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# FLUCTUATING ASYMMETRY IN COMMON TERN (*STERNA HIRUNDO*) CHICKS VARIES WITH HATCHING ORDER AND CLUTCH SIZE

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Abstract.—Fluctuating asymmetry (FA), small random deviation from bilateral symmetry, often increases with stress during development. Common Terns (*Sterna hirundo*) typically lay two to three eggs that hatch asynchronously. I predicted that C-chicks (last of three) should have greater FA than A- and B-chicks at hatching and that FA should be higher in chicks from smaller clutches, because of differences in parental quality. Tarsus length of newly hatched chicks was measured across three years, and middle toe length was measured in one year. Sample sizes exceeded 100 chicks in two of three years. Variation in tarsus FA with hatching order and clutch size was statistically significant in one year ($P < 0.01$) and nearly so in another ($P < 0.10$). No significant differences were present for toe FA. A-chicks from three-egg clutches appeared to have the lowest tarsus FA among categories of chicks in both years, and in one year they were significantly more symmetrical than B- and C-chicks from three-egg clutches. As predicted, A-chicks from three-egg clutches were also more symmetrical than A-chicks from two-egg clutches and singletons. However, C-chicks did not differ significantly from B-chicks in tarsus FA. Fluctuating asymmetry also varied with hatching date, but no clear pattern emerged. Fluctuating asymmetry was not associated with trait size or body mass, although there was significant variation in body mass and toe size among groups, C-chicks being relatively small and A-chicks and singletons relatively large. *Received 30 October 2008, accepted 28 April 2009.*

Key words: clutch size, Common Tern, fluctuating asymmetry, hatching asynchrony, parental quality, *Sterna hirundo*.

**La Asimetría Fluctuante en Polluelos de *Sterna hirundo* Varía con el Orden de Eclosión y Tamaño de la Puesta**

Resumen.—La asimetría fluctuante (AF), pequeñas desviaciones al azar de la simetría bilateral, generalmente aumenta con el estrés durante el desarrollo. Los individuos de *Sterna hirundo* generalmente ponen dos a tres huevos que eclosionan asincrónicamente. Predije que en el momento de la eclosión, los polluelos C (últimos de la secuencia de tres) tendrían una AF mayor que los polluelos A y B, y que la AF debería ser mayor en polluelos de nidadas pequeñas debido a diferencias en la calidad parental. Se midió la longitud de los tarsos de polluelos recién eclosionados durante tres años y en un año se midió la longitud del dedo del medio. El tamaño muestral superó los 100 polluelos en dos de los tres años. La variación en la AF con el orden de eclosión y el tamaño de la puesta fue estadísticamente significativa en un año ($P < 0.01$) y marginalmente en otro año ($P < 0.10$). No se encontraron diferencias significativas para la AF del dedo del medio. Entre las categorías de polluelos, los polluelos A provenientes de puestas de tres huevos tuvieron la menor AF en los tarsos en los dos años, y en un año fueron más simétricos que los polluelos B y C de nidadas de tres huevos. Como se había predicho, los polluelos A de nidadas de tres huevos fueron también más simétricos que los polluelos A de nidadas de dos o un huevo. Sin embargo, la AF de los tarsos de los polluelos C no se diferenció significativamente de la de los polluelos B. La asimetría fluctuante varió también con la fecha de eclosión, aunque no emergió un patrón muy claro. La asimetría fluctuante no estuvo relacionada con el tamaño del carácter o a la masa corporal, aunque hubo variación significativa entre grupos en la masa corporal y los tamaños del dedo medio. Los polluelos C fueron relativamente pequeños, y los polluelos A y los polluelos de nidadas de un huevo fueron relativamente grandes.

Fluctuating asymmetry (FA) is a measure of directionally random deviations from perfect bilateral symmetry and may be used as an indicator of stress during development (reviews in Leary and Allendorf 1989, Parsons 1990, Møller and Swaddle 1997, Lens and van Dongen 2002, Polak 2003). For example, among birds, FA has been shown to increase with parasite load (Møller 1992) and immune response (Fair et al. 1999), nutritional stress (Swaddle and Witter 1994), inbreeding (Grant and Grant 1995), poor habitat quality (Carbonell and Tellería 1998), exposure to pollution (Eeva et al. 2000), and thermal stress during incubation (Yalçin and Siegel 2003).

