

Sexual size dimorphism and the relationship between timing of breeding and size-assortative mating in a monogamous, marsh-nesting bird

David A. Shealer

Department of Biology, Loras College, Dubuque, Iowa, USA

ABSTRACT

Question: Can the process of mutual mate choice be inferred from patterns of size-assortative pairing?

Hypothesis: Mutual mate choice should result in a strong pattern of assortative mating early in the breeding season, with assortative pairing becoming weaker as the season progresses.

Organism: Black tern (*Chlidonias niger*), a semi-colonial, monogamous, marsh-nesting bird with substantial male parental care.

Study sites and dates: Wetland breeding sites throughout Wisconsin (USA) from 2000 to 2009.

Methods: Mated pairs ($n = 277$) of adults were captured and measured during incubation. I compared measures of body size between males and females to test for within-pair sexual size dimorphism. I used canonical correlation to test for size-assortative mating, with the sample divided into early (≤ 1 June) and late (≥ 2 June) breeding pairs.

Results: Males were larger than females (1–5%) for all measures of body size. Evidence for size-assortative mating was found in mated pairs, but only among late breeders. Hatching success did not depend on timing of breeding, total clutch mass or degree of size-assortative pairing.

Conclusions: Early breeding is not an expression of individual or pair quality. Black terns may exhibit mutual mate choice, but body size does not appear to be an important criterion for it. The pattern of size-assortative mating among late breeders only is difficult to reconcile with existing theoretical models.

Keywords: assortative pairing, black tern, *Chlidonias niger*, mate choice, mate retention, morphometry, sexual dimorphism.

INTRODUCTION

In animals, mating opportunities are assumed to limit male reproductive success (e.g. Bateman, 1948). Sexual selection, therefore, should act strongly on phenotypic traits that affect the

Correspondence: D.A. Shealer, Department of Biology, Loras College, 1450 Alta Vista, Dubuque, IA 52004, USA.
e-mail: david.shealer@loras.edu

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ability of males to acquire mates (Trivers, 1972; Emlen and Oring, 1977). Due to the costs and limitations of gamete production (eggs), females should be selected to exercise prudent choice by discriminating among males of variable quality via phenotypic or behavioural cues. Secondary sexual characteristics are common in many females (Clutton-Brock, 2009), however, suggesting that mate choice is not entirely female-driven, and that males also may take an active role in the process of mate selection under certain circumstances (Clutton-Brock, 2007; Edward and Chapman, 2011).

If mate choice is mutual, then one would expect a pattern of positive assortative mating, i.e. the tendency for males and females to pair according to some phenotypic characteristics indicative of individual quality. In species with biparental care, both sexes should seek the highest-quality mates possible, and high-quality individuals, regardless of sex, should be more selective than those of lower quality. In that case, one would expect assortative mating in the early part of the breeding season due to high-quality individuals pairing with each other. As the season progresses, unpaired lower-quality individuals should become less selective and assortative mating should weaken, although the cost associated with mate choice may alter this pattern (Johnstone, 1997). Assortative mating, however, may result from factors other than mutual mate choice, such as heterosis (Burley, 1983), intra-sexual competition (Hårdling and Kokko, 2005; Taborsky *et al.*, 2009), or even random pairing among individuals in a population (Barbraud and Barbraud, 1999).

Theoretical and empirical research on mate choice in animals has focused primarily on species with obvious sexual dimorphism. Monomorphic species have received considerably less attention, although they account for over half the world's bird species (Griffiths *et al.*, 1998). Monomorphism may result from the similar expression of secondary sexual characteristics in both males and females or from a lack of any obvious ornaments in either sex. In some auklets (Alcidae), mutual sexual selection may explain female ornamentation, as males and females each prefer mates with more elaborate traits (Jones and Hunter, 1993), which seem to function as a signal of dominance status in both sexes (Jones and Hunter, 1999). In other species, however, female ornamentation cannot be explained by mutual mate choice, such as in the turquoise-browed motmot (*Eumomota superciliosa*), which does not pair assortatively for tail ornamentation, body size or phenotypic condition (Murphy, 2008).

