Research article

Age-related differences in nest defense in common terns: Relationship to other life-history parameters

Jennifer Pearson¹, Ian C. T. Nisbet² & Mary Ann Ottinger^{1,*}

¹Department of Animal and Avian Sciences, University of Maryland, 3115 Animal Science Building, College Park, MD 20742, USA; ²I.C.T. Nisbet and Company, 150 Alder Lane, North Falmouth, MA 02556, USA

*Author for correspondence (e-mail: maotting@umd.edu; fax: +1-301-314-9059)

Received 1 October 2005; accepted in revised form 4 November 2005

Key words: age, chick growth, common tern, nest defense, productivity, seabird

Abstract

The Common Tern (*Sterna hirundo*) is a long-lived colonial nesting seabird. Previous studies have shown that chick growth and fledging success vary with age of the parental pair and with laying date, with older parents and those nesting earlier being more successful. This study investigated the dependence of breeding performance and one aspect of behavior, defense against conspecifics, on age and laying date. Nest defense behavior was evaluated by recording individual responses to a mirror placed 20 cm from the nest, simulating an unfamiliar intruder within the territory. Most study birds were of known age (3–21 years) from banding as chicks; they were divided into three groups: ≥ 12 , 8–11 and $\leq$ seven years. Responses to the mirror were examined during incubation and at the time of hatching. Older birds nested earlier than younger birds. Chicks reared by older parents gained mass more quickly and survived better than chicks of younger parents. Using a composite score reflecting both the intensity and duration of aggressive responses to the mirror, older birds responded more strongly than younger birds during incubation, but responses were similar at the time of hatching. Older birds reduced their aggressive responses between incubation and hatching, while younger birds increased their responses. We suggest that this contributes to the greater success of older birds, because younger birds expend more time and energy on territorial defense at a time when they need to feed chicks. Our findings are consistent with previous studies and show that Common Tern colonies are finely structured by age and laying date; older and earlier-nesting birds are superior to younger and later birds on several measures of performance. This study suggests that finely-tuned nest defense behavior is one component of the superior performance of old birds.

Introduction

The Common Tern (*Sterna hirundo*) is a particularly interesting subject for examining both the characteristics of long-lived species and some of the life-history strategies exploited for their success (Nisbet 2001, 2002; Nisbet et al. 2002; Haussmann et al. 2003; Apanius and Nisbet 2005). The Common Tern is a small (120 g), socially monogamous seabird that nests in large colonies; each pair must secure its one to three chicks in a limited territory and supply the

chick(s) with sufficient food for rapid growth and maturation. In order for an individual bird to maximize reproductive success, many different tasks such as territory acquisition, territorial defense, and chick rearing must be successfully completed. Several studies have shown that reproductive success varies strongly with the age of the parents (reviewed in Nisbet 2002; Becker and Ludwigs 2004). Mating is strongly age-assortative, older birds usually being mated together (Nisbet et al. 1984; González-Solís et al. 1999; Bridge and Nisbet 2004). Older pairs nest

earlier and occupy the prime nesting sites while younger pairs nest in less desirable sites (Nisbet et al. 1984). Older pairs are more efficient in foraging for their chicks, bringing more food per unit time without expending more energy (Galbraith et al. 1999), and older birds raise more young to fledging in better condition than young birds, even after controlling for differences in laying date (Nisbet et al. 2002). These changes are most rapid in the first few years of breeding (2–6 years), but increases in foraging efficiency continue until about age 12 years (Galbraith et al. 1999) and increases in productivity until the end of the life span at ages 18–23 years (Nisbet et al. 2002; Tims et al. 2004). However, the specific basis for the age-related changes in reproductive success has not been thoroughly delineated. Generally, this species provides an excellent model for the study of a long-lived avian species and investigations of lifetime physiology and reproductive strategies adopted by such species (Apanius and Nisbet 2003; 2005).

This paper reports on a study of one behavioral component of reproductive success in Common Terns: nest defense against conspecifics. Meehan and Nisbet (2002) reported that nest tenacity (defined as the speed of return to the nest after exposure to a model predator) increased with parental age, but was much more strongly related to early laying. We have found no previous studies of age-related changes in nest defense behavior of Common Terns towards conspecifics.

