

Opposing selective pressures may act on the colony size in a waterbird species

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Received: 8 November 2014 / Accepted: 31 December 2014 / Published online: 8 January 2015
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Abstract In theory, larger colony size should be favoured by lower per-capita predation rates, whereas smaller colony size should be favoured by reduced parasitism, social stress and competition for food. We conducted an experimental cross-fostering of young between colonies of different size to test whether differences in fitness had an environmental or genetic basis. We induced formation of one large (ca. 100 breeding pairs) and three small (30–40 pairs) Common Tern *Sterna hirundo* colonies by providing different size patches of nesting area (floating rafts). The larger colony had about 30 % higher reproductive success than the smaller colonies. However, offspring raised in the large colony were in poorer condition, which was indicated by the higher heterophil/lymphocyte ratios, lower hemoglobin concentrations in blood and slower growth rates, suggesting higher parasite loads or higher levels of social stress. By performing a cross-fostering experiment we confirmed that differences in chick condition were not inherited, but could be directly attributed to different rearing conditions experienced in the colonies of varying size. These results suggest that colony size in the Common Tern may be regulated by the opposing selective pressures (predation vs. parasitism/social stress).

Keywords Coloniality · Common Tern · Cross-fostering · Haematology · Natural selection · *Sterna hirundo*

Introduction

Coloniality is defined as breeding by a number of individuals among densely distributed territories which contain no other resource than nest sites (Perrins and Birkhead 1983). This social system occurs in different groups of vertebrates including fish, reptiles, and

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mammals, but it is most widespread in birds, as approximately 13 % of all avian species are classified as colonial breeders (Lack 1968). Avian coloniality is considered a labile form of social behaviour that has evolved independently many times from the ancestral state of solitary breeding (Rolland et al. 1998). Many studies have identified fitness benefits of reproducing in aggregations (Siegel-Causey and Kharitonov 1990), mainly reduced per-capita predation rates, as well as costs such as increased stress and competition for food. However, individuals could self-sort into colonies of different size based on their own genetic quality (poorer quality individuals may go to smaller colonies). Few studies have conducted cross-fostering experiments to test whether the differences observed between colonies of different size are due to these genetic effects or the environmental effects of colony size per se.

Theory predicts that some of the fitness benefits associated with breeding in aggregations should increase along with increasing size of breeding group, especially when reproduction is synchronized due to social stimulation (Darling 1938; Coulson 2011). One of the most commonly postulated benefits of colonial nesting is reduction in predatory pressure (e.g. Krebs and Davies 1993), which may operate by different mechanisms, such as a dilution effect (Murphy and Schauer 1996), group vigilance (Roberts 1996) or communal defence (Götmark and Andersson 1984). The dilution effect assumes that the individual probability of being attacked by a predator decreases in larger aggregations. Similarly, the costs of vigilance are likely to be lower in larger colonies, as per capita rate of scanning for predators decreases proportionally to group size. Lastly, the capacity of mobbing and deterring predators should also increase in larger colonies where more individuals can engage in active defensive behaviours, although these patterns may not be straightforward in mixed colonies of mobbing and non-mobbing species. However, taking all these into account, large colonies are likely to provide better safety from predation in comparison to smaller nesting aggregations, which has been supported by empirical evidence in birds (Raveling 1989; Wiklund and Andersson 1994). There is also experimental evidence from other taxa, such as fish, that nesting in aggregations reduces the costs of anti-predator efforts, thus providing further support for anti-predatory functions of animal colonies (Schädelin et al. 2012).

Colony size may change substantially between years and large colonies usually develop gradually over time from smaller nesting aggregations. However, the size of colonies can be limited by availability of suitable nesting habitat (Kaiser and Forbes 1992), as well as by several non-exclusive selective forces. Firstly, avian colonies are often surrounded by zones of lower food abundance which develop over the course of the breeding season as a consequence of foraging by birds from the colony (Ashmole 1963; Birt et al. 1987). These negative effects of competition for food resources have been demonstrated to be density-dependent and to constrain colony size in several seabirds (Forero et al. 2002; Votier et al. 2007; Davies et al. 2013). Similarly, deleterious effects of parasitism were suggested to be significantly elevated in large colonies, as the degree of parasite load and transmission rates are likely to increase proportionally to the density and abundance of hosts (Brown and Brown 1996; Brown et al. 2001). Finally, the physical condition of chicks raised in large and dense breeding aggregations may be negatively affected by increased social stress [e.g. in the Magellanic Penguin *Spheniscus magellanicus* (Tella et al. 2001)].