In species that exhibit hatching asynchrony, hatching order is a major determinant of chick survival. Common Terns (*Sterna hirundo*) typically have two or three young per nest, and third-hatched chicks ("C-chicks") suffer high mortality (Langham 1972, Nisbet 1973, Becker and Finck 1985, Bollinger et al. 1990, Bollinger

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1994). Much of this mortality occurs in the first week of life as a result of competition for food among siblings. Eggs are laid asynchronously, and C-chicks often hatch approximately three days later than the A-chick and one to two days later than the B-chick (Langham 1972, Nisbet and Cohen 1975, Courtney 1979, Bollinger et al. 1990). Not only do siblings that hatch earlier have a head start in growth, but differences among siblings may also be enhanced by possible biases in food provisioning with hatching order (Langham 1972, Rossell et al. 2000).

In addition to effects of hatching order that occur after hatching, C-eggs are smaller than A- and B-eggs (reviewed in Nisbet 2002, Becker and Ludwigs 2004), and incubation of C-eggs is likely to be less continuous close to hatching, because parents must feed older chicks that no longer stay inside the nest (Courtney 1979, Burger and Gochfeld 1991, Lee et al. 1993). In some locations, C-eggs have also been reported to contain higher levels of contaminants than A- and B-eggs (Nisbet 1982, French et al. 2001). Chick survival is positively correlated with egg size (Nisbet 1973, 1978), although in C-chicks a small egg may actually give a net survival benefit by decreasing the hatching interval (Bollinger 1994). I predicted that C-chicks should show signs of stress at hatching because of the differences in egg size and incubation frequency (and, perhaps, differences in contaminant concentrations). Thus, C-chicks should have higher levels of FA than A- and B-chicks, which would suggest that they start life with lower developmental stability. Differences in FA between A- and B-chicks may also be present, although the differences in egg size and timing of hatching are not as large as with C-chicks.

I also predicted that, when controlling for hatching order, chicks from two-egg clutches should have greater FA than chicks from three-egg clutches. Singletons should also show higher FA than first-hatched chicks from broods of two and three. These predictions at first seem counterintuitive, because as clutch size increases, parental investment would need to be divided up among more eggs during laying and more chicks after hatching. However, clutch size is correlated with parental quality (Coulson and Porter 1985), a major determinant of chick growth and survival in terns and gulls (Nisbet 1978, Coulson and Porter 1985, Bolton 1991, Bollinger 1994, Nisbet et al. 1998, Wendeln and Becker 1999, Arnold et al. 2004). Previous studies have demonstrated positive effects of clutch size on several aspects of reproductive success, such as fledging success, hatching success, growth of chicks controlled for hatching order, post-fledging survival, and maternal survival (Langham 1972, Coulson and Porter 1985, Burger et al. 1996, Hong et al. 1998, Nisbet et al. 1998; but see Arnold et al. 2006). Despite the presence of a larger number of mouths to feed, parental feeding rate per chick (Wiggins 1989) and daily growth rate per chick (Wendeln and Becker 1999) do not decline with increasing brood size. Langham (1972) demonstrated that in Common Terns the likelihood of an individual chick fledging (controlled for hatching order) can actually increase as brood size increases from one to two to three. Clutch size is also correlated with other aspects of parental quality, such as maternal body condition, early laying date, and parental age and experience (Nisbet et al. 1984, Coulson and Porter 1985, Burger et al. 1996).

To test the predicted relationships between hatching order, clutch size, and FA, I measured FA in newly hatched Common Tern chicks over three years. To the best of my knowledge, this is the first study to link FA with hatching asynchrony and parental quality. In addition, although there have been many previous studies of FA in passerine and galliform birds, very few authors have studied FA in charadriiforms, and I know of no previously published study of FA in terns.

## Methods

This study took place on Pettit Island (39°40′N, 74°11′W), a 0.3-ha salt-marsh island in Manahawkin Bay in Ocean County, New Jersey, over three years: 2002, 2007, and 2008. Data from 2007 are few, because of unusually high nest losses attributable to tidal flooding just as chicks were starting to hatch (Palestis 2009). The Common Tern colony consisted of ~200 breeding pairs in 2002, 210 in 2007, and 125 in 2008 (Palestis 2009). Nests were marked with numbered sticks, and their contents were checked approximately four days per week in 2002. In 2007 and 2008, nest checks were less frequent during incubation and after peak hatching but were of equal or greater frequency during peak hatching.

