DOI 10.21857/y26kecgpp9

Original scientific paper
Izvorni znanstveni članak
Received: 8.7.2024.
Accepted: 17.10.2024.

FACTORS AFFECTING NEST ATTENDANCE IN COMMON TERNS

Čimbenici koji utječu na prisutnost na gnijezdu kod crvenokljune čigre

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ABSTRACT

The Common Tern *Sterna hirundo* nests colonially in both marine and freshwater habitats with incubation and chick rearing being shared parental responsibilities. To research the dynamics of incubation behaviour in this species, a series of camera trap photographs taken between May 2021 and May 2023 were collected from three different colonies, one from marine and two from freshwater habitats. Photographs of seven nests were sorted into three states (incubating, near and absent) for which the state duration per day, the state duration until the change and the number of state changes were calculated. Incubation duration differed significantly among nests from the same and different habitats. Individuals on freshwater colonies spent a significantly longer time incubating, while birds from the marine habitat spent a longer time absent from nests, both of which can be related to more predictable prey availability at freshwater sites. Additional factors affecting incubation activity for this species are discussed.

Keywords: *Sterna hirundo*, marine habitat, freshwater habitat, camera traps, daily dynamic, incubation, foraging

INTRODUCTION

In birds, high nest attendance during incubation is essential for maintaining the adequate temperature and protection of eggs from thermal stress and predation. Such intensive parental effort involves high costs for parents. In birds

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with biparental care, partners may share incubation duties, coordinating their parental investment (Kavelaars *et al.* 2021). In seabirds, incubation stints and foraging patterns vary among species. While some pelagic species forage at considerable distances from the colony and are therefore absent for several days (Weimerskirch 1995), majority of seabirds forage at shorter ranges and exchange incubation duties several times per day (Becker *et al.* 1997). Nest attendance is affected by several factors, such as disturbance, predation, heat stress or foraging conditions (Frank & Becker 1992, Bluso-Demers *et al.* 2010, Amat *et al.* 2017, Olin *et al.* 2023).

The Common Tern *Sterna hirundo* is a monogamous colonial seabird with biparental care which breeds in both freshwater and marine habitats. It lays a single clutch with up to 4 eggs (mostly 2 – 3). Incubation lasts 21 – 23 days (Becker & Ludwigs 2004). Nocturnal nest desertion caused by predation or other factors may lead to an increasing length of the incubation period (Arnold *et al.* 2020). Incubation stints vary between less than a minute to several hours. Nocturnal incubation is mostly done by the female, while both sexes share diurnal incubation (Arnold *et al.* 2020). It has been shown that feeding conditions affect nest attendance in Common Terns (Frank & Becker 1992) and that freshwater and marine habitats differ in prey availability (Becker *et al.* 1997).

The aim of this work is to determine the difference in nest attendance of Common Terns from freshwater and marine colonies. By categorizing and analysing images collected by camera traps during the incubation period, we tested the hypothesis that terns spent more time at the colonies on freshwater habitats as a result of more predictable prey availability.

MATERIALS AND METHODS

Research area

The data was collected on three locations at different intervals: the islet of Školjić (43.98 N 15.36 E), Rakitje gravel pit (45.80 N 15.84 E) and Siromaja gravel pit (45.76 N 16.19 E). The Rakitje colony was surveyed during May 2021, Siromaja colony during May 2022, and Školjić during May 2022 and May 2023 (Fig. 1).

The islet of Školjić is a small rocky outcrop with sparse vegetation near the larger island of Pašman, belonging to the Zadar archipelago. During the years in which this colony was researched there were 23 and 32 pairs respectively. Rakitje gravel pit is comprised of four artificial lakes which are all frequently used for fishing. Common Terns have an established colony on a gravely island in one of the lakes, with 115 breeding pairs in 2021. Siromaja gravel pit is a cluster of three artificial lakes. One of the lakes houses an artificial breeding platform with 65 breeding pairs present in 2022. All three colonies were regularly monitored between 2021 and 2023.

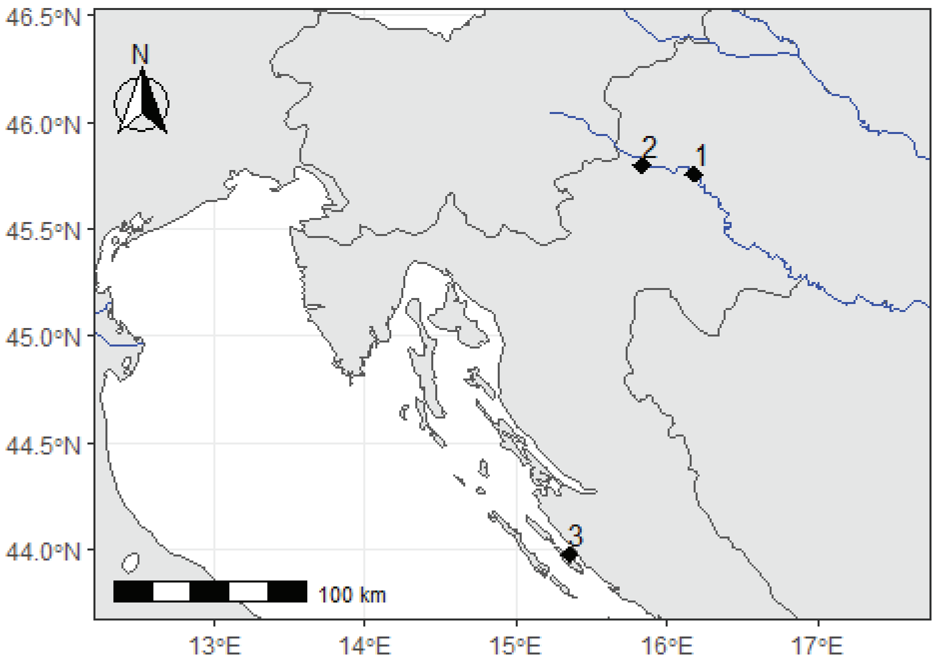

Figure 1. The position of studied Common Tern colonies: 1-Siromaja, 2-Rakitje, 3-Školjić.
Slika 1. *Položaj istraživanih kolonija crvenokljune čigre: 1-Siromaja, 2-Rakitje, 3-Školjić.*

Data collection

In each colony, one or two Spy-point Force-dark camera traps were placed a couple of meters from the nearest Common Tern nest, usually at an elevation of 0.5 m. Camera trap settings were set to the "multi-photo" setting, which allowed to record three consecutive photos after each recorded movement, usually within the same second. The cameras shot continuously and without pause regardless of the time between movement detection or the number of photos taken after each movement. The camera traps were active for the entire interval of colony surveillance, taking both diurnal and nocturnal photos. Each photo came coupled with the precise time (order of seconds) and date in which it was shot. To minimise the disturbance of adult Common Terns and ensure a quick return to incubation of their respective clutches, field visits for the instalment of camera traps and change of batteries and memory cards were kept brief.

Preparation of data for statistical analysis

Before filtering and processing the data, at least one nest was selected from each of the photo series. The nests were selected based on close proximity to the camera and good visibility throughout all times of the day. Nests caught only partially on camera were chosen for analysis only if they allowed a clear view of the individual's incubation behaviour. We selected three nests from Školjić (2022SKO1, 2022SKO2 and 2023SKO), two nests from Rakitje (R1 and R2) and two from Siromaja (SIR1 and SIR2).

In total, 170.883 photographs were filtered and statistically analysed in this work. The number of days covered at each nest was as follows: seven for SIR1 and SIR2, sixteen for R1, fifteen for R2, sixteen for 2023SKO, thirteen for 2022SKO1 and five for 2022SKO2. The photos were reviewed and filtered using the Photo Mechanic software (ver. 6.0.0.6552). Pictures in which a clear view of the nest and/or the incubating tern was obstructed, whether because of data corruption or blockages due to heavy fog, precipitation on the camera lens or foreign objects were excluded from the analysis. In addition, photographs taken during intermittent field visits were also excluded to prevent the occurrence of any Common Tern behaviour heavily modified by human presence. The analysis started with the first full day after the camera installation.

Filtering of the data was done on the account of three behaviour states present in the photographs. One state was assigned to each photo and those in which the state seemed ambiguous were compared to the pictures which immediately surrounded them in the time series. The behaviour states include "incubating", "near" or "absent". "Incubating" is defined as the state in which the individual completely covers the upper layer of the nest with their lower body, including any rotation and stretching performed by the bird. All the photographs which depicted an individual above or in the vicinity of the nest, but not incubating, were marked as the "near" state, but only if the individual could be clearly defined as one of the parents usually incubating on the given nest by analysing the individual's movement through the continuous time series of previous and ensuing photographs. In cases in which the adult birds were not present anywhere in the camera frame, or those present could not be surely associated with the given nests, the photographs were marked as "absent".

Statistical analysis

The collected data was used to calculate three parameters for statistical analysis: State duration per day (SDPD), State duration until change (SDUC) and Number of state changes (NOSC). The basis of all the parameters were the 24-hour periods of recorded colony behaviour and the internal periods of the day named "Morning", "Noon" and "Night". Internal daily periods were of similar, but varying length, depending on the date of their recording and the latitude of the nest site. Their exact duration was extrapolated from sunset and sunrise times specific for the colony area, obtained from the timeanddate website (Time and Date AS, 2024). Since that website couldn't supply sunrise and sunset data for the exact location of the colonies, nearby settlements were used as proxies: Mali Iž (44,03° N 15,14° E) was used as a substitute for the Školjić colony, whereas the settlements of Novaki Nartski (45,76° N 16,18° E) and Rakitje (45,79° N 15,82° E) were used for the Siromaja and Rakitje colony, respectively.

State duration per day is the sum of the duration of each behaviour state in a 24-hour period. The data for this parameter is shown as a percentage obtained by dividing the given duration in seconds by 86400 (the number of seconds in a day). Due to camera malfunctions or the presence of researchers in the observed colony, a certain amount of data had to be discarded, and the remaining data were used as a basis to measure state duration. However, days in which the recording didn't exceed six hours (21600 seconds) were deemed too short for analysis and were excluded except for when calculating internal daily intervals. State duration until change is the duration of any given state until the occurrence of a different state. SDUC is shown as the duration of the state measured in seconds. The Number of state changes represents the total amount of state changes recorded during a single day or a specific daily interval.

To determine the normality of the data Shapiro-Wilk tests were conducted for every parameter on all colonies during both the daily intervals and the entire day. Since data were mostly non-normally distributed, nonparametric tests were used for the comparison of parameters. The differences between freshwater and marine colonies were analysed using the Mann-Whitney U test, whereas the Kruskal-Wallis test was used to calculate the differences between the nests in colonies of the same habitat type. Certain night-time data had to be excluded from the Kruskal-Wallis test because of its scarcity. All analyses were done using the 4.3.1. version of the R programming language (R Core Team 2023).

RESULTS

The incubating state was the most common behaviour state across all seven analysed nests. The average time spent exhibiting this behaviour during the incubation period was 95.2% for freshwater and 55.9% for marine areas (Table 1). On average, Common Terns nesting in freshwater areas were absent less than their marine counterparts (1.4% compared to 26.7% of the time, Table 1).

The median duration of the incubating state was longer in freshwater colonies, whereas the absent state was longer in marine colonies (Table 2). The number of state changes was greater in freshwater colonies regardless of the observation interval (Table 3).

Differences in daily dynamics between nests of the same habitat types

The SDPD showed similar patterns for all nests, except for those observed on the islet of Školjić during the 2022 season. The incubating state was the most common, being present for more than 90% of the time and the absent state was the least common (Table 1). For the nests from Školjić in 2022 (2022SKO1 and 2022SKO2), the median of the incubating state was only 54% and 46%, respectively (Table 1). The absent state for those nests was recorded much more often compared to other nests and nesting seasons, having a median of 43% and 45% (Table 1). Kruskal-Wallis test showed statistically significant differences between nests of the same habitat in both freshwater and marine colonies for all calculated parameters (Table 4). The highest differences were found when comparing parameters during the entire day, and the lowest during the night. More significant differences were found among nests in freshwater than in marine colonies.

Differences in daily dynamics between nests of different habitat types

The SDPD showed large differences between nests of different habitat types: individuals nesting in the marine habitat spend less time at the colony (near and incubating states, Fig. 2). Mann-Whitney U test showed statistically significant differences for all three parameters (Table 5). The SDPD parameter was significantly different for the absent and incubating states in every interval, whereas the differences in the near state were mostly nonsignificant (Table 5). All states except incubating had statistically significant differences in the SDUC for every tested interval. The NOSC showed statistically significant differences only during the entire day and the night, with fewer state changes recorded in marine habitats (Table 5, Fig. 3).

Table 1. State duration per day during the incubation of common terns on different nest sites shown as a proportion of the observation interval. Values presented as median, first and third quartile. R1, R2 – nests on the Rakitje colony. SIR1, SIR2 – nests on the Siromaja colony. FR – combined result of freshwater colonies. 2022SKO1, 2022SKO2 – nests on the Školjić colony observed during 2022. 2023SKO – nest on the Školjić colony observed during 2023. MA – combined result of marine colonies.

Tablica 1. *Dnevno trajanje stanja tijekom inkubacije crvenokljune čigre prikazano kao udio trajanja razdoblja promatranja. Prikazani su medijani te prvi i treći kvartili. R1, R2 – gnijezda kolonije na jezeru Rakitje. SIR1, SIR2 – gnijezda kolonije na jezeru Siromaja. FR – gnijezda slatkovodnih kolonija. 2022SKO1, 2022SKO2 – gnijezda na otoku Školjiću promatrana 2022. 2023SKO – gnijezdo na otoku Školjiću promatrano 2023. MA – gnijezda morskih kolonija.*

	STATE DURATION PER DAY											
	ENTIRE DAY			MORNING			AFTERNOON			NIGHT		
	INCUBAT-ING	NEAR	ABSENT	INCUB ATING	NEAR	ABSENT	INCUBATING	NEAR	ABSENT	INCUBAT-ING	NEAR	ABSENT
R1	0.9491 (0.9177 – 0.9538)	0.0219 (0.0169 - 0.0365)	0.0211 (0.0169 - 0.0365)	0.9488 (0.9281 - 0.9629)	0.0245 (0.0141 - 0.0354)	0.0214 (0.0143 - 0.0407)	0.9299 (0.9138 - 0.9558)	0.0401 (0.0220 - 0.0630)	0.0234 (0.0079 - 0.0643)	0.9810 (0.9698 - 0.9900)	0.0058 (0.0028 - 0.0127)	0.0043 (0.0008 - 0.0152)
R2	0.9862 (0.9456 - 0.9811)	0.0142 (0.0111 - 0.0200)	0.0093 (0.0034 - 0.0144)	0.9831 (0.9787 - 0.9924)	0.0078 (0.0061 - 0.0172)	0.0055 (0.0027 - 0.0086)	0.9631 (0.9369 - 0.9773)	0.0318 (0.0142 - 0.0397)	0.0105 (0.0033 - 0.0306)	0.9908 (0.9559 - 0.9952)	0.0033 (0.0017 - 0.0077)	0.0043 (0.0011 - 0.0151)
SIR1	0.9378 (0.8058 - 0.9533)	0.0348 (0.0315 - 0.0473)	0.0031 (0.0017 - 0.0094)	0.9397 (0.8715 - 0.9773)	0.0456 (0.0238 - 0.0802)	0.0052 (0.0048 - 0.0120)	0.9805 (0.9669 - 0.9879)	0.0216 (0.0172 - 0.0369)	0.0022 (0.0020 - 0.0031)	0.9594 (0.7520 - 1.0000)	0.0404 (0.0283 - 0.0579)	0.0007 (0.0004 - 0.0011)
SIR2	0.9112 (0.8890 - 0.9505)	0.0230 (0.0140 - 0.0414)	0.0256 (0.0134 - 0.0393)	0.8586 (0.7925 - 0.9628)	0.1038 (0.0498 - 0.1552)	0.0453 (0.0143 - 0.3182)	0.9797 (0.9771 - 0.9917)	0.0154 (0.0047 - 0.0198)	0.0040 (0.0038 - 0.0119)	0.9853 (0.9475 - 0.9927)	0.0114 (0.0081 - 0.0202)	0.0547 (0.0257 - 0.0870)
FR	**0.9525 (0.9030 - 0.9686)**	**0.0202 (0.0127 - 0.0348)**	**0.0139 (0.0047 - 0.0310)**	**0.9626 (0.9281 - 0.9861)**	**0.0197 (0.0074 - 0.0377)**	**0.0120 (0.0050 - 0.0276)**	**0.9645 (0.9293 - 0.9806)**	**0.0269 (0.0152 - 0.0413)**	**0.0105 (0.0038 - 0.0349)**	**0.9853 (0.9475 - 0.9927)**	**0.0058 (0.0023 - 0.0127)**	**0.0046 (0.0008 - 0.0210)**
2023SKO	0.9255 (0.6167 - 0.9727)	0.0429 (0.0236 - 0.0935)	0.0078 (0.0041 - 0.0228)	0.9223 (0.8713 - 0.9934)	0.0477 (0.0142 - 0.1381)	0.0389 (0.0249 - 0.0529)	0.9287 (0.7558 - 0.9527)	0.0457 (0.0055 - 0.2425)	0.0052 (0.0017 - 0.0222)	/	/	/
2022SKO1	0.5429 (0.5192 - 0.5945)	0.0116 (0.0085 - 0.0261)	0.4362 (0.3845 - 0.4567)	0.8587 (0.8288 - 0.9102)	0.0178 (0.0136 - 0.0282)	0.1280 (0.0771 - 0.1599)	0.6378 (0.6091 - 0.6914)	0.0236 (0.0104 - 0.0441)	0.3437 (0.2962 - 0.3835)	0.1019 (0.0894 - 0.1746)	0.0172 (0.0024 - 0.0324)	0.8719 (0.4806 - 0.9031)
2022SKO2	0.4601 (0.4499 - 0.4860)	0.0586 (0.0507 - 0.0817)	0.4572 (0.2331 - 0.4892)	0.8326 (0.7329 - 0.8380)	0.0691 (0.0645 - 0.0707)	0.1447 (0.0864 - 0.1975)	0.6597 (0.6317 - 0.7322)	0.1017 (0.0913 - 0.1126)	0.2433 (0.1693 - 0.2899)	0.0338 (0.0160 - 0.0374)	0.0139 (0.0139 - 0.0139)	0.9626 (0.3972 - 0.9662)
MA	**0.5590 (0.4871 - 0.9098)**	**0.0251 (0.0128 - 0.0566)**	**0.2671 (0.0157 - 0.4476)**	**0.8682 (0.8135 - 0.9428)**	**0.0256 (0.0147 - 0.0685)**	**0.0821 (0.0365 - 0.1438)**	**0.7357 (0.6315 - 0.9036)**	**0.0585 (0.0178 - 0.1090)**	**0.1812 (0.0209 - 0.3233)**	**0.0969 (0.0338 - 0.1435)**	**0.0228 (0.0054 - 0.0337)**	**0.8836 (0.4745 - 0.9528)**

Table 2. State Duration until change during the incubation of common terns shown in seconds. Values presented as median, first and third quartile. R1, R2 – nests on the Rakitje colony. SIR1, SIR2 – nests on the Siromaja colony. FR – combined result of freshwater colonies. 2022SKO1, 2022SKO2 – nests on the Školjić colony observed during 2022. 2023SKO – nest on the Školjić colony observed during 2023. MA – combined result of marine colonies.

Tablica 2. *Trajanje stanja do pojave novog stanja tijekom inkubacije crvenokljune čigre prikazano u sekundama. Prikazani su medijani te prvi i treći kvartili. R1, R2 – gnijezda kolonije na jezeru Rakitje. SIR1, SIR2 – gnijezda kolonije na jezeru Siromaja. FR – gnijezda slatkovodnih kolonija. 2022SKO1, 2022SKO2 – gnijezda na otoku Školjiću promatrana 2022. 2023SKO – gnijezdo na otoku Školjiću promatrano 2023. MA – gnijezda morskih kolonija.*

	STATE DURATION UNTIL CHANGE											
	ENTIRE DAY			MORNING			AFTERNOON			NIGHT		
NEST	INCUBAT-ING	NEAR	ABSENT	INCUBAT-ING	NEAR	ABSENT	INCUBAT-ING	NEAR	ABSENT	INCUBAT-ING	NEAR	ABSENT
R1	991.0 (323.8 - 2369.0)	10.0 (5.0 - 46.0)	20.0 (10.0 - 85.0)	987.0 (354.0 - 2228.)	7.0 (4.0 - 41.0)	17.0 (10.0 - 41.5)	743.5 (221.3 - 1786.5)	12.0 (5.0 - 62.0)	21.0 (9.0 - 90.0)	3064.0 (1461.8 - 8190.3)	17.5 (5.0 - 33.3)	28.0 (10.0 - 128.0)
R2	1207.0 (448.3 - 2719.0)	9.0 (5.0 - 20.0)	16.5 (8.0 - 31.0)	1041.0 (454.0 - 2715.0)	8.0 (4.0 - 15.8)	15.0 (8.0 - 29.0)	988.0 (373.0 - 1978.0)	9.0 (5.0 - 24.0)	17.0 (7.8 - 32.8)	4868.0 (1918.3 - 8764.3)	10.0 (5.0 - 21.8)	27.0 (16.8 - 232.5)
SIR1	2086.0 (859.0 - 5995.0)	53.0 (5.0 - 298.0)	32.0 (17.0 - 81.0)	1166.0 (623.0-3871.0)	94.0 (17.0 - 393.0)	81.0 (42.0 - 208.0)	3338.0 (1123.0 - 6022.0)	35.0 (5.0 - 105.5)	34.0 (11.8 - 42.8)	8184.0 (1510.0 - 40526.5)	506.5 (128.5 - 1091.5)	20.0 (13.8 - 24.3)
SIR2	2998.5 (1280.0 - 9669.3)	68.0 (11.5 - 341.0)	134.0 (27.0 - 681.0)	2966.0 (1280.0 - 4243.0)	100.0 (25.0 - 363.0)	431.5 (148.8 - 673.5)	4223.0 (1500.0 - 6829.0)	38.0 (9.5 - 193.0)	36.0 (12.0 - 119.0)	22160.0 (772.0 - 26486.0)	68.0 (4.5 - 362.0)	702.0 (398.8 - 1546.0)
FR	**1172.0 (424.0 - 2767.0)**	**10.0 (5.0 - 40.3)**	**19.0 (9.0 - 67.0)**	**1091.0 (424.0 - 2621.0)**	**9.0 (4.0 - 37.0)**	**18.0 (10.0 - 53.0)**	**944.0 (296.5 - 2097.0)**	**10.0 (5.0 - 47.0)**	**18.0 (9.0 - 56.3)**	**2697.5 (1486.0 - 8862.75)**	**12.0 (5.0 - 32.0)**	**31.0 (16.0 - 243.0)**

2023SKO	1242.5 (414.8 - 3131.0)	20.0 (5.0 - 132.3)	74.0 (23.0 - 281.0)	1406.0 (490.0 - 3812.0)	16.0 (5.0 - 112.0)	51.5 (21.8 - 259.3)	1292.5 (399.0 - 2565.8)	30.0 (5.0 - 209.0)	93.0 (30.0 - 282.0)	/	/	/
2022SKO1	117.0 (407.0 - 2412.0)	22.0 (5.0 - 69.8)	39.0 (18.0 - 274.0)	1248.0 (338.0 - 2424.0)	20.0 (5.0 - 60.0)	42.0 (20.0 - 181.3)	1026.0 (396.5 - 1944.0)	20.0 (7.0 - 72.5)	34.0 (15.0 - 549.0)	3167.0 (1231.0 - 3601.0)	137.0 (86.0 - 900.0)	26068.5 (1476.8 - 29210.3)
2022SKO2	764.5 (230.5 - 1432.3)	14.5 (5.0 - 60.3)	29.0 (6.0 - 124.0)	673.0 (142.0 - 1448.0)	13.0 (5.0 - 41.5)	41.0 (21.0 - 131.0)	755.0 (260.5 - 1281.5)	18.0 (6.0 - 75.3)	22.0 (14.0 - 130.5)	1163.5 (668.5 - 2965.0)	1461.5 (957.8 - 1965.3)	31478.0 (12990.0 - 31595.0)
MA	**1016.0 (349.0 - 2229.0)**	**18.0 (5.0 - 78.8)**	**36.0 (17.0 - 210.3)**	**1019.0 (285.0 - 2290.5)**	**15.0 (5.0 - 60.0)**	**42.0 (20.0 - 180.5)**	**989.0 (338.5 - 2092.5)**	**21.0 (5.0 - 105.8)**	**31.0 (15.0 - 288.0)**	**2503.0 (1105.0 - 3573.5)**	**454.0 (111.5 - 1012.5)**	**27009.0 (4534.5 - 29701.0)**

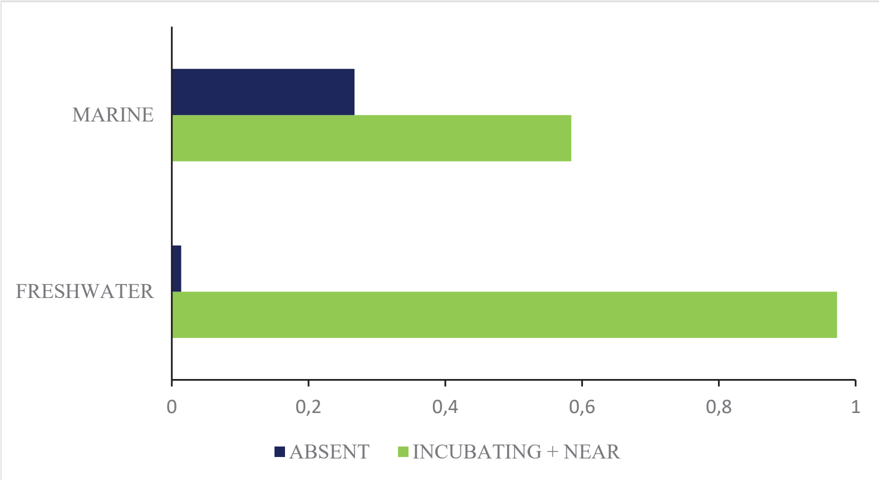

Figure 2. Average state duration per day during the incubation of common terns on different habitats shown as a proportion of total observed behaviour duration. Data for on-site behaviour (incubating and near states) is grouped.

Slika 2. *Prosječno dnevno trajanje stanja tijekom inkubacije crvenokljunih čigri na različitim tipovima staništa izraženo udjelom u ukupnom trajanju promatranja. Podaci za stanja bilježena na kolonijama (stanja "inkubira" i "blizu gnijezda") su grupirani.*

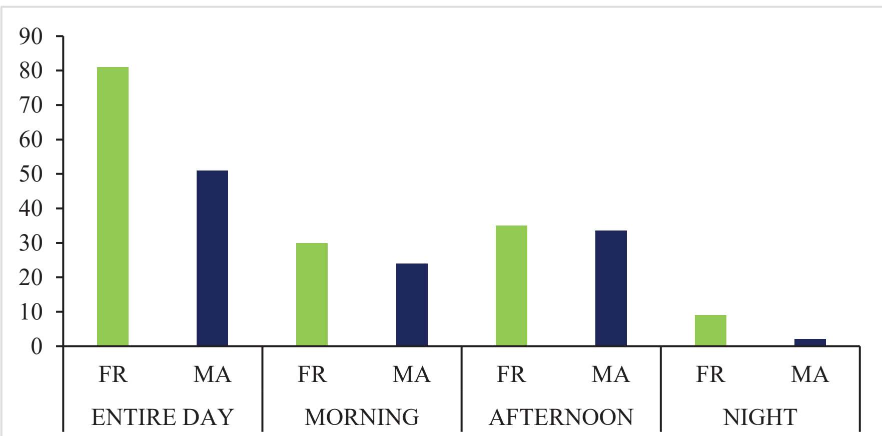

Figure 3. Number of state changes per day during incubation of common terns observed across different habitats during different time intervals. FR – Nests from freshwater colonies. MA – Nests from marine colonies.

Slika 3. *Broj promjena stanja po danu tijekom inkubacije crvenokljunih čigri po staništu tijekom različitih vremenskih intervala. FR – gnijezda slatkovodnih kolonija. MA – gnijezda morskih kolonija.*

Table 3. Number of state changes per day during the incubation of common terns. Values presented as median and first and third quartile. R1, R2 – nests on the Rakitje colony. SIR1, SIR2 – nests on the Siromaja colony. FR – combined result of freshwater colonies. 2022SKO1, 2022SKO2 – nests on the Školjić colony observed during 2022. 2023SKO – nest on the Školjić colony observed during 2023. MA – combined result of marine colonies.

Tablica 3. *Ukupni broj promjena stanja po danu tijekom inkubacije na gnijezdima crvenokljune čigre. Prikazani su medijani te prvi i treći kvartili. R1, R2 – gnijezda kolonije na jezeru Rakitje. SIR1, SIR2 – gnijezda kolonije na jezeru Siromaja. FR – gnijezda slatkovodnih kolonija. 2022SKO1, 2022SKO2 – gnijezda na otoku Školjiću promatrana 2022. 2023SKO – gnijezdo na otoku Školjiću promatrano 2023. MA – gnijezda morskih kolonija.*

	NUMBER OF STATE CHANGES			
NEST	ENTIRE DAY	MORNING	AFTERNOON	NIGHT
R1	106.0 (92.8 - 139.5)	43.0 (31.5 - 46.0)	51.5 (39.8 - 76.0)	14.0 (10.5 - 16.8)
R2	82.0 (76.0 - 102.0)	31.0 (24.0 - 33.0)	46.0 (29.0 - 60.0)	9.0 (8.0 - 12.0)
SIR1	19.0 (18.0 - 25.0)	10.0 (8.0 - 11.0)	10.0 (8.0 - 10.0)	0.0 (0.0 - 3.0)
SIR2	17.0 (12.0 - 24.0)	11.0 (2.0 - 14.0)	5.0 (4.0 - 10.0)	2.0 (2.0 - 4.0)
FR	**81.0 (40.0 - 105.0)**	**30.0 (18.0 - 39.0)**	**35.0 (17.0 - 60.0)**	**9.0 (5.0 - 14.0)**
2022SKO1	38.5 (26.0 - 49.0)	30.0 (21.0 - 40.5)	37.0 (30.0 - 41.0)	2.0 (2.0 - 5.0)
2022SKO2	67.0 (50.0 - 81.0)	43.0 (36.0 - 44.0)	61.0 (55.0 - 71.5)	2.0 (2.0 - 2.0)
2023SKO	91.0 (90.5 - 108.0)	14.0 (9.8 - 23.0)	22.0 (15.8 - 33.5)	/
MA	**51.0 (39.3 - 75.5)**	**24.0 (13.0 - 31.8)**	**33.5 (19.5 - 40.5)**	**2.0 (2.0 - 4.3)**

Table 4. Comparison of different behavioural parameters between common tern nests located within the same type of habitat. Data is presented as the degrees of freedom (df), chi square value (H) and p value (p) obtained using the Kruskal-Wallis test. SDPD – State duration per day. SDUC – State duration until change. NOSC – Number of state changes. MA – Nests from marine colonies. FR – Nests from freshwater colonies.

Tablica 4. *Usporedba trajanja stanja tijekom inkubacije među gnijezdima crvenokljune čigre na istom staništu. Prikazani su stupnjevi slobode (df), hi kvadrat (H) i p vrijednost Kruskal-Wallis testa. SDPD - Dnevno trajanje stanja. SDUC – Trajanje stanja do promjene. NOSC – Ukupni broj promjena. MA – gnijezda morskog staništa. FR – gnijezda slatkovodnog staništa.*

			KRUSKAL-WALLIS TEST											
			ENTIRE DAY			MORNING			AFTERNOON			NIGHT		
PARAMETER	STATE	HABITAT	df	H	p	df	H	p	df	H	p	df	H	p
SDPD	INCUBATING	MA	2	8.02	<0.05	2	1.88	0.17	2	0.40	0.53	1	2.85	0.09
		FR	3	5.57	0.13	3	13.15	<0.005	3	11.61	<0.01	3	0.93	0.82
SDPD	NEAR	MA	2	9.31	<0.01	2	6.94	<0.01	2	4.90	<0.05	1	0.86	0.35
		FR	3	7.87	<0.05	3	9.46	<0.05	3	7.00	0.07	3	9.90	<0.05
SDPD	ABSENT	MA	2	21.40	<0.001	1	0.02	0.88	2	4.92	<0.05	1	0.09	0.77
		FR	3	7.95	<0.05	3	13.09	<0.005	3	7.74	0.05	3	12.22	<0.01
SDUC	INCUBATING	MA	2	23.23	<0.001	2	21.65	<0.001	2	13.30	<0.005	1	1.26	0.26
		FR	3	49.78	<0.001	3	14.23	<0.005	3	6.78	0.08	3	4.88	0.18
SDUC	NEAR	MA	2	0.93	0.63	2	2.10	0.35	2	8.48	<0.05	1	1.35	0.25
		FR	3	71.52	<0.001	3	54.97	<0.001	3	7.10	0.07	3	6.46	0.09
SDUC	ABSENT	MA	2	4.76	0.09	2	0.06	0.97	2	6.84	<0.05	1	2.11	0.15
		FR	3	29.91	<0.001	3	27.58	<0.001	3	5.17	0.16	3	10.62	<0.05
NOSC	/	MA	2	16.69	<0.001	2	12.38	<0.005	2	13.10	<0.005	1	0.17	0.68
		FR	3	23.28	<0.001	3	22.06	<0.001	3	21.38	<0.001	3	24.03	<0.001

Table 5. Comparison of different behavioural parameters between common tern nests located across different habitat types. Data is presented as the number of samples (N), p value (p) and W value (W) obtained using the Mann-Whitney U test. SDUC – State duration until change. NOSC – Number of state changes. MA – Nests from marine colonies. FR – Nests from freshwater colonies.

Tablica 5. *Usporedba trajanja stanja tijekom inkubacije među gnijezdima crvenokljune čigre među staništima. Prikazani su N (broj uzoraka), p i W vrijednost Mann-Whitney U testa. SDPD - Dnevno trajanje stanja. SDUC – Trajanje stanja do promjene. NOSC – Ukupni broj promjena. FR – gnijezda slatkovodnih staništa. MA – gnijezda morskog staništa.*

		MANN-WHITNEY U TEST											
		ENTIRE DAY			MORNING			AFTERNOON			NIGHT		
PARAM-ETER	STATE	N (FR; MA)	W	p	N (FR; MA)	W	p	N (FR; MA)	W	p	N (FR; MA)	W	p
SDPD	INCUBATING	42; 31	1017.5	<0.001	44; 31	979.5	<0.005	44; 31	1183.5	<0.001	44; 17	740.0	<0.001
SDPD	NEAR	42; 30	486.5	0.10	39; 30	475.0	0.19	41; 30	409.0	<0.05	37; 6	74.5	0.24
SDPD	ABSENT	42; 30	311.0	<0.001	40; 14	221.5	<0.001	37; 31	277.0	<0.001	31; 18	3.0	<0.001
SDUC	INCUBATING	1243; 713	472839.5	<0.05	451; 331	79738.0	0.10	635; 383	121228.5	0.93	170; 23	2401.5	0.08
SDUC	NEAR	1364; 646	372831.0	<0.001	496; 286	60517.5	<0.001	698; 346	98165.0	<0.001	173; 7	91.5	<0.001
SDUC	ABSENT	561; 460	92292.0	<0.001	229; 207	14732.5	<0.001	280; 264	27202.0	<0.001	55; 23	80.5	<0.001
NOSC	/	37; 28	679.0	<0.05	45; 32	772.5	0.59	45; 32	765.0	0.65	45; 18	620.5	<0.001

DISCUSSION

Our study confirmed that Common Terns at freshwater habitats generally spent more time at the colonies, but also showed significant behavioural differences among birds from the same colony.

Behavioural differences of Common Terns nesting in freshwater habitats

Common Terns nesting in the Rakitje colony had more state changes than those nesting in the Siromaja colony. In addition, birds nesting in the Siromaja colony exhibited a longer state duration until change. The differences between these nesting sites can be explained by prey availability. Becker *et al.* (1997) observed that sites with easily available prey enabled Common Terns to increase their nest attendance and decreased the number of times they left their nests in search of prey. Thus, the longer duration of the incubation between state changes for the Siromaja colony (Table 2) could be caused by the colonies' proximity to favourable foraging grounds. This is corroborated by earlier research which has shown that terns from Siromaja spent less time foraging and covered shorter distances in search of prey (Martinović *et al.* 2023).

Predation was identified as an important factor altering nesting behaviour of the Common Tern (Becker & Ludwigs, 2004). During our study, the presence of predators was rarely noticed at any colony. Nest desertion due to the presence of predators mostly happens during the night, sometimes for several hours and during subsequent nights after the predation (Arnold *et al.* 2006). This would cause the birds in the predated colonies to exhibit the absent state more often, especially during the night. However, both colonies have a rather low percentage of absence state during the night (Table 1). Furthermore, no cases of nest predation have been caught on camera during the observation intervals, regardless of the time of day. The data collected so far indicates that nest predation isn't a factor in behavioural differences of Common Terns between these freshwater colonies. However, other unidentified disturbances could contribute to the differences in observed behaviours.

Behavioural differences of Common Terns nesting in a marine habitat

The data collected from the marine colony offers a comparison of Common Tern behaviour during two different breeding seasons in the same habitat. Nests from the marine colony showed statistically significant differences in the daily duration of all states (SDPD parameter, Table 1) the most notable being that of the absent state which was very prevalent for birds incubating during the 2022 season, especially during the night. On the other hand, birds incubating on the nest observed during 2023 followed a pattern of incubation behaviour similar to those from freshwater habitats (low percentage of absence, very high percentage of incubation, Table 1). As with Common Terns nesting on freshwater habitats, a higher degree of absence could indicate longer foraging duration (Becker *et al.* 1997, Danhardt *et al.* 2011).

While foraging opportunities serve as a plausible explanation for the diurnal absence, the collected data doesn't explain why the birds were leaving their nests during night-time in 2022. Foraging during the night is rare, but not unprecedented when the benefits outweigh the costs (Becker *et al.* 1997). Common Terns prefer to forage over the sea currents but mostly avoid windy situations with waves (Schwemmer *et al.* 2009, Militão *et al.* 2023). In the Adriatic Sea, wind-driven currents dominate over the other contributions to the current system (Orlić *et al.* 1992), therefore the daily dynamic of winds was suggested as an important factor affecting the foraging activities of Common Terns (Kralj *et al.* 2024). Increased tern foraging in the late afternoon might be a consequence of diurnal winds calming down towards the evening (Kralj *et al.* 2024), which under specific weather situations, might also affect prolonged foraging during the night-time. Nest desertion due to predation could explain the long periods of nocturnal absence, however, predation has not been recorded during our observation of the colony.

The prolonged period of absence could have been caused by a lack of camera triggers causing fewer photographs to be made. Bird *et al.* (2021) have found another model of SpyPoint camera traps to be prone to false triggers and extended periods of the night in which no photos are taken. Considering our methodology, the duration of the interval in which no photos were recorded would have been added to the state of the last recorded photo before the interval. However, the same type of camera trap was successfully used in other colonies. Another technical factor which could explain the low rate of photographs during the night is the ability of the camera trap to differentiate the heat signature of the animal being observed. The temperature has a significant impact on bird detection by camera traps, as does flock size, individual bird size and behaviour (Randler & Kalb 2018). It's possible that the specific distance, temperature during recording or an obstruction of the camera lens on Školjić caused the traps to trigger less frequently. The observed night time desertion likely stems from a cause which exceeds our current understanding of nightly incubation dynamics on Školjić.

Behavioural differences between Common Terns nesting in marine and freshwater habitats

Depending on the interval and the behaviour state, statistically significant differences between the behaviour of Common Terns on freshwater and marine habitats have been observed for all parameters. The absent state is especially noteworthy, being the only state with statistically significant differences for all parameters in each of the observed intervals (Table 5).

On average, Common Terns nesting on freshwater colonies spent almost 40% more time at or near their nests than those in the marine colony. We find it likely that this difference is caused by the difficulty of foraging due to prey availability and predictability. The effect of prey depletion around a bird colony (Ashmole's halo) can be neglected, as all the observed colonies were relatively small (Jovani *et al.*, 2016). In marine habitats Common Tern foraging lasts longer and ends later than in freshwater habitats (Becker *et al.* 1997, Kralj *et al.* 2024). This could, in part, explain the higher degree of absence from the marine colony, especially during the afternoon.