Most gulls and terns (Laridae) lack obvious secondary sexual characteristics, are monomorphic with respect to plumage, but usually exhibit some degree of sexual size dimorphism, with males generally larger than females (e.g. Chardine and Morris, 1989; Bosch, 1996; Fletcher and Hamer, 2003). Although size-assortative mating has been reported in some larids (Coulter, 1986; Chardine and Morris, 1989; Stern and Jarvis, 1991; Catry *et al.*, 1999; Helfenstein *et al.*, 2004; Ludwig and Becker, 2008; but see Phillips *et al.*, 2002; Nisbet *et al.*, 2007), the underlying mechanisms driving this process are not well understood. For example, patterns of size-assortative pairing may be confounded with age (e.g. Nisbet *et al.*, 2007), particularly if male and female birds join the breeding population at similar ages and form long-term pair bonds (Reid, 1988) and if mensural characteristics of adults change predictably over time (Bridge and Nisbet, 2004).

Here, I investigate the evidence for mutual mate choice in the North American black tern (*Chlidonias niger surinamensis*), a marsh-nesting larid. I examine patterns of sexual size dimorphism and assortative mating with respect to characteristics pertaining to body size and phenotypic condition, timing of breeding, and probability of breeding success.

Black terns recruit to the breeding population as early as 2 years of age (Shealer *et al.*, 2014). Adults of the North American subspecies exhibit little to no sexual plumage dimorphism

and only slight size dimorphism (Shealer and Cleary, 2007). Males and females form monogamous pairs, both socially and genetically, during the breeding season (Shealer *et al.*, 2014), and males contribute substantially to parental effort, often incubating entirely by themselves overnight while females depart the colony for a communal roost (Custer and Custer, 1996; Van der Winden, 2005a). Between-year mate retention is low (~20%), however (Shealer *et al.*, 2014), suggesting that most birds select a new mate each year or so.

Owing to these life-history characteristics, I predicted that both sexes should be choosy when selecting a mating partner. If so, I sought to confirm a prediction of Johnstone's (1997) model of mutual mate choice, that assortative mating would be more apparent among early-breeding (and presumably higher-quality) pairs and that assortative pairing would weaken as the season progressed. I also sought to determine whether phenotypic characteristics of adults change predictably over time, which potentially could confound pattern (e.g. size-assortative pairing) with process (e.g. age-assortative pairing).

METHODS

Field protocols

As part of a long-term study of population dynamics and reproductive success, my assistants and I captured adult black terns opportunistically during the incubation period using walk-in or drop-in traps placed over their eggs. Following capture of the first member of a pair, we tried to trap the mate during processing of the first bird. If we were unsuccessful, we tried again at a later date, if possible. To reduce the likelihood of nest abandonment, trapping efforts were concentrated during the latter half of the incubation period (Shealer and Haverland, 2000), which, for black terns in Wisconsin, ranges from 21 to 25 days (D.A. Shealer, unpublished data).

Immediately following capture, adult terns were transported away from the nest to a concealed location for processing. We banded each bird (under BBL permit #22827), and recorded various body measurements, including head-plus-bill length, length of exposed culmen, bill depth at gonys, wing chord, and body mass (for more detail, see Shealer and Cleary, 2007). Beginning in 2008, we scored arrested primary moult of the feathers in the right wing for each bird according to the system proposed by Van der Winden (2005b). Each bird received a numerical score corresponding to the number of primaries replaced during the second and third wave of moult. During the breeding season, the primaries (usually outer) developed during the first moult series the previous year are darker and more worn than the contrasting inner primaries, of which a variable number are replaced during the second, and sometimes a third, moult series (Van der Winden, 2005b). Bridge and Nisbet (2004) found a strong positive correlation in moult score for newly formed pairs of common terns (*Sterna hirundo*), but not for established pairs, and suggested that moult pattern may be an honest signal of individual quality in this species. Before release, a blood sample was collected from each bird for subsequent molecular sex determination (Fridolfsson and Ellegren, 1999; Shealer and Cleary, 2007). We released all birds immediately following processing. Adults recaptured in subsequent years were re-measured as for first-time captures, and their mates were identified whenever possible.