I measured paired traits of Common Tern chicks to the nearest 0.1 mm using calipers. Chicks were measured within one day after hatching to avoid variation in FA with post-hatching growth (Kellner and Alford 2003), and any chicks with an uncertain hatching date were excluded. Tarsometatarsus ("tarsus") FA was measured in 105 chicks in 2002, 35 in 2007, and 109 in 2008. Rather than the entire length of the tarsometatarsus, I measured from the joint with the tibiotarsus to a clearly visible horizontal depression just above the accessory metatarsus, which attaches to the hallux. Brown and Brown (2002) used similar landmarks. Toe FA was measured in 2002 only ($n = 105$) along the entire length (excluding the claw) of the middle of the three main, forward-facing digits. Wing FA, a common trait in FA research with adult birds, could not be accurately measured in newly hatched chicks, because the wings were flexible and covered in down. In 2007 and 2008, chicks were also weighed to the nearest gram.

I measured the traits twice per side for each individual, as is standard in FA studies, because the differences between sides are often so small that they can be similar in magnitude to measurement error (Palmer and Strobeck 1986, 2003; Palmer 1994). Only by measuring each side at least twice can one demonstrate that the differences between sides reflect actual asymmetry, rather than measurement error. To reduce variability, all measurements were made by one researcher, and to eliminate potential measurement biases, the calipers were closed after each measurement. Repeatabilities ranged from 0.82 (right tarsus 2002) to 0.94 (left tarsus 2008). It was not practical to perform blind measurements.

*Statistical analysis.*—Palmer and Strobeck (2003) recommend removing outliers before analysis of FA takes place, because they can have a disproportionately large effect on the analysis of symmetry and likely result from large measurement errors, recording errors, or injury rather than true FA (but see Leung and Forbes 1997). Grubb's test (Palmer and Strobeck 2003; see Acknowledgments) identified two significant tarsus FA outliers, one in 2002 ($P < 0.01$) and one in 2008 ($P < 0.01$). No outliers were present for 2007 tarsus and 2002 toe. Multiple traits were studied in 2002 (tarsus and toe), and the outlier remains significant with a sequential Bonferroni correction for multiple comparisons (Rice 1989, Palmer 1994, Palmer and Strobeck 2003). These two outliers are excluded from all subsequent analyses involving tarsus length and FA. (Excluding these outliers does not introduce any bias in favor of the predicted patterns. Keeping the outliers in would have increased mean tarsus FA for C-chicks in 2008 and increased the apparent difference between A-chicks from two- and three-egg clutches in 2002.)

The presence of significant FA (FA > measurement error) was determined using an Excel template (available online; see Acknowledgments) and is demonstrated by a significant *F*-test for a sides × individuals interaction in a mixed-model analysis of variance (ANOVA; Palmer and Strobeck 1986, 2003; Palmer 1994). Directional asymmetry (DA) is indicated by a significant effect of sides in the ANOVA model. This template also indicates whether significant skewness or kurtosis is present. When more than one trait was measured in a year (2002: tarsus and toe), *P* values were adjusted by the sequential Bonferroni correction for multiple comparisons (Rice 1989, Palmer 1994, Palmer and Strobeck 2003).

Significant DA was present in toe length and in 2008 tarsus length (see below). To ensure that statistical tests compared FA and were not biased by directional differences between sides, the following correction was made: [mean (right – left)]/2 was subtracted from the larger side and added to the smaller side (Palmer 1994). Although there was no significant directional bias in tarsus length in 2002 and 2007, the same correction was made for consistency and because the directional trends, though slight, were in the same direction as in 2008.

For analysis of variation in FA, trait size, and body mass with hatching order and clutch size, chicks were divided into the following categories: A-chick from three-egg clutch, A-chick from two-egg clutch, B-chick from three-egg clutch, B-chick from two-egg clutch, C-chick, and singleton. Additional analyses were performed on the basis of hatching order alone, combining A-chicks from two- and three-egg clutches and doing the same for B-chicks. Only categories with at least five chicks in a given year were included in the analyses (sample sizes for included groups are given below; see Table 1). Unsigned asymmetry values (absolute values of right – left) are used in all comparisons.