The median number of state changes was higher for the birds nesting on freshwater colonies. Since the daily duration of the incubating state was much longer on freshwater colonies the difference in the number of changes could indicate a higher degree of interaction between the members of the same colony caused by common returns from foraging trips. Freshwater habitats are known to support larger and denser Common Tern colonies (Cramp *et al.* 1974, Neubauer 1998), which was also the case in our study, and it could lead to a higher number of state changes during interactions between birds.

Even though no evidence of Common Tern nest predation has been recorded during our observation, the prolonged absence of terns from their nests during the 2022 season on Školjić raises some concerns. Gulls are recorded to lower the amount of deep sleep Common Terns get in their colonies and pose a threat to predation which causes them to temporarily abandon their nests (Diehl *et al.* 2020). Yellow-legged Gulls *Larus michahellis* present around Školjić could have played a role in the nightly abandonment of nests there, although the 2023 season saw a much larger tendency to incubate during the night, indicating a cause which can easily shift seasonally.

Potential behaviour altering factors beyond the scope of this research

Even though our findings are in accordance with previously conducted research a broader view is needed to bring forth any conclusions on the foraging and incubation habits of Common Terns nesting in the observed colonies.

The differences in incubation behaviour between the colonies could be partly caused by the breeding and foraging experience of individuals nesting there. As illustrated by Tims *et al.* (2004) it's possible that the difference between foraging at different colonies was affected by the age of the colony and the age of birds nesting there and not entirely by the prey availability. The colony at Siromaja has been established since 2018, whereas Rakitje had a continuous Common Tern colony on the same islet since 2009. This could explain some of the differences in behaviour for newer colonies such as Siromaja, which has already proven to have shorter foraging time and higher breeding success than Rakitje (Martinović *et al.*

2023, Martinović *et al.* 2019). On the other hand, Limmer & Becker (2009) have demonstrated that more experienced breeding pairs have a higher foraging success rate, enabling them to spend more time in their colony. This could explain significant differences in the nest attendance of birds at the same colony, but no conclusions can be drawn as monitored birds were not ringed and their age was not known. Additional research should also be focused on the sex of the incubating individuals. Several sources have shown that the complex roles of parental care in seabirds are best understood when coupled with data relating to the sex of the observed birds (Bluso-Demers *et al.* 2010, Reicher & Becker 2017).

Several climate factors could have influenced the observed behaviour as well. Higher temperatures are known to prolong the incubation time of Common Terns in order to lower the risk of clutch overheating (Amat *et al.* 2017). Conversely, at temperatures of 30 to 35 °C individual terns have been noticed to leave their nests for short periods during which they would immerse their lower body in water, presumably to further help the clutch stay cool (Arnold *et al.* 2020). As the observed colonies are situated in similar climates, temperature could have had a minor impact on the incubation behaviour of terns.

Conclusion

Our results showed statistically significant differences in incubation behaviour among Common Tern colonies from different types of habitats (marine and freshwater) as well as among different colonies and years on similar habitats (different freshwater sites and different years at a marine site). When comparing the data from different habitat types, terns nesting on freshwater sites spent about 40% more time at or near their nest than their marine counterparts (Table 1, Fig. 2).

Longer periods spent incubating infer a shorter time spent on activities such as foraging. Taking into account the results presented herein as well as previous findings of terns prioritising seasonally abundant food (Erwin 1977), foraging areas with high prey density such as commercial fishponds (Becker *et al.* 1997) and shallow, flowing water (Urmy & Warren 2018) we concluded that prey availability and predictability play a major role in Common Tern behaviour during incubation. The differences in nest attendance during the incubation period could affect reproductive success, which has already been proven for the two studied freshwater colonies (Martinović *et al.* 2019).

The presented research shows only a sample of Common Tern behaviour during incubation on a small number of sites. The noted behaviours, especially the nocturnal absence on the marine colony, can only be understood by additional, more robust research. Age and sex data, as well as observations on the most common prey items on these sites, are needed in order to define any concrete cause of the observed differences.

Acknowledgments

This work was supported by the Croatian Science Foundation under the project IP-2020-02-8793. The authors of this paper would like to express their gratitude to Sanja Barišić, Tomica Rubinić and Maja Bjelić Laušić who provided help and support during the fieldwork of this study.

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SAŽETAK

Crvenokljune čigre *Sterna hirundo* su morske ptice koje se kolonijalno gnijezde na morskim i slatkovodnim staništima. U inkubaciji i podizanju mladunaca sudjeluju oba roditelja. U svrhu istraživanja dinamike ponašanja na gnijezdima crvenokljunih čigri različitih staništa prikupljene su serije fotografija načinjene fotozamkama smještenim na tri kolonije: dvije slatkovodne i jednoj morskoj. Fotografije sa sedam gnijezda sortirane su temeljem stanja "inkubira, "blizu gnijezda" i "odsutna" temeljenih na položaju ptice na gnijezdu. Izračunato je dnevno trajanje svakog stanja, trajanje stanja do promjene i ukupni broj promjena, a analiza je napravljena i za dijelove dana. Analiza je provedena u programskom jeziku R koristeći se neparametarskim statističkim testovima. Utvrđena je značajna razlika u vremenu provedenom u inkubaciji među gnijezdima istog, ali i među različitim tipovima staništa. Ptice na gnijezdima slatkovodnih kolonija značajno su više vremena provodile inkubirajući, dok su ptice na morskim kolonijama značajno više vremena bile odsutne, što se povezuje s lakše dostupnim izvorima hrane na slatkovodnim staništima. Tehnički uvjeti snimanja foto zamkama, predacija, intraspecijsko antagonističko ponašanje, iskustvo jedinki u gniježđenju i meteorološki uvjeti mogući su dodatni utjecaji na vrijeme provedeno u inkubaciji.