Common Terns often nest at high densities and expend considerable time and effort in defending their territories against conspecific intruders, both at the time of territory establishment and during chick-rearing (reviews in Nisbet 2002; Becker and Ludwigs 2004). Territorial defense involves the defense of an established territory plus the protection of the eggs and the chicks. However, if the parent spends too much time defending the territory, this limits the time that can be spent foraging (Montgomerie and Weatherhead 1988). In order to effectively defend a territory it is essential that the territory holder accurately determine an intruder's identity and intentions and respond appropriately. Many factors have been found to play a role in determining the response of a territory holder to an intruder. One of the key factors is the type of intruder. Research in other species has shown that territory holders respond differently towards neighbors than non-neighbors (Wunderle 1978; Butler and James-Butler

1982; Dulude et al. 1989; Temeles 1990; Temeles 1994). The 'dear enemy' hypothesis developed by Fisher (1954) explains differences in response based on intruder type, specifically, that neighboring birds are more familiar with each other than with strangers and it is this familiarity which results in lower aggression towards neighbors.

Territorial responses also depend on the stage in the breeding cycle. Early in the breeding season, as territorial boundaries are being established, males exhibit increased aggression (Pierotti 1981). Many studies have also found a peak in aggression around hatching (Burger 1983). It is believed that this increase in aggression is likely to be a mechanism to protect the chicks. Finally, age has been shown to influence territorial defense. In some species, older birds more frequently engage in territorial defense (Pugesek 1983).

Based on this information, this study was designed to examine nest defense behavior in Common Terns and its relationship to parental age, laying date and breeding success.

Materials and methods

Study site

Studies were conducted in 1994 and 1995 on Bird Island in Buzzards Bay, Massachusetts (41°40' N, 70°43' W). Bird Island then supported about 1,800 pairs of Common Terns and about 1,200 pairs of Roseate Terns (*Sterna dougallii*). Common Terns nested on varied substrates of sand, shell and cobbles with scattered vegetation that became locally dense during the chick-rearing period. The mean nest density was about 0.7 nests m⁻², corresponding to a mean nest spacing of about 68 cm, which is unusually dense for the species (Nisbet 2002). Daily checks of the breeding area were conducted to establish the date of clutch initiation and the laying order within each clutch. Each new nest was marked with a numbered marker and each new egg was marked with a permanent marker to distinguish laying order within the clutch. The date on which the first egg was laid is referred to as the 'laying date' for that clutch and pair.

As a result of long-term banding of adults and chicks at this site, over 60% of the birds were banded and over 40% were of known age. Adults were

trapped in treadle traps placed over the nest, measured, weighed, and marked with a spot of color on the cheek to distinguish male from female within each pair. Ages of previously-banded birds were determined from banding records. Sexes were determined from the presence or absence of a palpable egg in the oviduct of birds trapped during egg-laying, or by measurement of culmen length or total head length in both members of a pair (Nisbet 2002; Nisbet and Cam 2002); pairs in which both members were in the overlapping parts of the distribution for head length were excluded from the study.

Chick growth and productivity

Chicks were banded on the day of hatching (day 0), marked with a spot of color for individual identification within the brood, and weighed daily thereafter. Study plots were enclosed within low wire fences to facilitate locating chicks on each visit. Most chicks were followed until they were ready to fledge at ages 22–27 days; some late chicks that could not be followed to fledging were considered fledged if they survived through day 10 and were gaining weight when last encountered. Productivity is defined as the number of chicks raised to fledging by each pair.

Nest defense behavior

Sex-related differences in nest defense behavior were examined at the time of hatching (from 1 day before to three days after the hatching of the first chick in the brood). Mirrors were used to simulate an unfamiliar intruder entering the study bird's territory. These observations took place in two steps, with each bird serving as its own control. The focal bird was first observed with no alterations to its environment for a period of 5 min, and then exposed to its reflection in a vertical mirror (30 cm × 30 cm) placed 20 cm from the center of its nest. The distance of 20 cm was selected based on a pilot study to maximize the variability in responses; it corresponded to an unfamiliar intruder appearing 40 cm from the focal bird and behaving reciprocally. The response of each focal bird to the mirror was observed for 5 min. The mirror was positioned based on the orientation of the sitting bird. If no response to the mirror occurred during the exposure, the mirror was rotated to the opposite side of the territory and the exposure was repeated. If during any stage in the

observation, the mate of the study bird returned, the exposure was stopped. Twenty-one males and 12 females, including 11 pairs, were studied in this part of the experiment.