Taking all this into account, we might expect that, under given environmental and ecological conditions, an optimal colony size should exist in each species, as a result of opposing selective pressures such as predation, parasitism or food availability. The aim of this study was to investigate how different selective forces act on colony size in the Common Tern *Sterna hirundo*, a ground-nesting colonial waterbird. For this purpose we

induced formation of breeding colonies that varied markedly in size by providing different size patches of attractive nesting area (floating rafts) at a site with limited availability of natural nesting habitat. By inducing establishment of all the colonies at the same site we could control for differences in environmental conditions that could affect breeding performance of birds, an assumption that is difficult to satisfy when comparing colonies from different locations (Ambrosini et al. 2002; Olea 2009). Usually, breeding aggregations of colonial birds are spread over large distances, and thus are often subjected to varying environmental and ecological pressures, which act simultaneously on reproducing birds and are difficult to disentangle in comparative analyses. Using a novel approach of inducing colonies formation under standardized environmental and ecological conditions, we could expect that any potential variation in breeding parameters or chick condition among the colonies should be directly related to their size, not to location-specific variation in factors such as predation or local food availability (all the colonies used the same foraging grounds). We predicted that under such conditions, large colony size was likely to promote better brood survival by providing reduced predation risk, although these benefits might be accrued at the expense of poorer chick condition (from increased parasitism or social stress). To test the latter prediction, we evaluated growth rates of chicks, as well as their physiological condition expressed with blood hemoglobin concentrations and heterophil/lymphocyte (H/L) ratios, which are considered reliable indicators of physiological stress in birds (Davis et al. 2008). In order to confirm whether any potential differences in offspring condition were not genetic, but could be directly attributed to different rearing conditions experienced in the colonies of varying size, a cross-fostering experiment was also conducted. So far, only few studies cross-fostered nestlings between colonies of different size, suggesting a heritable basis for choice of group size (Brown and Brown 2000; Møller 2002; Roche et al. 2011; but see Danchin et al. 2014). We are not aware of any cross-fostering experiments investigating the effects of colony size on physiological condition and stress in birds.

Methods

Study site

The study was conducted in 2012–2013 at the Jeziorsko reservoir (51°40'N, 18°40'E) in central Poland. Although Common Terns used to nest at the reservoir in the mid-1990s, the colony soon disappeared following the loss of nesting habitat due to the rapid development of riparian willow woodland. Consequently, at the time of this study no Common Terns were naturally nesting at the reservoir or in its immediate vicinity. For the purpose of the study, in 2011 we installed four artificial nesting rafts for Common Terns at the reservoir. In order to induce formation of colonies of different size we constructed one large nesting raft (ca. 40 m²) and three small rafts (ca. 10 m² each). All rafts were square-shaped and enclosed with a 15 cm high fence, so that the chicks could not leave the platforms until fledging. Mesh size of 0.3 mm was chosen to maximize chick safety by excluding any possibility of entanglement. The raft surface was covered with sand and gravel to an average depth of 2 cm. No vegetation was planted on the rafts nor was any other cover provided, so all chicks were equally vulnerable to predation. The rafts were anchored within the Jeziorsko nature reserve, in an area where human disturbance was negligible. All the rafts were placed in a similar distance from the shore of the reservoir (ca. 1 km) and to inundated willow shrubs (ca. 50 m), so they were equally accessible to different types of

predators. The placement of the rafts was also chosen so as to maximize the distances between them. The distance between any two neighbouring rafts was >130 m, and the distance between the two most distant rafts was ca. 0.5 km. As a result, each colony functioned as a fully independent unit in terms of antipredatory defence, which was supported by the following observations: (1) communal vigilance of birds from different colonies was largely precluded, as nesting rafts were visually isolated with patches of willow shrubs; (2) individuals were not observed to interrupt their breeding activities in response to the alarming calls and antipredatory behaviours of conspecifics from neighbouring colonies; (3) individuals from neighbouring colonies were not observed cooperating in the communal defence against predators; (4) the presence of researchers at one nesting raft did not affect behaviour of birds nesting on other rafts. We did not make replicates of the large nesting raft to limit availability of nesting area, so that individuals could not spread themselves over all the rafts and form low density colonies. As such, there would not be sufficient differences in the size of the colonies to test the colony size hypotheses that we put forward. The applied experimental design (1 large raft, 3 small rafts) allowed us to obtain similarly high nesting densities in all established colonies (2012: 2.4 nests/m² on the large nesting raft vs. 2.5–2.9 nests/m² on the small nesting rafts; 2013: 2.7 nests/m² on the large nesting raft vs. 2.5–3.0 nests/m² on the small nesting rafts; all measured at the height of the breeding season in the second half of June).

Field procedures

Although all the rafts were immediately colonised in 2011 (ca. 120 tern pairs altogether), research disturbance was limited that year so as to maximize probability that permanent colonies would establish. In 2012, a population-wide study was conducted to evaluate reproductive output and different components of chick condition in the colonies established on the large and small rafts. The colonies were visited at 5-day intervals starting from 1 May, when the first adult Common Terns started to settle on the rafts. During each visit, all new clutches were recorded and all eggs were individually marked. The length (L) and breadth (B) of each egg was measured with callipers to the nearest 0.1 mm and these measurements were used to calculate egg volume according to the formula of Coulson (1963): $V = 4.866 \times 10^{-4} \times L \times B^2$. The clutches were monitored until hatching and all egg losses were recorded. All living chicks were ringed during the first visit after hatching. During the main hatching period the colonies were visited more frequently (each 2–3 days) to appropriately assign hatchlings to their natal nests. Chicks have low mobility during the first few days post-hatching, so we could identify natal nests without application of special nest enclosures. We chose wing length to characterize growth of chicks (following LeCroy and Colins 1972; Ricklefs and White 1981). During each visit wing lengths of all living chicks were measured with a wing ruler (± 1 mm). Sixteen chicks (6.3 %, $N = 253$) were ringed and measured immediately after hatching. Measurements of these chicks were used to calculate the wing length growth curve, and determine a general equation [wing length = $191.06/(1 + 11.43 \times \exp(-0.18 \times \text{age}))$]; $R^2 = 0.99$] used to estimate age at ringing and hatching dates of all other chicks. During each visit all dead chicks were recorded and assigned to their natal nests if not ringed. Since nesting rafts were fenced and all living nestlings could be recaptured during each visit until the moment of their fledging, we could construct chick survival curves for the colonies of different size. Fledging success was measured as the number of chicks that reached 20 days of age (Becker and Wink 2003) and left the rafts.

Brood growth rates

To compare brood growth rates between large and small colonies, we fitted logistic curves of the form $y = A/[1 + B \times \exp(-KT)]$ to the collected measurements of chick wing length, where y is the body measurement at age T , A is an asymptotic value, B is a constant of integration, and K is the growth rate constant (Richner 1989). We could not fit the curves separately for each chick, as the number of individual measurements was often too low to obtain reliable estimates of curve parameters. For this reason, we decided to fit separate growth curves to data obtained from all chicks from each brood altogether. This approach allowed us to include measurements from chicks that did not survive until fledging. Such methodology was necessary to avoid over-estimating mean growth rates in broods where at least one of nestlings grew slowly and died because of starvation at the early stages of development. The growth curves were fitted only for broods in which no less than five individual measurements were obtained and at least one chick was measured after the age of 20 days, when morphological parameters of Common Tern chicks start to reach asymptotic values (LeCroy and Colins 1972). These conditions were fulfilled for 99 broods, out of which 46 were located in the small colonies and 53 in the large colony. We used parameter K from the fitted curves as an indicator of average chick growth rate for each brood (hereafter brood growth rates).

Hemoglobin concentrations

To assess the effect of colony size on physiological condition of tern chicks, we measured blood hemoglobin concentration, which is considered a robust indicator of physiological health and quality in birds (Bañbura et al. 2007; Pryke and Griffith 2010; Minias et al. 2014). We collected approximately 5 μ l of blood from the ulnar vein of each bird. The concentration of hemoglobin was determined using a portable HemoCue Hb 201 + photometer (HemoCue Hb, Ängelholm, Sweden). Not all broods were sampled to reduce researcher disturbance and avoid chick losses. Broods for the haematological analyses (both hemoglobin concentrations and H/L ratios) were chosen at hatching. Prior to each visit we randomly selected equal numbers of broods from each colony type, however, relatively high (and unpredictable) mortality of chicks immediately after hatching resulted in slightly different final sample sizes from the large and small colonies. In total, hemoglobin concentrations were determined for 145 chicks from 65 broods (32 broods with 72 chicks from the large colony and 33 broods with 73 chicks from the small colonies). Since hemoglobin concentration is known to change substantially along the pre-fledging period of development in birds (Eklom and Lill 2006) we conducted all measurements of chicks between 2 and 8 days of age in order to reduce age-related variation.

Heterophil/lymphocyte ratios

To measure physiological stress of chicks from the colonies of different size, we performed leukocyte counts and calculated H/L ratios for a randomly chosen subsample of chicks (70 chicks per colony size, 88 broods altogether). It has been demonstrated that the relative number of heterophils (innate immune system) in the peripheral blood increases, while the number of lymphocytes (acquired immune system) decreases (Gross and Siegel 1983) in response to different external stressors. Therefore, H/L ratio is known to increase in response to parasite load, infectious diseases, starvation or physiological disturbance (Gross and Siegel 1983), and it was suggested to be a more reliable stress indicator in birds

than individual cell numbers or corticosterone level (Maxwell 1993). High validity of H/L ratio as a proxy of physiological stress in vertebrates has been recently confirmed with a comparative analysis (Davis et al. 2008).

For the purpose of analysis, we made a blood smear slide from selected chicks between 2 and 8 days of age. Blood smears were stained using the May–Grünwald–Giemsa method and scanned at 1000× magnification under a light microscope. A sample of 100 leukocytes from each blood smear was classified into five categories (heterophils, lymphocytes, eosinophils, basophils, and monocytes), counted, and used to calculate H/L ratios.

Cross-fostering experiment

The experiment was carried out in 2013 using 20 randomly selected pairs of clutches to be exchanged between the rafts of different size. Each swapped nest was paired with another according to clutch size (only two- and three-egg clutches included) and laying date (within 2 days). Forty clutches were also selected as controls (20 clutches per each raft size), which were handled to account for potential effects of disturbance and replaced in the nest of origin. We could not exchange control clutches within the colonies, as there were not sufficient clutches in the small colonies to match by clutch size and laying date. After controlling for the random effect of nest identity ($F_{77,156} = 3.41$, $P < 0.001$), we found no difference in the mean egg size between experimental groups ($F_{1,156} = 0.10$, $P = 0.75$). Due to high losses of clutches during incubation, only 56 clutches successfully hatched out of 80 clutches selected for the experiment (24 foster and 32 control clutches). Brood growth rates of wing length could be calculated for 20 foster and 26 control broods.

Statistical analyses

Since the size of all three small colonies was similar (see Results for details) and there were no differences in basic breeding parameters between small rafts (Kruskal–Wallis test, laying dates: $H_{2,104} = 1.89$, $P = 0.39$; clutch size: $H_{2,104} = 1.92$, $P = 0.39$; mean egg size: $H_{2,104} = 0.07$, $P = 0.97$; reproductive success: $H_{2,104} = 2.22$, $P = 0.33$), we analysed all data gathered from the small colonies jointly.

Due to non-normal distributions and different variances, differences in laying dates between the large and the small colonies were assessed with Mann–Whitney U test ($M-W$). Laying dates from each colony were divided in quartiles; values below the lower quartile (hereafter early breeders) were used to assess the timing of breeding initiation, while laying dates above the upper quartile (hereafter late breeders) indicated length of nesting activity (e.g. Laurenço et al. 2011). Between-colony differences in the variances of laying dates were assessed with Levene's test.

Differences in clutch size between the colonies of different sizes were analysed with generalized linear model (GLM) with binomial distribution and logit link, since only full clutches of two and three eggs were included in the analysis ($N = 157$). All clutches consisting of one egg ($N = 34$) were abandoned during or immediately after laying and, thus, were considered incomplete, while four-egg clutches ($N = 6$) were considered likely to contain parasitic eggs. Laying date was included as a covariate in this model. Egg size ($N = 423$) was analysed with general linear mixed-model (GLMM) with laying date entered as a covariate, clutch size and colony size entered as fixed factors, and nest identity entered as a random factor to avoid pseudoreplication (Hurlbert 1984). GLMMs with nest identity included as a random factor were also used to analyse chick hemoglobin

concentrations and H/L ratios, while general linear model (LM) was used to analyse brood growth rate. For all these models hatching date was entered as a covariate, while brood size and colony size were entered as fixed factors. Hemoglobin concentration was log-transformed to improve normality prior to the analysis. The results of the cross-fostering experiment were also analysed with GLMMs (haemoglobin concentration, H/L ratio) and LM (brood growth rate), with the size of the colonies where eggs were laid and where chicks were raised included as fixed factors. The effects of hatching date and chicks age were entered as covariates where necessary. Cox–Mantel test was used to compare chick survival curves between the colonies of different size. The results of the full models with no interaction terms are reported in all the cases and all values are presented as mean \pm SE. The character and strength of significant linear relationships was assessed with β coefficients. GLMMs were analysed with JMP Pro 10 (SAS Institute Inc., Cary, NC, USA) and all other statistical analyses were done with STATISTICA 10.0 (Statsoft, Tulsa, OK, USA).

Results

Colony size

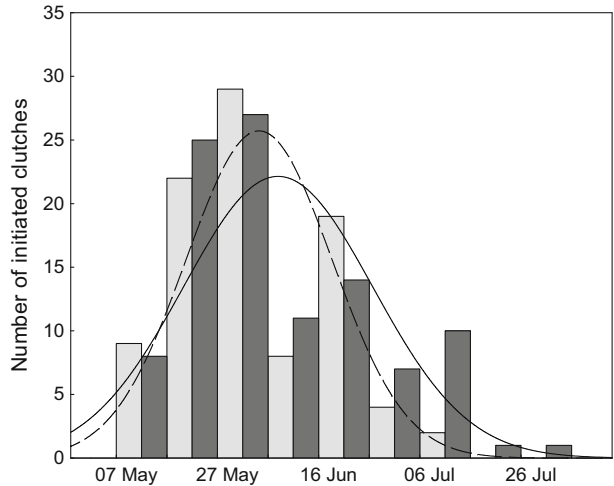
In 2012, throughout the entire breeding period we recorded 93 initiated Common Tern clutches on the large nesting raft (hereafter the large colony). Sizes of the colonies on the small rafts (hereafter the small colonies) were about 60–70 % smaller (30, 33, and 39 clutches laid per raft). In 2013, we recorded 107 initiated Common Tern clutches on the large nesting raft and the sizes of the colonies on the small rafts were, similarly to 2012, about 70 % smaller (28, 33, and 36 clutches laid per raft).

Laying dates, clutch size and egg size

In 2012, variance of laying dates was significantly higher in the small colonies when compared with the large colony ($S^2 = 351.14$ vs. $S^2 = 208.13$; Levene's: $F_{1,195} = 9.66$, $P = 0.002$), which indicated that clutches in small colonies were less synchronized in time. There were no differences in the time at which early breeders initiated laying in the colonies of different sizes (M–W: $U = 258$, $P = 0.42$; Fig. 1), and all colonies were initiated on 7 May. One quarter of all clutches were laid by 15 May in the large colony and by 16 May in the small colonies. In contrast, we found that laying period was significantly prolonged in the small colonies (M–W: $U = 113$, $P < 0.001$). In the large colony, the last clutch was laid on 03 July, whereas in small colonies laying lasted until 22 July.

We found that both clutch size and egg volume decreased with laying date (clutch size: $W = 22.89$, $N = 157$, $P < 0.001$, $\beta = -0.06 \pm 0.01$; egg volume: $F_{1,265} = 4.12$, $P = 0.044$, $\beta = -0.013 \pm 0.007$). After accounting for within-seasonal variation, we found no differences in clutch size between the colonies of different sizes (2.76 ± 0.05 eggs/nest in large colony vs. 2.66 ± 0.05 eggs/nest in small colonies; $W = 0.40$, $N = 157$, $P = 0.53$). Similarly, controlling for the effects of laying date and clutch size, we found no significant differences in the mean egg volume between the large and the small colonies (18.40 ± 0.16 cm³ in large colony vs. 18.65 ± 0.15 cm³ in small colonies; $F_{1,265} = 1.51$, $P = 0.22$).

Fig. 1 Laying dates of Common Terns nesting in the large (*light grey columns*) and in the small colonies (*dark grey columns*) in 2012. *Dashed and solid curves* indicate fitted normal distributions for the large and small colonies, respectively



Growth rates and physiological condition

Brood growth rate of wing length was negatively affected by brood size ($F_{1,94} = 10.37$, $P = 0.002$, $\beta = -0.010 \pm 0.003$), while the effect of hatching date was non-significant ($F_{1,94} = 1.10$, $P = 0.30$). After accounting for these effects, we found that chicks raised in the small colonies grew faster in comparison to chicks from the large colony ($K_{\text{small}} = 0.196 \pm 0.003$ vs. $K_{\text{large}} = 0.179 \pm 0.003$; $F_{1,94} = 15.24$, $P < 0.001$).

Hemoglobin concentrations of chicks declined over the course of the breeding season ($F_{1,78} = 4.40$, $P = 0.040$, $\beta = -0.0022 \pm 0.0010$) and were positively related with brood size (75.23 ± 0.03 vs. 81.06 ± 0.02 g/l for two- and three-chick broods; $F_{1,78} = 5.60$, $P = 0.021$, $\beta = 0.037 \pm 0.015$). After accounting for these effects, we found that offspring raised in the small colonies had higher hemoglobin concentrations in comparison to offspring

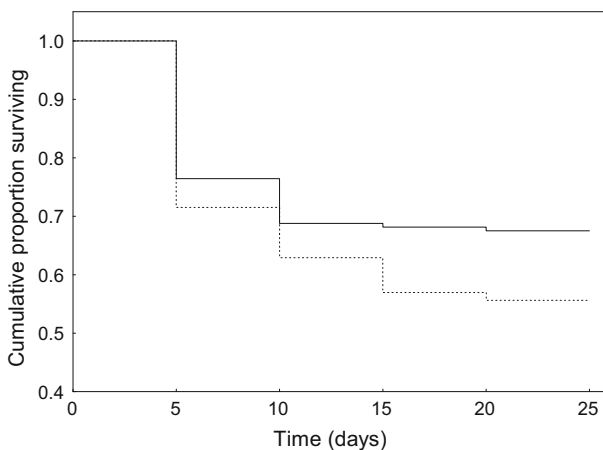


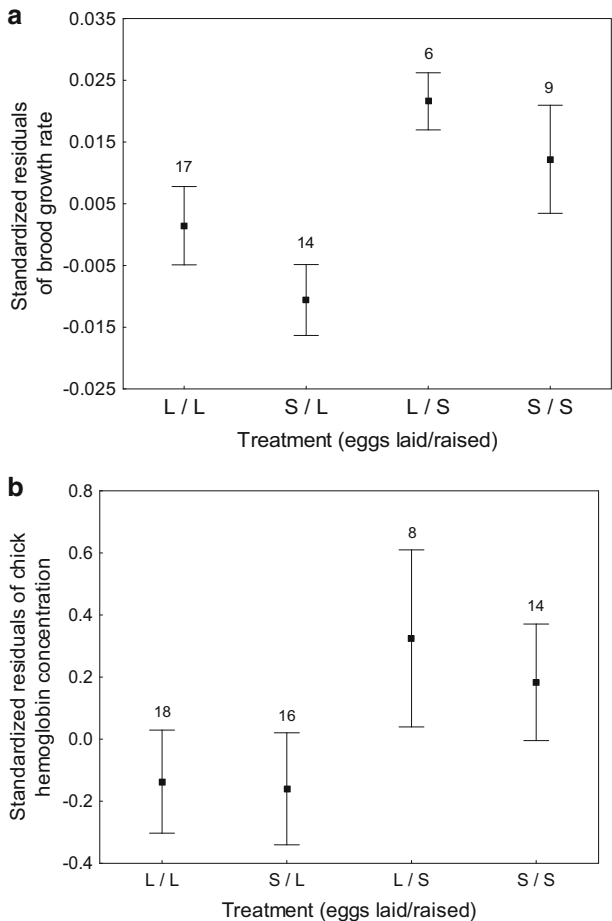
Fig. 2 Survival curves for Common Tern chicks hatched in the large (*solid line*) and small (*dotted line*) colonies in 2012

raised in the large colony ($Hb_{small} = 80.44 \pm 0.02$ vs. $Hb_{large} = 75.82 \pm 0.02$ g/l; $F_{1,78} = 4.07$, $P = 0.048$). Significantly lower average H/L ratio was found in chicks from the small colonies ($H/L_{small} = 0.62 \pm 0.06$ vs. $H/L_{large} = 0.83 \pm 0.06$; $F_{1,50} = 6.28$, $P = 0.014$). There was no significant effect of hatching date ($F_{1,50} = 0.01$, $P = 0.91$) and brood size ($F_{1,50} = 0.06$, $P = 0.81$) on the H/L ratio.

Chick survival and reproductive success

Although there were no significant differences in the hatching success between the colonies of different size ($F_{1,195} = 2.22$, $P = 0.14$), we found that chicks had higher survival rate in the large colony than in the small colonies (Cox–Mantel: $Z = -2.04$, $P = 0.041$; Fig. 2). Consistently, after accounting for hatching date which negatively affected fledging success ($F_{1,194} = 14.15$, $P < 0.001$, $\beta = -0.015 \pm 0.004$), we found that terns nesting in the large colony fledged more young than terns from the small colonies (1.14 ± 0.11 vs. 0.79 ± 0.09 fledglings; $F_{1,195} = 5.64$, $P = 0.019$).

Fig. 3 Standardized residuals of brood growth rates of wing length against hatching date (a) and standardized residuals of chick hemoglobin concentration against hatching date and age (b) in cross-fostered and control clutches in 2013. The size of the colony where eggs were laid and raised is indicated (S small colonies, L large colony). Mean \pm SE are presented. Number of clutches above bars



Cross-fostering experiment

The cross-fostering experiment carried out in 2013 indicated that the size of the colony where chicks were raised had a significant impact on their condition and the level of physiological stress. After controlling for hatching date ($F_{1,46} = 11.29$, $P = 0.001$) and chick age ($F_{1,46} = 20.27$, $P < 0.001$), we found that chicks (both fostered and control) raised in the small colonies had higher hemoglobin concentrations in comparison to chicks raised in the large colony ($F_{1,46} = 4.22$, $P = 0.045$; Fig. 3a). A similar relationship was found for brood growth rates of wing length, which after accounting for hatching date ($F_{1,42} = 13.91$, $P < 0.001$) were higher in foster and control broods raised in the small colonies ($F_{1,42} = 8.66$, $P = 0.005$; Fig. 3b). Finally, controlling for hatching date ($F_{1,30} = 1.31$, $P = 0.26$) and chick age ($F_{1,30} = 6.10$, $P = 0.016$), significantly lower levels of stress indicated by lower H/L ratios were recorded in chicks (both fostered and control) raised in the smaller colonies ($F_{1,30} = 4.28$, $P = 0.044$). In contrast, we found that the size of the colony where eggs were laid had no significant effect on chick hemoglobin concentrations ($F_{1,46} = 0.10$, $P = 0.76$), brood growth rates ($F_{1,42} = 2.38$, $P = 0.13$), and chick physiological stress ($F_{1,30} = 1.33$, $P = 0.25$), indicating that the differences in chick condition were not inherited, but could be directly attributed to different rearing conditions experienced in the colonies of varying size.

Discussion

In this study, we provided empirical evidence that opposing selective pressures may simultaneously act on colony size in birds. Our results suggest that large colony size promotes better survival of Common Tern broods, but reduces the quality of offspring. As chicks from the larger nesting aggregation grew more slowly and were in poorer physiological condition than chicks in the smaller colonies, they were likely to experience higher mortality rate during the post-fledging period (Sagar and Horning 1998; Mougin et al. 2000). In fact, Schaub and Becker (2008) found that slow development rate of Common Tern nestlings was associated with lower post-fledging survival. Consequently, the greater fledging success observed in large colonies may be negated by lower survival afterwards. A similar mechanism of opposing selective pressures acting on the colony size has been reported by Wiklund and Andersson (1994), who demonstrated that predation on Fieldfare *Turdus pilaris* eggs and young selected for larger colony size, whereas a higher likelihood of chick starvation selected for smaller colonies.

In this study we recorded ca. 30 % lower fledging success in the small colonies (30–40 breeding pairs) in comparison to the large colony (ca. 100 breeding pairs) and this pattern was consistent with differences in chick survival between the colonies. Since all the colonies were located at the same site, the differences in chick survival could not likely be attributed to between-colony variation in the density or type of predators. Higher fledging success and chick survival in the large colony could be plausibly explained by more effective antipredatory behaviours of adult birds. Common Terns are known to readily use mobbing to deter predators (Becker 1995), although effectiveness of defence is likely to depend on the number of individuals involved in this behaviour (Brunton 1999; Hernández-Matías et al. 2003). Thus, terns nesting in smaller aggregations may fail to effectively deter predators, especially if predators selectively choose to forage in the smaller colonies.

It is important to stress that between-colony differences in the intrinsic quality of breeding adults were unlikely to explain the observed variation in survival and condition of

offspring. Our experimental cross-fostering manipulation demonstrated that the size of the colony where chicks were raised strongly affected their condition, growth rates and levels of physiological stress, but the size of the colony of origin had no significant impact on the quality of raised offspring. Higher physiological quality of control and foster broods raised in the smaller colonies suggests that all measured components of offspring quality were not inherited, but reflected more favourable developmental conditions prevailing in nesting aggregations of smaller size. This also seems to contradict previous reports on a strong heritable component to colony size choice based on individual ability to withstand parasites (Brown and Brown 2000), which is consistent with the results of the recent simulation study by Danchin et al. (2014).

Very similar distribution of low- and high-quality pairs between the colonies of different size was also supported by lack of differences in clutch size and mean egg volume between the large and small colonies. Both of these traits are widely acknowledged as reliable proxies of female phenotypic quality (Amundsen and Stokland 1990; Slagsvold and Lifjeld 1990), reflecting their condition (Newton et al. 1983; Bolton et al. 1993) and increasing with age or experience (Nisbet et al. 1984; González-Solís et al. 2004). Therefore, it might be assumed that there were no major differences in the age and condition of adult terns nesting in the colonies of different size and, thus, individual variation in quality was unlikely to account for the observed differences in chick condition and survival. This hypothesis was further supported by simultaneous initiation of laying at the large and small rafts, considering that the timing of breeding is known to be quality-dependent (Arnold et al. 2004). The prolonged laying period in the small colonies was most likely due to reneesting after earlier failed breeding attempts, rather than a consequence of poorer quality adults preferentially breeding on the smaller rafts.

We suggest that the poorer physical condition of chicks raised in the large colony could result from increased social stress or parasitic pressure. This hypothesis is supported by the higher H/L ratios, lower hemoglobin concentrations and slower growth rates found in offspring from the large colony compared to the small colonies. The H/L ratios indicated that chicks from the large colony were subjected to higher physiological stress than offspring raised in small nesting aggregations. Although we collected no direct data on the parasite load of Common Tern chicks, lower hemoglobin concentrations of chicks raised in the large colony may provide a circumstantial support for the positive association between parasitic pressure and colony size in the studied tern population. Increased hemoglobin levels have been associated with parasite load in nestlings and adults of several avian species (e.g. Clark and Mason 1988; Sergent et al. 2004; Słomczyński et al. 2006). Slower growth rates of chicks from the large colony could also indicate their higher infestation with parasites, however, this pattern could be alternatively explained by the necessity of parents to invest more in nest defence. It has been demonstrated that the fighting rate and the time devoted to intraspecific nest defence increases with the size of waterbird colonies (e.g. Hötker 2000), constraining such activities as foraging and food provisioning, which may reduce chick growth rates and their physical condition (Phillips et al. 1998). Our results are consistent with patterns observed in the Magellanic Penguin, where offspring raised in large colonies showed lower body condition and poorer immune response in comparison to chicks from smaller colonies (Tella et al. 2001). Since the studied tern colonies were located at the same site and adults used the same foraging grounds, differences in food availability could be excluded as a potential explanation for colony-related variation in chick growth rates and condition.

Since nesting densities were similar for all the rafts, we assumed that reported differences in the reproductive traits were primarily attributable to the variation in the size of the

colonies. In natural conditions, the size of breeding aggregations may be positively associated with nesting density (Møller 1982), as in large colonies there is intensified competition for the attractive central nesting sites (Coulson 1968; Minias 2014), which can produce locally high densities. For this reason, the effects of colony size and nesting density on reproductive performance are often difficult to separate and could be easily confounded. In our study, similar nesting densities on both large and small nesting rafts suggested that the colony size could be directly responsible for the differences in chick condition and survival between the colonies. Since the crèche size on the large raft was several times higher than on the small rafts (max. 120 chicks vs. 30–40 chicks) and all grown-up chicks could move freely around each colony, the frequency of interactions between unrelated chicks, as well as between chicks and non-parental adults was undoubtedly higher in the larger colony, likely increasing the level of social stress and decreasing chick survival. Similar conclusions were reached in a recent study on Common Terns in Germany, demonstrating that reproductive parameters are primarily determined by colony size, and not necessarily by nesting densities (Szostek et al. 2014).

As it is difficult to identify all benefits and costs of colonial breeding, it has been proposed that research on the adaptive functions of colony size should focus on reproductive success as an integrative measure of the balance between all advantages and disadvantages of coloniality (Danchin and Wagner 1997). Parameters, such as post-fledging or adult survival, are rarely included in studies aiming to explain intraspecific variation in the colony size (Serrano et al. 2005). This study supports the view that focusing solely on reproductive success may easily produce spurious interpretations. Although we found that larger colony size favoured brood survival in the Common Tern and, consequently, per capita fledging success of terns nesting in small aggregations was significantly lower, we also demonstrated that birds from small colonies raised fledglings in better condition, which likely enhances post-fledging survival (Schauroth and Becker 2008). Therefore, we may expect that the final fitness balance of terns nesting in the colonies of different size should be much more similar than indicated by the analysis of reproductive success at the moment of fledging. However, since Common Terns can breed in the colonies of up to several thousand pairs in nature (Szostek et al. 2014), studies on much broader range of colony sizes would be needed to unequivocally confirm this conclusion.

Acknowledgments We would like to thank all the participants of the fieldwork, especially Marta Paśiek. We thank Bartosz Lesner for designing and constructing nesting rafts. Regional Fund for Environmental Protection and Water Management in Łódź and ICOPAL S.A. gave financial support for constructions of the rafts. PM was financially supported by the Scientific Foundation of the University of Łódź. We appreciate constructive suggestions on the earlier draft of the manuscript by Neil Metcalfe, Peter Dunn, and Richard Wagner. We also thank an anonymous reviewer and the Associate Editor, Martin Reichard, for helpful comments on the manuscript. The experiments comply with the current laws of Poland, where the study was performed under the permissions of the Bioethical Commission and the General Environmental Protection Directorate.

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