Table 1. Trait size and body mass (means ± SE) across chick categories (see text for definitions of categories).

| Chick category | Tarsus length (mm) | | *n* | Toe length (mm) | | *n* |
|---|---|---|---|---|---|---|
| **2002** | | | | | | |
| A2 | 10.27 ± 0.11 | | 25 | 11.01 ± 0.13 | | 26 |
| A3 | 10.37 ± 0.11 | | 21 | 11.05 ± 0.14 | | 21 |
|   A | 10.31 ± 0.08 | | 46 | 11.03 ± 0.10 | | 47 |
| B2 | 10.38 ± 0.11 | | 19 | 11.05 ± 0.14 | | 19 |
| B3 | 10.37 ± 0.14 | | 19 | 10.73 ± 0.20 | | 19 |
|   B | 10.38 ± 0.09 | | 38 | 10.89 ± 0.12 | | 38 |
| C3 | 10.19 ± 0.12 | | 18 | 10.51 ± 0.16 | | 18 |
| Comparison | *F* | df | *P* | *F* | df | *P* |
| All categories | 0.95 | 4 and 77.8 | 0.44 | 3.42 | 4 and 76.1 | 0.013 |
| A vs. B vs. C | 1.73 | 2 and 66.7 | 0.18 | 4.33 | 2 and 62.2 | 0.017 |
| Chick category | Tarsus length (mm) | | *n* | Body mass (g) | | *n* |
| **2007** | | | | | | |
| A2 | 10.44 ± 0.13 | | 13 | 13.31 ± 0.33 | | 13 |
|   A | 10.36 ± 0.12 | | 16 | 13.38 ± 0.29 | | 16 |
| B2 | 10.43 ± 0.06 | | 13 | 12.31 ± 0.29 | | 13 |
|   B | 10.41 ± 0.06 | | 14 | 12.29 ± 0.27 | | 14 |
| Comparison | *F* | df | *P* | *F* | df | *P* |
| A2 vs. B2 | 0.22 | 1 and 23.0 | 0.65 | 9.90 | 1 and 16.7 | 0.006 |
| A vs. B | 0.13 | 1 and 27.0 | 0.73 | 10.09 | 1 and 19.1 | 0.005 |
| Chick category | Tarsus length (mm) | | *n* | Body mass (g) | | *n* |
| **2008** | | | | | | |
| A2 | 10.40 ± 0.09 | | 28 | 14.43 ± 0.34 | | 28 |
| A3 | 10.60 ± 0.11 | | 20 | 15.05 ± 0.43 | | 20 |
|   A | 10.48 ± 0.07 | | 48 | 14.69 ± 0.27 | | 48 |
| B2 | 10.33 ± 0.10 | | 19 | 13.90 ± 0.37 | | 19 |
| B3 | 10.44 ± 0.13 | | 19 | 14.95 ± 0.47 | | 19 |
|   B | 10.38 ± 0.08 | | 38 | 14.42 ± 0.31 | | 38 |
| C3 | 10.47 ± 0.13 | | 15 | 13.56 ± 0.49 | | 16 |
| S | 10.58 ± 0.24 | | 5 | 16.40 ± 0.98 | | 5 |
| Comparison | *F* | df | *P* | *F* | df | *P* |
| All categories | 0.74 | 5 and 90.4 | 0.60 | 2.63 | 5 and 99 | 0.028 |
| A vs. B vs. C vs. S | 0.43 | 3 and 85.7 | 0.73 | 2.81 | 3 and 101 | 0.043 |

Note: Results of *F*-tests are from linear mixed models with date as a covariate and nest included as a random factor. Only means for groups included in the analyses are shown above ($n \geq 5$).

Because colony censuses were not performed daily, it is possible that some nests that I have labeled as one- or two-egg clutches were actually larger clutches that lost an egg before the nest was marked (Nisbet 2002). Hatching-order comparisons also are affected if, for example, the first egg laid in a nest is lost. These problems, which are widespread in field research, should only make it less likely that differences based on clutch size and hatching order would be detected (i.e., increased type II error) and, thus, should not have led to any spurious findings (Type I error) (Wrege and Emlen 2005).

When testing for variation among chick categories, *F*-tests were performed using linear mixed models in SPSS, version 12.0 (SPSS, Chicago, Illinois), with hatching date of the A-chick as a covariate. Nest was included as a random factor in these models to control for the presence of chicks from the same nest and, thus, to avoid pseudoreplication. If variation among chick categories was statistically significant, multiple comparisons among groups were performed with Fisher's protected least significant difference (PLSD) test. All tests are two-tailed.

## Results

*Tarsus asymmetry.*—Fluctuating asymmetry in tarsus length exceeded measurement error in all three years: the sides * individuals interactions were highly significant (2002: $F = 3.67$, df = 103 and 208, $P < 0.0001$; 2007: $F = 4.11$, df = 34 and 70, $P < 0.0001$; 2008: $F = 4.47$, df = 107 and 216, $P < 0.0001$). (Results for toe FA are described below.) Except for small but significant DA in 2008 (right > left), the distributions were normally distributed, with a mean of approximately zero. The mean difference (± SE) between right and left tarsi (signed asymmetry) was 0.022 ± 0.046 mm in 2002 ($n$ = 104), 0.026 ± 0.046 mm in 2007 ($n$ = 35), and 0.093 ± 0.026 mm in 2008 ($n$ = 108). The mean absolute value of the difference between right and left tarsi (unsigned asymmetry) was 0.385 ± 0.025 mm in 2002, 0.211 ± 0.028 mm in 2007, and 0.222 ± 0.018 mm in 2008. All subsequent analyses use unsigned FA values corrected for DA. The differences between sides reported here comprise 3.7% of mean tarsus length in 2002, 2.0% in 2007, and 2.1% in 2008.

To compare among years, the following variables were included in a linear mixed model: year (2002, 2008) and chick category (A-chick from three-egg clutch, A-chick from two-egg clutch, B-chick from three-egg clutch, B-chick from two-egg clutch, C-chick), with date included as a covariate and nest as a random factor. (Hereafter, the chick categories are abbreviated A3, A2, B3, B2, and C3, respectively.) Because of the small number of chicks measured in 2007, only 2002 and 2008 data are included here. Singletons (S) are excluded, because only two singletons were measured in 2002. The analysis showed highly significant effects of chick category, year, and date, with no significant category * year interaction (Table 2). Nest dropped out of the model. Because of the difference among years, data from each year are treated separately when comparing among chick categories. Singletons are included only for 2008 in all analyses below.

Chick category showed significant variation among groups in 2008 ($F = 3.35$, df = 5 and 99, $P = 0.008$; Fig. 1) but was not quite statistically significant in 2002 ($F = 2.40$, df = 4 and 47.6, $P = 0.063$; the non-integer degrees of freedom here and below result from the presence of nest as a random factor in the model; Fig. 1). There was

Table 2. Linear mixed model testing for variation in fluctuating asymmetry of tarsi of Common Tern chicks with year (2002, 2008) and chick category (A2, A3, B2, B3, C3), with date as a covariate.

| | *F* | df | *P* |
|---|---|---|---|
| Year | 39.64 | 1 and 192 | <0.0001 |
| Category | 4.37 | 4 and 192 | 0.002 |
| Category * year | 0.90 | 4 and 192 | 0.47 |
| Date | 8.21 | 1 and 192 | 0.005 |

a significant effect of date in both years (2002: $F = 5.80$, df = 1 and 94.5, $P = 0.018$; 2008: $F = 6.16$, df = 1 and 99, $P = 0.015$) and of nest in 2002 (Wald $Z = 2.92$, $P = 0.003$). Nest dropped out of the model in 2008. The following significant differences were present in comparisons among chick categories in 2008: A3-chicks had significantly lower FA than A2, B3, C3, and S, and B2 was significantly

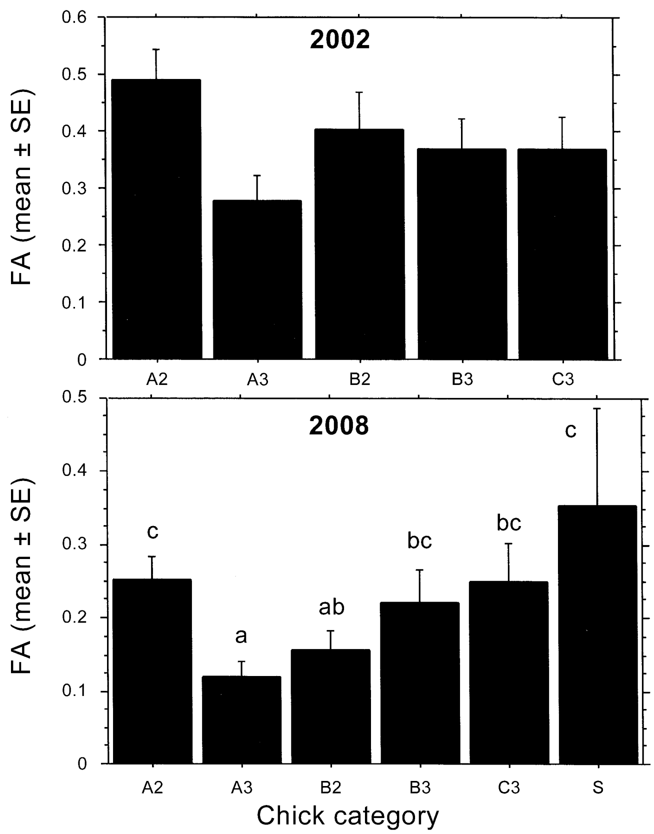


Fig. 1. Variation in fluctuating asymmetry (FA; given as means ± SE unsigned asymmetry) across Common Tern chick categories is shown for 2002 and 2008. Letters along the *x*-axis represent chick categories: A2 = A-chick from two-egg clutch, A3 = A-chick from three-egg clutch, B2 = B-chick from two-egg clutch, B3 = B-chick from three-egg clutch, C3 = C-chick, and S = singleton. Singletons are excluded in 2002 because only two were measured. Sample sizes are given in Table 1. Letters above the bars indicate statistical significance: categories that do not share a letter are significantly different (Fisher's PLSD test, following a significant *F*-test in a linear mixed model with date as a covariate and nest as a random variable).

more symmetrical than S and A2 (Fig. 1). A3-chicks also appeared to have the lowest FA in 2002 (Fig. 1).

Results for hatching order were similar when comparisons were made within nests (among pairs of siblings) rather than across the colony, although the sample sizes were much smaller. For example, A3-chicks had significantly lower FA than their C3 siblings in 2008, and the effect size was very large (mean difference in unsigned FA = 0.15; paired *t*-test, $t = 2.35$, df = 9, $P = 0.043$, Cohen's $d = 1.03$), whereas in 2002 the difference was nearly significant and the effect size was moderate (mean difference = 0.13, $t = 2.03$, df = 9, $P = 0.073$, Cohen's $d = 0.72$).

For 2007, the only meaningful comparison that can be made among categories is between A- and B-chicks from two-egg clutches (both $n = 13$; all other categories $n < 5$). These two categories did not differ in tarsus FA (A2: 0.186 ± 0.055 mm, B2: 0.198 ± 0.032 mm; $F = 0.35$, df = 1 and 4.2, $P = 0.59$). As in 2008, singletons were the category with the numerically highest mean FA (0.287 ± 0.080 mm, $n = 4$). There was no significant effect of date or nest in 2007 (date: $F = 2.27$, df = 1 and 19.5, $P = 0.15$; nest: Wald $Z = 1.32$, $P = 0.19$).

Fluctuating asymmetry did not vary significantly if clutch size was ignored and A- and B-chicks from two- and three- egg clutches were combined. With date as a covariate and nest included as a random factor, the following results occurred for hatching order: 2002 (A vs. B vs. C), $F = 1.70$, df = 2 and 32.8, $P = 0.20$; 2007 (A vs. B), $F = 0.45$, df = 1 and 5.5, $P = 0.53$; 2008 (A vs. B vs. C vs. S), $F = 1.79$, df = 3 and 101, $P = 0.15$.

*Toe asymmetry.*—Significant FA and DA were present in toe length in 2002, the one year that toe length was measured (sides * individuals: $F = 3.83$, df = 104 and 210, $P < 0.0001$; sides: $F = 5.61$, df = 1 and 208, $P = 0.039$). The mean difference between right and left toes was −0.108 ± 0.047 mm (left > right), and mean unsigned asymmetry was 0.394 ± 0.029 mm, corresponding to 3.6% of mean toe length. Toe FA did not vary significantly across chick categories ($F = 1.29$, df = 4 and 97, $P = 0.28$). There also was no significant variation in toe FA among A-, B-, and C-chicks regardless of clutch size ($F = 0.29$, df = 2 and 99, $P = 0.59$) or when comparing A-chicks and C-chicks within nests (mean difference = −0.053, paired $t = 0.047$, df = 9, $P = 0.65$, Cohen's $d = -0.20$).

*Trait size and body size.*—There was no significant variation in tarsus length in any year, whether comparing across categories or comparing across ranks, regardless of clutch size (Table 1). Toe size varied (Table 1), in that C-chicks had significantly shorter toes than A3-, A2-, and B2-chicks. There was no relationship between FA and trait size in any year (Spearman rank correlations, all $r_s < 0.1$, all $P > 0.45$) and no relationship between tarsus FA and body mass (2007: $r_s = 0.17$, $Z = 1.02$, $P = 0.31$; 2008: $r_s = -0.16$, $Z = -1.61$, $P = 0.11$).

Body mass in 2008 varied among chick categories, with singletons significantly heavier than all but A3 and B3, and A3 significantly heavier than C3 (Table 1). When combining A- and B-chicks from two- and three-egg clutches (A vs. B vs. C vs. S), variation in body mass remained significant, with singletons significantly heavier than B- and C-chicks (Table 1). In 2007, A-chicks were significantly heavier than B-chicks (Table 1). Singletons (excluded from analysis) tended to be heavy (13.75 ± 0.25 g, $n = 4$; compare Table 1). (Only one C-chick was measured in 2007; body mass was not measured in 2002.)

## Discussion

Tarsus FA in newly hatched Common Tern chicks varied with both hatching order and clutch size. In 2008, A-chicks from three-egg clutches were significantly more symmetrical than B- and C-chicks from three-egg clutches, A-chicks from two-egg clutches, and singletons, as predicted. A-chicks from three-egg clutches also appeared to have the lowest FA among categories in 2002 (see Fig. 1), but variation among chick categories was not quite statistically significant ($P = 0.063$). Unfortunately, there were too few singletons, the category that tended to have the highest FA, present in 2002 to include in the analysis. The observed differences in tarsus FA likely reflect underlying differences in developmental stability as a result of stress during development: A-chicks hatch first and typically come from larger eggs than their siblings (reviewed in Nisbet 2002, Becker and Ludwigs 2004), and, therefore, development should proceed with less stress. Because clutch size is associated with parental quality (Coulson and Porter 1985), an A-chick from a three-egg clutch benefits both from the ideal hatching order and from high-quality parents.

However, not all the results matched predictions. C-chicks did not have significantly elevated FA compared with B-chicks. In addition, A-chicks from two-egg clutches had higher FA than expected, compared with other categories, in both 2002 and 2008 (see Fig. 1). Why that would be the case is unclear. This unexpected result may be spurious, given that A-chicks from two-egg clutches did not have elevated FA in 2007. Unlike tarsus FA, there was no significant variation in toe FA among groups, but it is common for a relationship with FA to be evident in some traits and not others (Bjorksten et al. 2000, Lens et al. 2002).

Directional asymmetry, which was present in toe length and tarsus length for one of three years, complicates interpretation of patterns in FA (Palmer and Strobeck 1986, 2003; Palmer 1994; Graham et al. 1998). Although most authors have avoided studying FA in traits exhibiting DA or have statistically removed DA, as I have done here, some have suggested that DA can also be used as an indicator of developmental stability (Graham et al. 1998, Cuervo and Restrepo 2007). Tarsus DA has been previously reported in some species (Cadée 2000, Brown and Brown 2002, Cuervo and Restrepo 2007) but not in others (Carbonell and Tellería 1998, Eeva et al. 2000, Cuervo and Restrepo 2007). Kellner and Alford (2003) found that DA was present in newly hatched Domestic Chickens (*Gallus gallus domesticus*) but disappeared within a few days of hatching. Whether the directional differences between sides reported here for newly hatched Common Terns reflect true DA or a slight directional bias due to researcher handedness (Cadée 2000, Helm and Albrecht 2000, Brown and Brown 2002) is unknown. Although statistically significant, the observed DA was very small, with one side measured as ~0.1 mm larger than the other. According to Palmer and Strobeck (2003), if mean (right − left) is smaller in magnitude than $0.798\sqrt{(\text{variance in right} - \text{left})}$, then the directional difference between sides is less than the average deviation around (right − left); in other words, DA is less than FA. That is the case here: 2008 mean tarsus right − left = 0.093 mm, $0.798\sqrt{(\text{variance in right} - \text{left})} = 0.220$; 2002 mean toe right − left = −0.108 mm, $0.798\sqrt{(\text{variance in right} - \text{left})} = 0.384$. Because FA was greater than DA and any small directional bias was factored out before making comparisons, the patterns found represent variation attributable only to FA and should reflect differences in developmental stability.

A large difference between years was present in the magnitude of tarsus FA, with FA significantly lower in 2008 than in 2002. Although survival to fledging was not rigorously studied, 2008 appeared to be an unusually good year at this site. In 2008, only 15 of 169 banded chicks (8.9%) were later found dead, compared with 62 of 220 (28.2%) in 2002 (2 × 2 contingency chi-square with continuity correction: $\chi^2 = 21.242$, df = 1, $P < 0.0001$), or 19.8% excluding 23 chicks whose deaths could be directly attributed to a storm ($\chi^2 = 10.850$, df = 1, $P = 0.0010$). It is therefore possible that the difference among years reflects an ecological difference, such as in food availability.

Breeding success in terns is typically higher among pairs that nest early (Burger et al. 1996; Arnold et al. 2004, 2006), and late nests mainly include a mixture of nests from young parents and renesting parents that lost nests early in the breeding season (Nisbet and Cohen 1975, Nisbet et al. 1984, Wendeln et al. 2000, Nisbet 2002, Arnold et al. 2004). Because of the associations between laying date, parental quality, and breeding success, I have included date as a covariate in the analyses (with hatching date of the A-chick as a proxy for laying date). Although date emerged as a significant covariate, examination of scattergrams and weekly means revealed no consistent pattern throughout the breeding season (data not shown), with one exception: there was a surprising trend for chicks from late nests to have relatively low FA in both 2002 and 2008, and FA was also low in 2007, when most data came after a flood. If this pattern is real, it adds support to evidence that replacement clutches tend to be produced by high-quality parents (Wendeln et al. 2000) and fits with data on parental behavior from 2002 (and 2001) at the same site (Palestis 2005). In 2008, few replacement clutches were present, because few nests were lost to flooding. If late nests were excluded from analysis, the variation in FA among chick categories followed the same patterns and remained significant ($F = 2.81$, df = 5 and 68, $P = 0.023$).

In addition to comparisons of FA among chicks, trait size and body mass were analyzed. The means for body mass reported here are similar to those reported previously for newly hatched Common Terns (Nisbet 2002, Becker and Ludwigs 2004), but the tarsus lengths are smaller than reported by Cymborowski and Szulc-Olechowa (1967), because I did not include the entire length of the tarsometatarsus. Toe length has not been reported elsewhere. Fluctuating asymmetry was not associated with trait size or body mass, although there was variation in toe size (but not tarsus size) and body mass with hatching order. C-chicks had significantly shorter toes than A- and B-chicks and were significantly lighter than A-chicks from three-egg clutches and singletons. A-chicks were also significantly heavier than B-chicks in one year, and singletons were significantly heavier than all but A- and B-chicks from three-egg clutches in another year.

The chicks studied were all within a day of hatching, to control for changes in FA with growth; therefore, sibling competition for food had not yet had a large effect. As Common Tern chicks age, C-chicks are consistently out-competed by their siblings and suffer high early mortality (Langham 1972, Nisbet 1973, Becker and Finck 1985, Bollinger et al. 1990, Bollinger 1994). In addition, parental quality has a large influence on chick growth and survival (Nisbet 1978, Bollinger 1994, Wendeln and Becker 1999, Arnold et al. 2004). The results presented here suggest that subtle differences among chicks are present very early in life because of differing levels of stress during development and small differences in initial body size. These subtle differences must contribute to the large differences in growth and survival that occur after hatching. It would be interesting to determine how fluctuating asymmetry changes as tern chicks age and whether the patterns observed vary with the fate of the chicks.


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