Age-related differences in nest defense behavior were studied using 53 males early in incubation and 50 males at hatching. Study males ranged in age from 3 to 21 years and were divided into three age categories: ≥ 12 , 8–11 and $\leq$ seven years. Six birds that were of unknown age but had been banded as breeding adults eight or more years earlier are included in the ≥ 12 years group. Five birds that were of unknown age but were mated to birds three to four years old were included in the $\leq$ seven years group, based on previous data on age-assortative mating (Nisbet et al. 1984). Observations with the mirror were completed in three stages, again with each bird serving as its own control. The focal bird was first observed with no alterations to its environment for a period of 5 min (control), then (sham control) to a covered mirror 20 cm from the center of its nest for 2.5 min, then (experimental) to the uncovered mirror for 5 min. For each stage, the response of the bird was recorded beginning when the study bird returned to the nest site. Observing the males at chick hatching was difficult because many of the females were at the nest. Therefore, some females were trapped and held until exposure of the male to the mirror was completed.

Measures of response

The response of each bird was recorded on two scales: intensity and duration. Intensity was scored as follows: 0, no response; 1, vocal response without body movement; 2, threat call with extended neck or other body movement; 3, crouch display or slight contact with mirror; 4, physical attack. Responses 1 and 3 were infrequent, so for most analyses responses 1–3 were grouped as 'intermediate' responses. Duration was scored as the number of 30 s intervals (up to 5 min) in which the bird gave a response. The product intensity * duration was used as a composite measure of response.

Statistical analysis

Statistical analysis was conducted using SAS[®] (1996) and STATISTICA[™] (Stasoft Inc. 2001) software. Spearman rank correlation coefficients (r_s)

Figure 1. Correlation between male age and laying date. As males age, they nest significantly earlier in the breeding season ($r = -0.497$, $n = 63$, $P < 0.0001$). The laying date is shown as the number of days laid after the first nest was found (12 May).

were used to test the relation between parental age and laying date. Pearson correlation coefficients (r) were used to test the relation between chick growth rate and laying date. Sex- and age-related differences in intensity and duration of response to the mirror were analyzed using Fisher's exact tests. Age-related differences in composite response scores were analyzed using analysis of variance (ANOVA), except that changes in composite scores within individuals were analyzed using a Kruskal–Wallis test because of small sample sizes. Analysis of covariance (ANCOVA) was used to analyze the dependence of changes in composite scores on age and laying date simultaneously.

Table 1. Sex-related differences in the intensity of response to the mirror at hatching.

Group	Physical attack (4)	Intermediate (1–3)	No response (0)
Male ($n = 21$)	7 (33%)	11 (52%)	3 (15%)
Female ($n = 12$)	1 (8%)	8 (67%)	3 (25%)

Table 2. Age-related differences in intensity of response to the mirror by males during incubation.

Age group	Physical attack (4)	Intermediate (1–3)	No response (0)
12+	8 (53%)	5 (33%)	2 (13%)
8 to 11	11 (44%)	8 (32%)	6 (24%)
7 and below	5 (38%)	3 (23%)	5 (38%)

Results

Correlation between age and laying date

As in previous studies of Common Terns at Bird Island and elsewhere (see Discussion), there was a negative correlation between parental age and laying date ($r_s = -0.497$, $n = 63$, $P < 0.0001$; Figure 1). Therefore, date of laying the first egg was used in some analyses as a surrogate measure of age as well as an index of the timing in the season.

Nest defense

No study birds exhibited aggressive behavior towards neighbors or intruders during the 5-min control periods, nor towards the covered mirror during the 2.5-min sham control periods. Table 1 compares the responses of males and females to the uncovered mirror at the time of hatching. More males than females responded with physical attacks, but the difference was not statistically significant (Fisher's exact test, $P = 0.12$). Intensity of male versus female response was compared in 11 pairs of birds. In seven pairs (64%) males and females responded similarly, and in three pairs (27%) males responded more intensely. Only one female exhibited relatively more intensity and this female was older than her mate.

Table 3. Age-related differences in duration of response to the mirror by males during incubation.

