not significant ($F_{7,405}$ = 1.14, P = 0.34). Chick-rearing attendance bouts averaged 91.1 ± 14.0 min. Male and female terns averaged bout lengths of 94.8 ± 31.5 min and 84.2 ± 31.0 min, respectively, but this difference was not significant between the sexes ($F_{1,412}$ = 3.41, P = 0.065). Chick-rearing attendance bouts varied by time of day ($F_{7,412}$ = 3.42, P = 0.001). The shortest bouts began in the four 3-h intervals 3:00–14:59 (52.8 ± 4.4 min) and the longest bouts began in the 3-h interval 21:00–23:59 (112.5 ± 23.5 min; all $t_{412} \geq 3.20$, $P \leq 0.03$; Fig. 3).

Both members of a pair overlapped in colony attendance 2.7 ± 0.4 times/24-h period and the overlaps averaged 122.2 ± 35.9 min in duration. The duration of overlaps did not differ by breeding stage ($F_{1,99}$ = 1.04, P = 0.31), but varied across the day ($F_{8,99}$ = 7.96, P < 0.001). The interaction between breeding stage and time of day was not significant ($F_{6,93}$ = 1.55, P = 0.17). The shortest overlaps began during the two 3-h intervals 12:00–17:59 (35.4 ± 1.8 min) and the longest began during the two 3-h intervals 18:00–2:59 (164.3 ± 32.7 min; all $t_{99} \leq 3.40$, $P \leq 0.02$).

On average, both members of a pair were absent from the colony 6.0 ± 0.13 times/24-h period (range per pair: 2.9–12.8). During the nocturnal hours between 21:00 and 5:59, both members of a pair were absent on average 2.5 ± 0.45 times/night. The average duration of time when both members of a pair were absent from the colony was 96.4 ± 28.6 min. The duration absent from the colony did not vary by breeding stage ($F_{1,348}$ = 2.65, P = 0.10), but differed by time of day ($F_{7,348}$ = 3.05, P = 0.004), after the non-significant interaction between breeding stage and time of day ($F_{7,341}$ = 1.26, P = 0.27). Pairs were absent for the least amount of time during the 3-h interval 0:00–2:59 (44.5 ± 17.8 min) and missing for the most time during the two 3-h intervals 6:00–11:59 (133.8 ± 28.9 min; all $t_{348} \geq 3.17$, $P \leq 0.04$).

DISCUSSION

We successfully obtained 24-h records of colony attendance for Forster's Terns in South San Francisco Bay using an automated data-logging system. Because of the high detection rate of the reference transmitter and the infrequent detections of false frequencies, we are confident the data-logging system functioned well. Additionally, the data-logging system overcomes limitations of observational studies, which are often restricted by daylight, by allowing full 24-h records of colony attendance. These nocturnal records are important to fully assess colony attendance patterns. For example, without continuous colony attendance records, overall colony attendance rates by female Forster's Terns would appear to be much lower than we report here, due to relatively low rates of diurnal attendance (25.9%) by females. However, once we incorporated nocturnal records of attendance, overall attendance for females was 45.1% and 39.1% of their time during incubation and chick-rearing, respectively.

This study is the first to document colony attendance patterns of Forster's Terns and one of a few studies to document these rates for any tern species. Similarly, Anderson *et al.* (2007) obtained daytime colony attendance of radio-marked Caspian Terns

Hydroprogne caspia using a comparable data-logging system and reported attendance varying during their two years of study between 37% and 52% of an individual's time during the chick-rearing period. We found similar chick-rearing colony attendance rates for Forster's Terns. However, we also found significant differences between the sexes, with female and male Foster's Terns averaging attendance rates between 9:00 and 14:59 of 23.0% and 61.8 %, respectively, throughout the duration of the study. Despite these sex-specific differences, the length of the attendance bouts did not differ between the sexes. This highlights the importance of examining multiple variables in order to assess patterns of colony attendance.

During the day, pairs infrequently overlapped in their colony attendance and both members of a pair were often missing. However, nocturnal colony attendance was high for pairs and individuals, regardless of sex, and both members of a pair often attended the colony together at night. In contrast, female Black Terns often did not attend their colony at night, leaving the incubation and brooding responsibilities solely to the males (van der Winden 2005). The instances that both members of a Forster's Tern pair were missing at night occurred infrequently, but, when it occurred, averaged 44.5 ± 17.5 min in duration. Similarly, Arnold *et al.* (2006) documented Common Tern *Sterna hirundo* pairs nocturnally abandoning nests for an average of 54 minutes, and attributed these desertion behaviours to predation events.

The data-logging system functioned well and we determined it is a reliable method to monitor colony attendance patterns of radio-marked Forster's Terns. The system has advantages over direct observations, which are limited by daylight and other factors that limit visibility. Also, the system is more effective than using temperature sensors, since those devices cannot distinguish between individuals, are affected by ambient temperatures, and only detect presence on the nest rather than on the colony. Despite the benefits of this system, there are some associated limitations. First, the temporal resolution of the system may obscure some patterns of colony attendance if a foraging trip or other absence occurs within the 15 min logger cycle. In our study, Forster's Terns from the N7 colony range 4–5 km from the nest during incubation and chick-rearing stages (Bluso-Demers *et al.* 2008), therefore, if terns travel at the flight speed reported by Cottam *et al.* (1942; 16 km/h), they may require 15 min to travel those distances. Similarly, observations on Common Tern in colonies in the Wadden Sea showed feeding rates by both parents of on average well below 3 per h (Frank 1992). For these reasons, we believe the instances of the logger failing to record absences from this colony to be limited. However, we suggest that others considering use of a data-logging system take into account the foraging range and flight speed of their study species, as well as time needed for the data-logging system to scan through the frequencies of marked individuals. Second, the data-logging system could detect the presence of radio-marked terns within 150 m of the system; therefore, our measure of colony attendance only includes attendance within this range. Although, tern colonies often have nests aggregated very closely together, this distance may be unsuitable to determine colony attendance in other species. Third, the data-logging system collects only presence/absence data; therefore, it is difficult to link these records to on-colony activities or specific parental care behaviours at the nest without incorporating observational data. Where practical, we suggest supplementing the data collected from the data-logging systems with observational data. In this case, our goal was to obtain 24-h records of colony attendance for paired terns at a remote site with limited access, and this system was successful in achieving that goal.

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SAMENVATTING

Om een compleet beeld van de broedzorg van vogels te krijgen zijn waarnemingen gedurende het gehele etmaal nodig. In dit onderzoek werd de aanwezigheid van Forsters Sterns *Sterna forsteri* in een broedkolonie in de baai van San Francisco, Californië, Verenigde Staten, vastgelegd met behulp van een geautomatiseerd systeem om radiosignalen op te pikken. Hiertoe werden tien vogels (vijf paren) gevangen en voorzien van een zendertje dat was bevestigd op een ring rond de poot. Op grond van de registraties werden vijf maten voor de aan- en afwezigheid berekend: de tijd dat een van beide partners en elke partner afzonderlijk tijdens een etmaal in de kolonie doorbracht, de duur van elk koloniebezoek en de duur dat beide partners gezamenlijk aanwezig of afwezig waren. Het percentage van de tijd dat minstens een van de partners in de kolonie aanwezig was, was het hoogst in de broedtijd en nam na het uitkomen van de jongen af. Mannetjes waren overdag meer tijd in de kolonie aanwezig dan vrouwtjes. Vrouwtjes brachten echter 's nachts (bijna negen uur in het onderzoekgebied) meer tijd in de kolonie door dan mannetje. Zonder de nachtregistraties zou de totale tijd van vrouwtjes in de kolonie sterk zijn onderschat. De verblijfsduur in de kolonie per koloniebezoek verschilde niet tussen de seksen. 's Nachts waren beide partners vaak gezamenlijk aanwezig in de kolonie, maar overdag bestond er weinig overlap in de aanwezigheid. Zij waren vaak overdag beide afwezig. Het zenderregistratiesysteem werkte naar behoren. De verkregen gegevens onderstrepen het belang van 24-uurregistraties van de aanwezigheid in de broedkolonie. (JP)

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