The total sample consisted of 277 mated pairs of black terns captured at eleven different colony sites in Wisconsin from 2000 to 2009 and sexed by molecular markers. Colony sites and number of pairs captured and measured at each site included: Horicon Marsh (Dodge

Co.), $n = 149$ pairs; Grassy Lake (Columbia Co.), $n = 68$; Grand Lake (Green Lake Co.), $n = 22$; Mud Lake (Columbia Co.), $n = 14$; Theresa Marsh (Dodge Co.), $n = 6$; Sandhill State Wildlife Area (Juneau Co.), $n = 6$; Rose Lake (Jefferson Co.), $n = 5$; Mead State Wildlife Area (Marathon Co.), $n = 3$; Allequash Lake (Vilas Co.), $n = 2$; Keyeser Marsh (Columbia Co.), $n = 1$; Vernon Marsh (Waukesha Co.), $n = 1$.

Follow-up visits to each nest on, or just after, the projected date of hatching provided information on hatching success. All chicks were banded at first encounter and assigned to particular nests whenever possible. For newly hatched chicks (i.e. within 2 days post-hatch), nest assignment was relatively straightforward as chicks remain in or near the nest cup. When an empty nest was encountered, a reasonable determination of nest fate often could be made based on the condition of the nest (intact, disturbed, flooded) or indirect evidence of hatching success (e.g. fresh faeces from nestlings around the nest substrate, aggressive behaviour by the putative parents). Empty nests or nests that disappeared before day 20 were recorded as failed (for more detail on assignment of nest fate, see Shealer *et al.*, 2005).

Data analysis

Measures of body size were compared statistically between males and females within pairs with paired-samples *t*-tests. In addition to the morphometric measures described previously, two additional metrics were compared: same-day body mass, and a scaled mass index. Same-day body mass was a subset of the data from which both pair members were trapped and weighed on the same day (usually in the same hour). I made this comparison to test for the relative temporal plasticity in this measure, which I assume is sensitive to variation in local food abundance. I computed a scaled-mass index (SMI) for each individual as an index of body condition (body mass corrected for skeletal size) at the time of capture during the incubation period. Of the skeletal measures recorded, head-plus-bill length was most strongly correlated with body mass for both males ($r = 0.438$, $n = 271$, $P < 0.001$) and females ($r = 0.337$, $n = 274$, $P < 0.001$) and was therefore used as the single linear measure to compute the SMI, according to Equation (2) in Peig and Green (2009).

In addition to comparing univariate measures of body size between the sexes, I used canonical correlation to test for assortative pairing, with the two latent variables comprising the following individual variables for each sex: total head, culmen, and wing chord lengths, depth of bill at gonys, and body mass. As a test of Johnstone's (1997) model of mutual mate choice, the data set was divided into early (≤ 1 June) and late (≥ 2 June) nesting pairs, based on the laying date of the first egg in the clutch. This cut-off date resulted in two sample groups of approximately equal size; canonical correlations were run separately for each group.

Previous studies have reported negative correlations between various measures of body size and laying date in black terns (Shealer and Cleary, 2007) and common terns (Nisbet *et al.*, 2007), suggesting that late-nesting birds are either younger or of poorer quality than early nesters. I examined the relationship between several potential predictor variables and hatching success using a generalized linear model that included the following covariates: date of first egg laid (1 = 1 May), total clutch mass (for three-egg clutches only), SMI difference (the difference in the scaled-mass index between the male and female of a mated pair), and culmen difference (the difference in standardized culmen length between the male and female of a pair). The rationale for including the latter two variables was to explore the possibility that differences in the degree of size-assortative mating might be correlated with

breeding performance. That is, small or negative relationships between differences in mass or culmen length and the probability of hatching success would indicate that size-assortative mating confers little to no benefit with regard to breeding performance (for a similar application of this analysis, see Forero *et al.*, 2001).

Over the course of the 10-year study, 78 adults were recaptured at least once in a subsequent year following the year of initial capture. Measurements taken of recaptured birds were used to test for age-related changes in morphometry. For birds recaptured only once, the values from measurements recorded during the year of recapture were subtracted from the values recorded during the year of initial capture, then divided by the number of years between capture to derive an annualized rate of change. For birds recaptured multiple times, the slope of the least-squares regression line (regardless of statistical significance) was used as the estimated annual rate of change. Values for each metric were then subjected to one-sample *t*-tests, against the null hypothesis of no change over time.

For all parametric statistical tests, assumptions of normality and equal variances were verified before analysis. I assessed differences in moult score between the sexes with the non-parametric Wilcoxon signed-ranks test, and used Spearman's rank correlation to test for assortative mating by this character. I used SPSS v.13.0 for Windows (SPSS, Inc., 2004) for all statistical analyses presented here.

RESULTS

Sexual size dimorphism

Mated pairs of black terns displayed sexual size dimorphism, with males, on average, 1–5% larger than females in measurements related to head and bill traits, wing chord, and body mass (Table 1). Moult score, which is not a size-related characteristic, did not differ significantly between the sexes. For early-laying females, standardized canonical loadings indicated that wing length had the strongest relationship to the underlying size construct, but the correlation was inverse; for both sexes, body mass was the strongest variable related positively to overall body size (Table 2). For late-nesting pairs, gonys was the variable most positively related to the underlying size construct for each sex; other variables with high standardized loadings were negatively related to size (Table 2).

Test for assortative mating

Canonical correlation indicated little to no evidence of size-assortative pairing for early-laying birds (≤ 1 June). The multivariate test was not significant (Wilks' $\lambda = 0.767$, $P = 0.19$), and the first canonical correlation ($r = 0.37$) indicated that only 13% of the variation in female size could be accounted for by male size. In univariate comparisons among the variables comprising the size constructs for the two sexes, the only significant relationship was that of female gonys to male mass ($P = 0.01$).

Relationships were stronger, however, for later-laying pairs (≥ 2 June), and the overall multivariate test was significant (Wilks' $\lambda = 0.658$, $P = 0.01$). The first canonical correlation ($r = 0.44$), however, again indicated that only about 20% of the variation in female size could be accounted for by male size. Univariate *F*-tests indicated that both culmen length and mass of females were related significantly ($P = 0.02$ for each) to the underlying male size construct. For individual pair-wise comparisons among the variables, the

Table 1. Within-pair comparisons of morphometry of adult black terns

Measure	<i>n</i> (pairs)	Males		Females		<i>t</i> -score (paired)	<i>P</i>	Male larger (% of cases) ^a	SDI ^b
		Mean	S.D.	Mean	S.D.				
Head plus bill length (mm)	275	60.1	1.2	57.9	1.3	21.5	<0.001	89	1.04
Exposed culmen (mm)	277	27.0	1.0	25.8	1.1	14.7	<0.001	80	1.05
Bill depth at gonys (mm)	253	5.4	0.3	5.2	0.3	9.85	<0.001	70	1.04
Wing chord (mm)	274	211.0	5.3	207.9	5.3	6.67	<0.001	62	1.01
Body mass (g)	268	59.7	4.5	58.7	3.8	3.03	0.003	59	1.02
Same-day body mass (g) ^c	236	59.7	4.7	58.7	3.8	2.96	<0.001	60	1.02
Scaled mass index (g) ^d	274	59.9	2.9	58.7	3.6	4.63	<0.001	60	1.02
Moult pattern ^e	42	6	(5–6)	5	(5–6)	0.74	0.46		

^a Includes ties (male = female).

^b Sexual dimorphism index, calculated as mean male/mean female.

^c Body mass of each member of a mated pair trapped and weighed on the same day.

^d See Methods.

^e Number of replaced inner primary feathers. Reported for this measure are medians (25th and 75th percentiles), and Z-score from Wilcoxon signed ranks test with associated probability.

Table 2. Standardized canonical loadings for variables pertaining to the underlying constructs of female and male body size for pairs laying early (≤ 1 June) or late (≥ 2 June)

Variable	Early breeders		Late breeders	
	Female	Male	Female	Male
Head plus bill	0.512	-0.031	-0.191	0.223
Culmen	0.008	-0.073	-0.276	-0.622
Gonys	0.324	0.301	0.660	0.692
Wing	-0.666	-0.337	-0.016	-0.071
Mass	0.606	0.908	-0.664	-0.498

following relationships were statistically significant between males and females within mated pairs:

- culmen length ($\beta = 0.49 \pm 0.14$ [S.E.], $t = 3.47$, $P = 0.001$);
- gonys ($\beta = 0.23 \pm 0.09$ [S.E.], $t = 2.48$, $P = 0.015$);
- body mass ($\beta = 0.35 \pm 0.13$ [S.E.], $t = 2.72$, $P = 0.008$)

Sample size was too small to include moult pattern in the canonical correlation analysis, but the total sample revealed no evidence of assortative mating for this character (Spearman's $\rho = 0.164$, $n = 42$ pairs, $P = 0.30$)

Timing of breeding and hatching success

Of the 277 pairs included in the sample, confident determinations about hatching success could be made for 201 nests (71%). Of these, at least one chick hatched from 83 of 113 (73%) early nests, as well as from 60 of 88 (68%) late nests.

The chi-square test of association with Yates' correction was $\chi^2_1 = 0.44$, $P = 0.51$, indicating no difference in hatching success between early and late nests. At a finer scale, the generalized linear model constructed to evaluate parameters related to hatching success fit the data no better than the null model that included only the intercept (likelihood ratio chi-square = 9.02, d.f. = 4, $P = 0.06$); thus, none of the individual parameters included in the model was a significant predictor of hatching success (Table 3). Early-breeding males and females were heavier, on average, than late-breeding birds of the respective sex, but did not differ with respect to head- or bill-size measurements (Table 4).

Test for age effects on morphometry

The comparison of repeated measurements taken from recaptured birds over the 10-year study revealed little evidence that univariate measures of body size change with age in adult black terns (Table 5), as all of these mean differences were well below normal measurement error. The one possible exception is the bill depth at the gonys, which exhibited a significant positive change over time, and for which late-nesting pairs did tend to mate assortatively.

Table 3. Results of generalized linear model^a for variables predicting hatching success of black tern nests

Parameter ^b	β	S.E.	Wald χ^2	P-value
Intercept	-6.30	2.91	4.68	0.03
Lay date	0.01	0.02	0.57	0.45
Total clutch mass	0.16	0.09	2.89	0.09
SMI difference (M – F)	-0.10	0.05	3.43	0.06
Culmen difference (M – F)	0.20	0.18	1.36	0.24

^a Omnibus test comparing fitted model against intercept-only model: likelihood ratio $\chi^2 = 9.02$, d.f. = 4, $P = 0.06$.

^b All parameters = 1 degree of freedom.

Table 4. Body size comparisons between males and females tending early (≤ 1 June) and late (≥ 2 June) nests

	Body mass (g)	Head + bill (mm)	Culmen (mm)	Gonys (mm)	Wing (mm)
Males					
Early	60.5 $\pm$ 3.1 (137)	60.1 $\pm$ 1.2 (138)	26.9 $\pm$ 0.9 (138)	5.4 $\pm$ 0.3 (126)	211.8 $\pm$ 5.5 (138)
Late	59.2 $\pm$ 3.2 (121)	60.1 $\pm$ 1.2 (122)	27.1 $\pm$ 1.0 (124)	5.4 $\pm$ 0.3 (116)	210.0 $\pm$ 5.1 (122)
	$t_{256} = 3.31$ ($P = 0.001$)	$t_{258} = -0.56$ (N.S.)	$t_{260} = -1.62$ (N.S.)	$t_{240} = 1.01$ (N.S.)	$t_{258} = 2.88$ ($P = 0.004$)
Females					
Early	59.3 $\pm$ 3.9 (135)	58.0 $\pm$ 1.3 (138)	25.8 $\pm$ 1.2 (138)	5.2 $\pm$ 0.2 (127)	208.4 $\pm$ 5.1 (138)
Late	58.2 $\pm$ 3.8 (124)	57.9 $\pm$ 1.2 (124)	25.8 $\pm$ 1.1 (124)	5.2 $\pm$ 0.3 (115)	207.4 $\pm$ 5.4 (121)
	$t_{257} = 2.34$ ($P = 0.02$)	$t_{260} = 1.01$ (N.S.)	$t_{260} = -0.03$ (N.S.)	$t_{240} = -0.53$ (N.S.)	$t_{257} = 1.65$ (N.S.)

Note: Values are means $\pm$ 1 standard deviation, with sample sizes in parentheses (N.S. = not significant, $P > 0.05$).

Table 5. Annualized differences in morphometry of adult black terns captured at least twice in separate years

Measure	<i>n</i>	Mean difference (mm)	S.D.	<i>t</i> ^a	<i>P</i>	95% confidence limits	
						Lower	Upper
Head plus bill length	78	-0.003	0.404	-0.57	0.95	-0.094	0.089
Exposed culmen	78	-0.014	0.778	-0.16	0.88	-0.189	0.162
Bill depth at gonys	67	0.048	0.181	2.18	0.03	0.004	0.092
Wing chord	78	0.374	2.530	1.31	0.20	-0.196	0.945

^a One-sample *t*-test against $H_0: \mu_{\text{difference}} = 0$.

DISCUSSION

Although statistically significant for all comparisons, differences in morphometry between the sexes were small (1–5%), with males on average larger than females for all measures (Table 1). This finding confirms two earlier reports of sexual size dimorphism in black terns (Stern and Jarvis, 1991; Shealer and Cleary, 2007), and is consistent with other species of terns in general (Craik, 1999; Fletcher and Hamer, 2003). The largest dimorphisms were in measures related to the head

and bill, as reported previously for black terns (Stern and Jarvis, 1991; Shealer and Cleary, 2007) and other larids (Chardine and Morris, 1989; Helfenstein *et al.*, 2004). With the exception of early-breeding females, however, head and bill lengths did not contribute substantially, in terms of standardized canonical loadings, to the underlying body size construct. Body mass received high positive loading scores for early-breeding males and females, whereas gonys depth was strongly and positively related to size for later-breeding pairs (Table 2).

Black terns exhibited size-assortative mating, but the effect sizes were small and the relationship was significant only among late breeding pairs. None of the models of mutual mate choice I am aware of predict precisely this pattern, although Johnstone's (1997) model generates lower positive correlations between the qualities of mates under a relatively high cost of mate choice and/or low sensitivity to small differences in mate quality. The fitness costs to black terns of searching for a new mate are unknown but presumably are not negligible, as males perform elaborate courtship flights and provision potential mates with food during courtship (Heath *et al.*, 2009). The degree of error during the mate-sampling period also may be rather high, as females do not possess any obvious secondary sexual characteristics or display any other physical traits that might advertise quality. The weaker size-assortative mating pattern seen among early breeders would make sense if the fitness benefits of early breeding superseded any inherent phenotypic attributes of quality (e.g. body size), but hatching success did not differ between early and late breeders. Conversely, if late-arriving birds are of lower quality, they would be restricted in their choice of a mate to other low-quality birds, because the earlier arrivals already would be paired. Johnstone (1997) assumed that late arrivals represent lower-quality individuals, a reasonable assumption given the vast body of literature (reviewed in Bried and Jouventin, 2002) pertaining to timing of breeding and breeding performance in a variety of birds. If body size is an expression of individual quality in black terns, the present study found little evidence that late-breeding birds are of lower quality than early breeders (Table 4). The only consistent difference was that of a lower body mass among late-breeding pairs, but such a measure likely is sensitive to seasonal effects of food availability. Early-breeding pairs also might have shown a mass decline had they been re-weighed later in the season. The results reported here, then, suggest either that body size is not a reliable indicator of individual quality in black terns, or that late-arriving individuals are not particularly of lower quality. For terns in particular, behavioural specializations related to foraging proficiency are known to be reliable indicators of parental quality (Nisbet, 1973; Shealer *et al.*, 2005; Garcia *et al.*, 2011, 2013), often overriding more traditional measures such as early breeding, body size or egg size.

An alternative for a late-arriving, low-quality female might be to form a social bond with a low-quality male, then seek extra-pair copulations from already-mated males of higher quality (Johnstone, 1997). There are costs associated with this behaviour, however, such as the risk of desertion by the social mate or a reduction in parental effort corresponding to the degree of certainty of paternity. Furthermore, a genetic study conducted on black tern family groups in which the putative males varied considerably in body size found no evidence of any nestlings being sired by extra-pair males (Shealer *et al.*, 2014). Again, the equivalent hatching success between early and late breeders suggests that delayed breeding does not necessarily imply low quality.

Male black terns court unpaired females by feeding them and engaging them in courtship flights (Heath *et al.*, 2009). Thus, as in most species, females exercise some degree of mate choice. The question is whether males pair with females indiscriminately or exercise some degree of choice in the process. Theoretically, male mate choice is more likely to occur when males

encounter available females simultaneously instead of sequentially (Barry and Kokko, 2010). Under such a scenario, assortative mating is predicted to be stronger early in the season and decrease with time, as high-quality males and females pair first, leaving unpaired individuals, regardless of quality, to become less discriminating as time passes and opportunities for mating decrease (Johnstone, 1997). Conversely, assortative mating may be maintained throughout the breeding season if the cost of mate choice increases over time. If high-quality males and females pair early, the pool of females available for mating declines over time, such that low-quality males are left to select among remaining low-quality females, either by default or as an adaptive tactic to avoid being outcompeted in mate choice by higher-quality males (Fawcett and Johnstone, 2003; Härdling and Kokko, 2005).

I applied the results of the canonical correlation analysis for size-assortative mating among black tern pairs to the prudent choice model of Härdling and Kokko (2005). Recall that the body-size correlation was 0.37 and 0.44 for early and late breeders, respectively. From Figure 3 in Härdling and Kokko (2005), the only similar correlations correspond to a relatively low probability of encountering a mate, a relatively high rate of female takeover by large males over small males, and a low cost to small males of losing a takeover contest (high survival, S). The model solution for this set of conditions is positive assortative mating, with large males attracted only to high-quality females and small males attracted to females of both high and low quality (Solution C, Figure 2 in Härdling and Kokko, 2005). Do these criteria apply to black terns? A more biologically sound combination would be a high encounter rate (black terns breed colonially), a low rate of mate takeover (no evidence of EPP), and a high probability that small males survive a takeover (fighting among males is observed rarely). Such a combination predicts much stronger assortative mating ($r = 0.8\text{--}1.0$) than what this study revealed, resulting from the attraction of both large and small males to high-quality females, and large males sometimes usurping high-quality females from small males (Solution D, Figure 2 in Härdling and Kokko, 2005).

Spurious patterns of size-assortative mating (in the absence of active mate choice) may result from assortative mating by age (Reid, 1988; Bridge and Nisbet, 2004). Similar recruitment ages in the two sexes, coupled with low mortality and strong inter-year mate fidelity, could produce positive age correlations (Reid, 1988). Some long-term studies of terns (Bridge and Nisbet, 2004) and other seabirds (reviewed in Bried and Jouventin, 2002) report statistically significant age correlations within mated pairs, particularly among younger birds (Ludwig and Becker, 2008). Barbraud and Barbraud (1999) also found a strong age correlation within pairs of European white storks (*Ciconia ciconia*), but these birds paired in proportion to the relative availability of experienced and inexperienced birds in the population, and therefore the age correlation could be explained simply by random mate selection rather than active choice. The ages of most adults in this study were not known precisely, so I was unable to test for age associations. The tendency for size-assortative pairing among late breeders, however, likely was independent of any age associations because the morphometric characters recorded from recaptured birds showed no consistent changes with increasing age. The one possible exception to this was the depth of the gonys, which showed a slight but statistically significant increase over time (Table 5). The gonys in black terns, however, is not well developed, it is difficult to measure precisely, and therefore it is likely prone to a high degree of measurement error.

In summary, sexual size dimorphism was confirmed within mated pairs of black terns. Size-assortative mating was evident only among late-breeding pairs, but timing of breeding was not related to the body size of either sex, egg size or hatching success.

Substantial male parental effort (Van der Winden, 2005a), and apparent genetic monogamy together with low inter-annual mate retention (Shealer *et al.*, 2014) in this species implies strong selective pressure on decisions relating to adaptive mate choice, not only for females but for males as well (Clutton-Brock, 2007, 2009; Edward and Chapman, 2011). The criteria for such choices, however, remain elusive, but probably they are not related strongly to body size or timing of arrival at the breeding site. Future searches for evidence of mutual mate choice in monogamous, monomorphic birds should devote more attention to behavioural traits, such as male effort during the courtship period (e.g. Nisbet, 1973; Garcia *et al.*, 2011) or more cryptic traits, such as UV reflectance (e.g. Nolan *et al.*, 2010), that exceed the capabilities of human sensory perception.

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