Age Group	4–5 min	0.5–3.5 min	≤1 min
12+	5 (38%)	3 (23%)	5 (38%)
8–11	1 (5%)	10 (55%)	7 (39%)
7 and below	1 (13%)	6 (75%)	1 (13%)

One bird included in Table 2 is not included in this table because the duration of response was not recorded precisely.

Table 4. Age-related differences in intensity of response to the mirror by males at hatching.

Age group	Physical attack (4)	Intermediate (1–3)	No response (0)
12+	6 (35%)	5 (29%)	6 (35%)
8 to 11	5 (33%)	1 (6%)	9 (60%)
7 and below	7 (38%)	1 (5%)	10 (55%)

Tables 2 and 3 summarize the intensity and durations of responses by males to the mirrors during incubation. There was a tendency for both the intensity and duration of responses to be greater in older males, but neither tendency was statistically significant (Fisher exact tests, $df = 2$, $P = 0.690$ and $P = 0.061$, respectively). However, the composite scores were significantly higher among older males (≥ 12 years: mean 16.7 ± 2.8 SD, $N = 15$; 8–11 years: mean 9.0 ± 2.2 , $N = 24$; $\leq$ seven years: mean 6.1 ± 3.0 , $N = 13$; ANOVA, $F_{2,49} = 3.87$, $P = 0.027$).

No age-related differences were observed in the intensity or duration of the response to the mirror at the time of hatching (Fisher's exact tests, $df = 2$, $P = 0.321$ and $P = 0.906$, respectively; Tables 4 and 5). Only 50% of the birds that were tested responded to the mirror. Nor were there significant differences in the composite response score (≥ 12 years: mean 10.5 ± 3.0 SD, $N = 17$; 8–11 years: mean 7.9 ± 3.3 , $N = 15$; $\leq$ seven years: mean 10.5 ± 3.1 , $N = 18$; ANOVA, $F_{2,47} = 0.27$, $P = 0.765$). However, there was a strong tendency for older birds to decrease their responses between incubation and hatching and for younger birds to increase their responses. Table 6 lists composite scores for 14 males that were tested at both periods. The differences among age groups in changes in composite scores were statistically significant (Kruskal–Wallis $\chi^2_2 = 7.78$, $P = 0.020$). The changes in composite scores were also strongly related to laying date ($r = 0.578$, $df = 12$, $P = 0.029$), but ANCOVA indicated that the relationship was primarily with age ($F_{2,10} = 4.36$, $P = 0.043$) and not with laying date ($F_{1,10} = 0.66$, $P = 0.435$).

Chick growth and productivity

Using the increase in body-mass between day 0 and day 4 as an index of early chick growth, significant negative correlations were found between laying date and mass gain in both A- and B-chicks (Figures 2

and 3; A-chicks: $r = -0.347$, $n = 33$, $P = 0.048$; B-chicks: $r = -0.417$, $n = 22$, $P = 0.05$). Chicks hatched early in the breeding season gained more weight than later chicks. Productivity (chicks raised per pair) was higher in early-nesting pairs (Figure 4), but the difference was only marginally significant ($\chi^2_1 = 3.11$, $P = 0.07$).

Discussion

This study has documented a negative correlation between parental age and laying date, and negative correlations between laying date and chick growth and probably productivity (Figures 1–5; see summary in Table 7). These correlations have been documented previously in Common Terns nesting on Bird Island (Nisbet et al. 1984, 2002; Galbraith et al. 1999; Arnold et al. 2004; Tims et al. 2004) and elsewhere (Hays 1978; Nisbet et al. 1984; Nisbet and Welton 1984; Wendeln 1997; Ludwigs and Becker 2002; González-Solís et al. 2004); see reviews by Nisbet (2002) and Becker and Ludwigs (2004). These and other studies have shown that Common Tern colonies are finely structured by both age and breeding date: older birds lay earlier than younger birds, pair with older mates, obtain better nest sites, feed their chicks more frequently, and raise more chicks to fledging in better condition; early-laying birds are older than later-laying birds, obtain better nest sites, feed their chicks more frequently, and raise more chicks to fledging in better condition. Attempts to separate the effects of laying date and age, either by experiment or by using multivariate statistical methods, have suggested that both are important: early-laying birds perform better regardless of age, but older birds perform better even after laying date is considered (Nisbet et al. 2002; Arnold et al. 2004; Tims et al. 2004). Structuring of colonies by age and laying date has been reported in several other colonial seabird species – e.g., the Black Legged Kittiwake (*Rissa tridactyla*: Coulson and Thomas

Table 5. Age-related differences in duration of response to the mirror by males at hatching.

Age Group	4–5 min	0.5–3.5 min	≤ 1 min
12+	5 (45%)	4 (36%)	2 (18%)
8–11 years	2 (33%)	3 (50%)	1 (16%)
7 & below	4 (50%)	3 (38%)	1 (12%)

Table 6. Individual changes in nest defense behavior during incubation and hatching. The composite score is the product of the intensity and duration scores.

Nest	Laying date (1 May = 1)	Group	Incubation: composite score	Hatching: composite score	Change
117	13	Old (≥ 12 years)	40	16	-24
274	15	Old (≥ 12 years)	40	8	-25
996	23	Old (≥ 12 years)	14	0	-14
1,061	23	Old (≥ 12 years)	20	0	-20
170	14	Intermediate (8–11 years)	8	8	+4
854	21	Intermediate (8–11 years)	0	0	0
875	21	Intermediate (8–11 years)	24	0	-24
716	19	Young (≤ 7 years)	5	0	-5
1,108	23	Young (≤ 7 years)	0	16	+16
1,128	24	Young (≤ 7 years)	20	28	+8
1,180	24	Young (≤ 7 years)	6	6	0
1,206	24	Young (≤ 7 years)	0	4	+4
1,263	25	Young (≤ 7 years)	8	40	+28
1,268	26	Young (≤ 7 years)	0	32	+32

1985) and the Great Skua (*Catharacta skua*; Hamer and Furness 1991) – and is probably characteristic of long-lived species in which breeding performance is influenced strongly by experience and individual

‘quality’ (Coulson 1968; Wendeln and Becker 1999). However, these phenomena have been documented and analyzed in more detail in Common Terns than in most other species.

Figure 2. Gain in body-mass for the B-chick between days 0 and 4. Mass gain was significantly correlated with laying date ($r = 0.417$, $n = 22$, $P < 0.05$).

Figure 3. Gain in body-mass for the A-chick between days 0 and 4. Mass gain was significantly correlated with laying date ($r = 0.347$, $n = 33$, $P = 0.04$).

Our study appears to be the first to investigate the relationship between nest defense behavior (versus conspecifics) and age. Using mirrors to simulate the intrusion of an unfamiliar conspecific into an established territory, we found that older birds gave stronger aggressive responses than younger birds during incubation, but that responses were similar at the time of hatching; older birds reduced their aggressive responses between incubation and hatching, but younger birds increased their aggression (Tables 2–6). Multivariate analysis indicated that this difference was primarily related to age *per se* rather than to the fact that older birds lay earlier. We suggest the hypothesis that this reduction in aggressive responses to intruders by older Common Terns may have contributed to their superior chick-raising ability. Under this hypothesis, a high level of aggression is required by older birds during incubation to prevent intruders from encroaching on their territories at the time when many other pairs are

Figure 4. Productivity (number of chicks surviving at least through day 10) for pairs nesting early (12–22 May; Group 1) and late (≥ 23 May; Group 2). The difference was marginally significant ($\chi^2 = 3.11$, $P = 0.07$). Bars represent 95% confidence limits.

Table 7. Summary of age-related differences in reproduction of Common Terns.

Factor	Old	Young
Laying date	Earlier	Later
Defense at incubation (unfamiliar intruder)	Higher	Lower
Defense at hatching (unfamiliar intruder)	Reduced	Increased
Chick weight gain ^a	Higher	Lower
Chick survival ^a	Higher	Lower

^aDocumented in this paper as variations with laying date; variations with age were reported by Tims et al. (2004).

attempting to establish their own territories. By the time the eggs of older birds are hatching, however, most pairs are already incubating, so that the threat of such encroachment is small and aggressive responses to intruders are less necessary. Under this hypothesis, the lower aggressive responses by younger birds early in incubation would reflect their failure to obtain high-quality territories (Nisbet et al. 1984), and their increased aggressive responses at the time of hatching would represent wasted effort. