

**Male-built nest volume varies with colony and the timing of the breeding
season but not with the nesting-substrate quality and egg production in
whiskered terns**

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Abstract

Nest building can represent an energetically-costly activity for a variety of animal taxa. Besides, the determinants of within-species variation in the design of nests, notably with respect to natural and sexual selection, are still poorly known although the situation has been partly remedied recently. Based on an observational study, we examined the influence of nesting conditions (nesting-substrate quality, colony, laying date, and year) on the volume of male-built nests and its potential role as a post-mating sexually-selected display in the whiskered tern *Chlidonias hybrida*, a monogamous species with obligate bi-parental care breeding on unstable aquatic vegetation beds. No relationship was found between the nest volume and the nesting-substrate quality (i.e. nest stability) indicating that the density of white waterlily leaves was large enough when whiskered terns breed. In contrast, building a large nest likely constitutes a selective advantage since nests were larger in less densely populated colonies and for early breeders whatever the year. Since being influenced by nesting conditions, the volume of male-built nests was unlikely to be a sexually selected trait in whiskered terns. The reproductive effort by females (the probability of laying one, two or three eggs, and variation in mean egg volume per clutch) was indeed not correlated with the volume of male-built nests. The fitness consequences of building a large nest are yet to be studied and additional investigations are recommended to better depict the participation of males early during breeding (including notably courtship feeding) and later to chick provisioning.

Keywords

Chlidonias hybrida · Colony size · Egg number and/or size · Laying date · Nesting-substrate quality · Post-mating sexual signal

Introduction

Nest building is a critical stage in the lifetime of a variety of animal taxa. Nests can exhibit large between- and within-species variation in their design, but their causes and the relative fitness consequences are not still well determined (Hansell 2000). The primary function of a nest is to provide a secure structure for eggs during their development and nestlings during rearing (in the case of altricial species). Additional functions include environmental adjustment, crypsis against predators, and parasite control (e.g. Hansell 2000, Deeming and Mainwaring 2015). This, in turn, make it more difficult to determine the, sometimes conflicting, selective pressures responsible for variation in nest characteristics. Nest features (materials, form, structure, size, placement, and duration of nest building) have been indeed shown, mainly in birds, to be influenced by a variety of environmental (extrinsic) factors including the local availability of materials, the microclimatic conditions, the nature and/or quality of the substrate, the time of year, and the risk of nest predation (Collias and Collias 1984; Hoi et al. 1994; Persson and Öhrström 1996; Palomino et al. 1998; Deeming and Mainwaring 2015). They are also influenced by individual state variables including sex, body size, experience, and quality (Soler et al. 1998, Hansell 2000; Muth and Healy 2011).

For species nesting colonially, an increasing body of literature supports the idea that a variety of life-history (e.g. clutch size, body condition and/or size) and behavioural (e.g. aggressiveness or, conversely, tolerance toward conspecifics, vigilance) traits and their fitness consequences vary with social environment, notably with group size (i.e. a phenotypic sorting of individuals based on their competitive ability, see the review of Brown (2016) and references therein). Although a large panel of phenotypic traits tend to vary among colonies (but not necessary with colony size; Brown 2016), variation in the design of nests with colonial nesting remains a neglected issue whereas nest characteristics may substantially

affect various indicators of reproductive success (Hansell 2000; Deeming and Mainwaring 2015). More precisely, given that nest building behaviours can be energetically costly due to the numerous trips that individuals make to gather the necessary nesting materials (Collias and Collias 1984; Hansell 2000; Mainwaring and Hartley 2013) and that nesting materials can be limited, competition for nesting materials is expected to be exacerbated in large colonies (Carrascal et al. 1995). Furthermore, Moreno et al. (1995) reported that nesting-material stealing by conspecifics is particularly associated with colonial nesting. Hence, colony size may influence nest size (Carrascal et al. 1995).

Nest building has also been proposed to have a sexually-selected component (e.g. Soler et al. 1998). In birds, the energy costs during breeding are among the highest throughout their lifetime (Williams 1996), breeders may therefore trade their effort between current breeding, their own survival, and upcoming breeding events (as predicted by life-history theory: Stearns 1992; Gustafsson et al. 1994; Liker and Székely 2005). In this respect, adults able to assess the quality of their mates as future parents on the basis of sexual signals would experience a critical advantage adjusting their own reproductive effort (Burley 1986; Hoelzer 1989; Møller 1994; Soler et al. 1998). An extensive body of literature has provided evidence that, in monogamous species with obligate bi-parental care, the activity of males early during the breeding season (e.g. nest building and courtship feeding performance) may serve as a post-mating sexually-selected display allowing females to assess the quality of males (reviewed in Collias and Collias 1984; Hansell 2000; Wachtmeister 2001). For instance, Soler et al. (2001) showed that Eurasian magpie *Pica pica* females laid larger clutches when nests were experimentally enlarged to simulate increased nest-building effort by males. A number of studies, notably in passerines, support the idea that sexual selection would favour large nests (e.g. Moreno et al. 1994, Palomino et al. 1998; Soler et al. 1998).

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95 The whiskered tern *Chlidonias hybrida*, is a colonial long-lived migratory monogamous
96 bird with obligate bi-parental care that, by contrast to most terns (Collias and Collias 1984;
97 Gochfeld and Burger 1996), builds floating open-nesting platforms on aquatic vegetation beds
98 (Bakaria et al. 2002; Paillisson et al. 2006). It makes its nests particularly vulnerable to
99 environmental conditions (floods, and wave and wind actions). Notably, it may be less
100 adaptive to build a small nest in sparsely aquatic vegetated beds (e.g. Collias and Collias
101 1984). Previous works showed that, during early breeding, whiskered tern females spend the
102 major part of their time at the nesting place (Paillisson et al. 2007, Chambon et al. 2020)
103 whereas males nearly alone bring nesting-plant materials (85% in Chambon et al. (2020)).
104 Nest building *per se* is often not very sophisticated since both members of a pair loosely
105 gather plant materials to constitute a floating platform (Figure 1). The nest size rather results
106 from the accumulation of plant materials brought by whiskered tern males.

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108 The aims of this study are threefold. First, we document the extent of nest size variation
109 in the whiskered tern; this aspect of its breeding biology has been little documented to date
110 (but see Mužinić and Delić 1997; Bakaria et al. 2002, Figure 1). Second, we consider a
111 variety of environmental and social factors to explain nest size variation. The nest support
112 hypothesis posits that nesting materials are used to form a solid base for the nest, increasing
113 its stability (Collias and Collias 1984, Palomino et al. 1998). This hypothesis predicts that the
114 amount of nesting material is negatively correlated with the nesting-substrate stability. Hence,
115 we expect that nest volume is negatively correlated with the density of aquatic plant beds as
116 the theory predicts. In addition, we examine a possible laying date effect on nest volume.
117 Early breeders are expected to access to better quality nesting places (Ketterson and Nolan
118 1983); i.e. dense aquatic vegetation in the whiskered tern) and would build small nests as the

nest support hypothesis suggests. An alternative prediction would be that early breeders, also considered as high-quality individuals (Verhulst and Nissson 2008) take more time to build nests and, in turn, build larger nests (Deeming and Mainwaring 2015). Moreover, opposing forces can influence the nest size for late breeders. As the season progresses, breeders have less time to build nests (referring to the optimal breeding time hypothesis, Mainwaring and Hartley 2008), hence, we expect that late breeders build smaller nests. At the same time, late breeders may settle in less densely vegetated beds (i.e. suboptimal nesting places) and be constrained to build large nests as the nest support hypothesis predicts. We also expect that nest size varies with colony; more specifically, high competition for nesting materials is intended in large colonies and would select for, or favour, smaller nests. Third, we examine the potential benefit of nest size in terms of sexual selection. We hypothesize that, whether the nest-building activity of males provides reliable information on their participation to future parental effort that females are able to assess, females would adjust their own reproductive effort accordingly. Hence, a positive relationship would exist between nest size and egg production. To test these various hypotheses, we conducted a three-year observational study in a French breeding area supporting several whiskered tern colonies. All studied colonies were characterized regarding their size; colony, laying date and year, together with nest volume, were used as predictors of females' egg production (see also Paillisson et al. 2007).

Materials and Methods

Study site and fieldwork

The study was conducted at the Lake of Grand-Lieu, in northwestern France (47°05' N, 1°39' W), which supports one of the major breeding populations of whiskered terns in the country (900–1,460 breeding pairs over the study period, 25–39% of the national population size). Grand-Lieu is a very large (ca. 4,000 ha in summer), shallow and eutrophic natural freshwater

lake with extensive beds of floating macrophytes (around 700 ha depending on the year), including mainly white waterlily *Nymphaea alba* beds where whiskered terns settle in well-spaced colonies (see Paillisson et al. (2008) for more details). Whiskered terns build nesting platforms from macrophyte fragments, mainly waterlily leaves and stems, and sometimes from common club-rush *Scirpus lacustris* stems (depending on the proximity of colonies to this nesting-material source). The almost circular platforms are generally completed before egg-laying. However, the nest cup (when present) is built by both members of a pair when incubating eggs using soft plant materials (water chestnut *Trapa natans*, yellow-floating heart *Nymphoides peltata*, and primrose yellow *Ludwigia grandiflora*).

JMP visited all the active nests of eight colonies by boat in 2008, 2009 and 2018 only once during egg incubation to limit disturbance (see basic information on colonies in Table 1). The measurement of nest size and egg size takes less than five minutes per nest. Field observations showed that parents came back to the nest within 1–15 minutes then after. The largest external diameter of the nests was measured using a giant caliper (d , to the nearest 1 cm), and their maximum height above the water line using a bracket equipped with a spirit level (h , to the nearest 0.1 cm). Nest size was approximated using the formula of the volume of a cone: $(d/2)^2 \times \pi \times h/3$ (cm³). The dominant plants used for nest building were recorded. A small number of platforms were made mostly of club-rush (< 5% of the total number of nests once all selection criteria are applied, see below); they were discarded from the dataset because they were larger than nests composed of waterlily (data not shown) and were too few to represent a competing factor in subsequent analyses. The quality of the nesting substrate was visually estimated by determining the leaf density of white waterlily in a 1-m radius around the nests (i.e. a proxy of its biomass, see Paillisson and Marion (2006) for more

details). Two classes were defined: low (when one leaf layer covers the water surface totally or not), or high (when several floating and aerial leaf layers cover the total water surface).

Egg number and egg size are classically used to describe females' reproductive effort (Birchard and Deeming 2015; Brulez et al. 2015). As whiskered terns typically lay up to three eggs (Paillisson et al. 2007), clutches with more than three eggs were discarded ($< 1\%$ of the total) because they probably resulted from conspecific brood parasitism (Paillisson et al. 2008) and, hence, did not reliably represent the reproductive effort by the host females. Egg volume (cm^3) was calculated based on the measurement of egg length and width (using a Vernier caliper, to the nearest 0.01 mm) using the formula provided in Coulson (1963). Egg weight (measured using an electronic scale to the nearest 0.1 g) was used to estimate egg age using the linear egg density/age relationship we published elsewhere (Paillisson et al. 2007). Egg age was used to determine whether one- and two-egg clutches were complete, knowing that an interval of at least one day is necessary between the laying of successive eggs. Only clutches defined as complete with certainty were kept for subsequent analyses (see Paillisson et al. 2007). Egg age was also used to estimate the clutch initiation date (i.e. the laying date of the first egg of a clutch). We took the clutch initiation date into account in the analyses because egg number and/or size may vary as the season progresses (due to, for example, changes in food availability (Parsons 1975; Sydeman et al. 1991) or replacement clutches (Coulson and Thomas 1985; Wendeln 1997)). To do this, we converted the estimated clutch initiation dates (i.e. Julian dates) into residual laying dates (i.e. relative dates) to control between-year differences in the egg-laying period. More exactly, the estimated clutch initiation dates were expressed in pentades (5-day time intervals, beginning May 20) and converted into residual laying dates by subtracting each clutch-laying date (in pentades) from the peak laying date of all nests of each year (pentades 5, 7 and 7 in 2008, 2009 and 2018,

respectively). Finally, clutches were classified into three classes: early (pentades ranging from – 6 to – 2), peak (– 1 to 0) and late (+ 1 to + 5) clutches. The number of nests assigned to the early-laying class was too small (4% of the total number of nests finally used for analysis) to be retained for subsequent statistical analyses. Lastly, given that nesting platforms are composed of slowly decaying plant fragments, we assumed that we reasonably evaluated males' nest-building effort by keeping only nests with ≤ 10 -day old eggs (i.e. nests whose size was measured during the first half of the egg-incubation stage). An alternative approach would have been to control the effect of egg age on nest volume to consider the complete dataset for subsequent analyses, but we had no idea whether it would accurately reflect the plant breakdown rate. Overall, the dataset used for analysis included 297 nests, for 4–6 colonies per year (see details in Table 1). In addition, behavioural observations of focal nests were made in 2008 to provide an extensive overview of the activity of males before egg-laying with respect to sexual selection aspects (see Appendix 1 and the discussion section).

Statistical analyses

We used Linear Models (LMs) to investigate the effects of the aforementioned variables potentially influencing nest size in birds: time of year (peak or late laying; Mainwaring and Hartley 2008; Britt and Deeming 2011), year (Britt and Deeming 2011), nesting-substrate quality (Collias and Collias 1984), and colony (colony identity refers both to local and environmental conditions). These analyses were performed on the 297 nests. We also examined whether egg production varied according to nest volume (after controlling for the effects of the aforementioned variables on nest volume), year, colony, and laying date (i.e. a proxy of breeders' quality: Verhulst et al. 1995; Wendeln 1997; Verhulst and Nilsson 2008). For this purpose, we used multinomial models and LMs to examine the probability of laying one, two or three eggs, and variation in mean egg volume per clutch, respectively, as a

function of the candidate variables. Egg number was also considered as a candidate predictor in models investigating variation in mean egg volume per clutch. Due to small or unbalanced sample size issues, the analyses on egg production were performed on a subset of four colonies ($n = 225$ nests, see Table 1).

For all analyses, we tested all possible additive combinations of up to two candidate variables to limit the complexity of the models. Interaction effects were not tested as no biological hypothesis seemed prevalent. Models were ranked by the Akaike information criterion corrected for small sample sizes (AICc), and the models with the lowest AICc were identified as the best models when their AICc was at least two units lower than those of all other models. A multi-model inference approach was used when several models were with $\Delta\text{AICc} \leq 2$ to calculate model-averaged parameter estimates (with 95% Confidence Intervals, 95% CIs) for the variables included in the selected models. An explanatory variable was considered as significant when its parameter estimate (the slope of the relation, for a quantitative variable) or at least one of all parameter estimates (the differences in the estimated values of the response variable between a reference factor level and all the other levels, for a qualitative variable) was different from zero (when the 95% CI excluded zero). Pairwise post-hoc comparisons of the adjusted estimates of a response variable (means \pm SE, based on estimated marginal means from the models) according to the retained effects were performed using Tukey's multiple comparison tests.

All statistical analyses were performed with R 3.5.2 (R Development Core Team 2018) using the *AICcmodavg*, *car*, *emmeans*, *lme4*, *MuMIn*, *nnet*, *r2glmm* and *RVAideMemoire* libraries. The significance level was fixed at $\alpha = 0.05$.

Results

Estimated nest volumes ranged from 477 to 8,701 cm³, with a mean value of $2,618 \pm 63$ SE cm³. The first-ranked model explaining variation in nest volume was better supported than the other models (Table 2); it included laying date and colony ($R^2 = 0.19$). Nest volume was on average smaller for late clutches than for peak clutches ($2,013 \pm 148.2$ and $2,853 \pm 94.7$ cm³, respectively; Figure 2a). Nest volume was particularly low in large colonies ($1,739 \pm 218$ and $1,820 \pm 153$ cm³ in colonies VII and V (see Table 1), respectively), it was twice as high in colony IV ($3,673 \pm 165$ cm³, a less densely populated colony), and intermediate in all the other colonies (Figure 2b).

One-egg clutches were much less represented (18%) than two- (39%) and three-egg clutches (43%) across the complete dataset ($n = 297$ nests). Proportions were very similar in the subset of four colonies (colonies I, IV, V and VI) used to examine the drivers of egg production (19, 38 and 43%, respectively). Nest volume was the only variable included in the best model explaining the propensity for whiskered tern females to lay one, two or three eggs (Table 3). However, the estimated equal probabilities for all egg numbers we found whatever the nest volume (post-hoc comparisons) revealed that nest volume did not exert an influence on egg number. Four models best explained mean egg volume per clutch (Table 3); nevertheless, colony was the only significant variable ($R^2 = 0.07$; 95% CIs of its estimates using colony I as the reference level: 0.51 to 1.53 for colony IV, -0.06 to 1.08 for colony V, and 0.24 to 1.24 for colony VI; Figure 3). Egg volume was the lowest in colony I (mean \pm SE = 14.39 ± 0.20 cm³), the highest in colonies VI and IV (15.20 ± 0.11 and 15.39 ± 0.16 cm³, respectively), and intermediate in colony V (14.93 ± 0.13 cm³) without any relationship to colony size (Table 1).

Discussion

Nesting platforms exhibited large variation in size between whiskered tern breeding pairs. This was attributed to laying date and colony but not to the nesting-substrate quality. Therefore, nest volume is not very likely to be sexually selected in whiskered terns since partly depending on nest site conditions. Moreover, no relationship was shown between nest volume and females' egg production.

Contrary to our expectations, nest volume was not correlated to the leaf density of white waterlily as the nest support hypothesis posits. However, whiskered terns are known to be sensitive to nesting-substrate quality (Paillisson et al. 2006, see a similar conclusion in Van der Winden et al. (2004) in black terns *Chidonias niger*). More exactly, birds settle every year when a minimum waterlily biomass is reached (Paillisson et al. 2006). Therefore, we conclude that nesting-substrate quality was surely high enough when most whiskered terns settled over the present study period. Moreover, large nests take time and energy to build (Soler et al. 1998; Hansell 2000; Mainwaring and Hartley 2013). This is a critical issue notably for migrant species because of the optimal breeding time constraint (Mainwaring and Hartley 2008). Our results are consistent with this hypothesis since we showed that late breeders built smaller nests. An alternative explanation would be that poorer-quality birds breed later in the season and therefore build small nests. In all cases, the prediction that late breeders would build large nests because they access to poor-quality plant beds (i.e. suboptimal nesting places) is refuted. Besides, it is generally admitted that early breeders are high-quality parents (Verhulst and Nisson 2008); they are thought to access to better quality nesting places and to initiate nest building well before egg-laying. Thus, they may have a long nest building period, and, in turn, build larger nests (see Mainwaring and Hartley (2008), and Smith et al. (2013) in passerines). Large nests may constitute a selective advantage for

whiskered terns because they are better anchored to floating plants. As a result, they are more stable and may better survive wind and wave action and water level fluctuations. Future investigations would be required to explore this issue.

Nest volume also varied between whiskered tern colonies: small nests were noted in colonies with high challenging social conditions (i.e. a high number of breeders or a high density of nests depending on the year), and occurred in less densely populated colonies. These results support the idea that whiskered terns in densely populated colonies (being however moderate compared to elsewhere; Minias et al. 2014; Chambon et al. 2020) face increased competition for the nest material available. Another explanation could be that colonies with smaller nests were suboptimal sites (e.g. more exposed to the wind and the waves), or colonies supporting poor-quality parents. In addition, nest predation pressure that is known to favour small nests (Mainwaring et al. 2015 and references therein) is low in our study site. Magpies *Pica pica* and black kites *Milvus migrans* are occasionally observed and when an individual is detected close to a colony whiskered terns alarm and massively attack it.

To function as a sexually selected male trait, nest may primarily reflect significant participation of males to build it. Time-activity budgets showed that whiskered tern males indeed made practically alone all trips to gather nesting materials (97% of the total number of nesting-material deliveries, Appendix A1). Time-activity budgets also revealed that males can highly provision their mate before egg-laying. The functions of courtship feeding have long been debated in the past, and several hypotheses have been supported by empirical data including the post-mating sexual signal hypothesis (Wachtmeister 2001, and notably Nisbet (1973) and Wiggins and Morris (1986) in common terns *Sterna hirundo*). Hence, two displays

(nesting-material delivery and courtship feeding) would potentially act simultaneously as sexual signals in whiskered terns (see also Yoon et al. (2015) in oriental storks *Ciconia boyciana*). We found that males exhibiting the most intensive courtship feeding brought nesting material at a low rate (no negative relationship was however observed, Figure A1). Therefore, the information gathered by a female from the activity of its mate during early breeding is highly complex. What is more, males' effort may vary in the course of the nest-building period, so that the 3-day period during which their activities were recorded may not have coincided with the period of maximum energy requirements of females for all studied breeding pairs (peak energy requirements occurring, for instance, only 1–2 days before laying in common terns; Moore et al. 2000). Additional investigations are needed to clarify the relationship between nesting-material and food supply throughout the whole pre-laying period and to provide a better understanding of the functions of courtship feeding in whiskered terns.

Besides, it is also admitted that in order to be a reliable post-mating sexual signal, a parent's display has to convey its ability to provide parental care to its partner; the partner, in turn, adjusts its reproductive effort accordingly to acquire direct fitness benefits. This means that data on chick provisioning by males are needed to examine whether males that invest more in nest building (i.e. build a large nest) also invest more in chick provisioning or not. Unfortunately, we do not possess such data. This requires trapping, banding and sexing adults because it is frequently impossible to differentiate sexes when chicks require intense provisioning (see for instance Ledwoń and Neubauer 2017). Additional investigations are needed to examine whether the activities of males before egg-laying well inform on their future investment in chick provisioning.

342 Lastly, we found no evidence for a link between nest volume and egg number and size.
343 More broadly, variation in females' egg production (egg number and size) was poorly
344 correlated to the candidate predictors considered. At most, egg volume was colony-dependent,
345 without any straightforward explanation; no apparent relationship indeed occurred with the
346 number and density of active nests. Other factors, notably the own phenotypic quality of
347 females, have been suggested to explain differences in females' reproductive effort (Coulson
348 and Porter 1985; Slagsvold and Lifjeld 1990; Hipfner et al. 1999). Unfortunately, such data
349 are not available in the present study.

351 In conclusion, our findings contribute to the knowledge of the drivers of within-species
352 variation in nest size in birds. Nest building behaviours by whiskered tern males were mainly
353 influenced by nest site conditions (colony and laying date, this latter variable could indicate
354 changes in nesting conditions as the season progresses). Since whiskered terns build large
355 nests when nesting conditions are suitable (early in the season and in less densely populated
356 colonies), they likely take advantage of this increased costly activity later in the season.
357 Hence, the next step would be to assess the relative fitness consequences of nest size. In
358 addition, nest building is unlikely a sexual signal in whiskered terns. By contrast, courtship
359 feeding may be an important cue for females before egg-laying; future investigations are
360 needed to explore this issue, and, in turn, to contribute to a better understanding of the
361 breeding ecology of this monogamous bird.

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Conflict of interest

None declared.

Author contributions

Jean-Marc Paillisson: conceptualization (lead), methodology (lead), project administration (lead), writing-original draft (equal). Remi Chambon: data analysis (lead), writing-original draft (equal).

Data Accessibility statement

Data supporting the results (nest volume, egg production and potential predictors) are supplied as supplementary materials at the Dryad repository (the link will be provided upon acceptance).

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535 **Tables**

	Colony size (nests)			Nest density (nests.ha ⁻¹)			Number of nests to study nest volume and egg production										
Colony	Year			Year			Year			Waterlily leaf density		Laying date		Egg number			Total
	2008	2009	2018	2008	2009	2018	2008	2009	2018	Low	High	Peak	Late	1	2	3	
I	57	20	19	7.7	10.9	10.7	13	–	13	18	8	7	19	6	13	7	26
II	–	–	18	–	–	61.7	–	–	12	12	0	12	0	2	4	6	12
III	12	12	–	11.5	33.7	–	6	–	–	0	6	6	0	1	4	1	6
IV	22	38	43	8.4	7.3	2.7	12	15	16	22	21	6	37	11	15	17	43
V	–	91	–	-	9.4	–	–	61	–	54	7	60	1	11	24	26	61
VI	84	61	88	26.8	6.9	17.6	19	37	39	42	53	78	17	15	33	47	95
VII	61	23	–	96.2	13.3	–	14	11	–	25	0	25	0	3	10	12	25
VIII	18	46	–	6.9	9.4	–	7	22	–	17	12	14	15	5	12	12	29
Total	178	291	168	–	–	–	71	146	80	190	107	208	89	54	115	128	297

536

537 **Table 1** Basic description of the colonies over the study (colony size and nest density) and summary of the number of nests ($n = 297$) among the

538 levels of factors used for exploring variation in nest volume and egg production (only colonies I, IV, V, and VI for this latter case; $n = 225$).

539 Colonies (I, II, III, IV, V, VI, VII, VIII) represent well-delimited areas where whiskered terns settle sometimes for several years, otherwise a dash is used. Year:
 540 2008, 2009 and 2018. Waterlily-leaf density: low or high. Laying date: residual clutch initiation date classified as peak or late laying (too few data for the early
 541 laying class). Egg number: one, two, or three eggs.

542 **Table 2** Models tested to explain the nest volume of whiskered terns.

Explanatory variable	AICc	Δ AICc	ω AICc
Laying date + Colony	4956.10	0.00	0.91
Year + Colony	4960.86	4.76	0.08
Year + Waterlily density	4965.43	9.32	0.01
Colony + Waterlily density	4970.63	14.52	0.00
Colony	4976.82	20.71	0.00
Waterlily density	4984.58	28.48	0.00
Laying date + Waterlily density	4985.40	29.29	0.00
Year	4989.01	32.91	0.00
Laying date + Year	4990.63	34.52	0.00
Laying date	5003.87	47.77	00.0

543 Laying date: residual clutch initiation date classified as peak
544 or late laying (too few data for the early laying class). Year:
545 2008, 2009 and 2018. Colony: I, II, III, IV, V, VI, VII, VIII.
546 Waterlily-leaf density: low or high. Δ AICc (the difference in
547 AICc units between the first-ranked model and a given
548 model); ω AICc, Akaike weight.

549

Table 3 Models tested to explain the egg production (egg number and size) of whiskered tern females.

Response variable	Explanatory variable	AICc	Δ AICc	ω AICc
Egg number	Nest volume	472.19	0.00	0.78
	Laying date + Nest volume	476.06	3.87	0.11
	Year + Nest volume	478.48	6.30	0.03
	Laying date	478.91	6.73	0.03
	Colony + Nest volume	479.04	6.85	0.03
	Year	480.99	8.81	0.01
	Colony	481.91	9.73	0.01
	Year + Laying date	484.22	12.04	0.00
	Colony + Laying date	485.45	13.26	0.00
	Year + Colony	487.67	15.48	0.00
Egg volume	Colony + Laying date	659.40	0.00	0.33
	Colony	659.62	0.21	0.30
	Colony + Nest volume	660.67	1.26	0.18
	Colony + Year	661.24	1.84	0.13
	Egg number + Colony	662.91	3.50	0.06
	Year	671.20	11.79	0.00
	Laying date	671.42	12.02	0.00
	Nest volume	671.44	12.03	0.00
	Nest volume + Laying date	672.51	13.10	0.00
	Year+ Nest volume	672.69	13.29	0.00
	Egg number	672.89	13.48	0.00
	Year + Laying date	673.00	13.60	0.00
	Egg number + Year	673.81	14.41	0.00
	Egg number + Laying date	674.07	14.66	0.00
	Egg number + Nest volume	674.36	14.95	0.00

Nest volume was controlled for the effects of laying date and colony (see the text for more details). Laying date: residual clutch initiation date classified as peak or late laying (too few data for the early laying class). Year: 2008, 2009 and 2018. Colony: I, IV, V and VI (see the text and also Table 1). Δ AICc (the difference in AICc units between the first-ranked model and a given model); ω AICc, Akaike weight. Multinomial and linear models were used to explain variation in egg number and mean egg volume per clutch, respectively.

Figure Legends

Figure 1. A whiskered tern pair on a dense white waterlily bed (a), and a variety of nests (b, c).

Figure 2. Nest volume (mean \pm SE, in cm³) according to: (a) laying date (after controlling for the colony effect), and (b) colony (after controlling for the laying-date effect). Different letters above bars indicate significant post-hoc differences between factor levels for laying date and colony. See sample sizes in Table 1.

Figure 3. Model-averaged parameter estimates (with 95% Confidence Intervals) for variables explaining the mean egg volume per clutch (model selection with $\Delta AICc < 2$). Laying date: peak or late classes. Year: 2008, 2009 and 2018. Colony: I, IV, V and VI (see also Table 1). Parameter estimates are provided for each factor level (the difference in estimated values to a reference level, i.e. colony I, 2008, and late clutches for colony, year, and laying date, respectively). The estimate for nest volume is the slope of the linear regression. A variable was considered as significant when the 95% CI of its parameter estimate (or at least one of all parameter estimates for a qualitative variable) excluded zero (the dashed line).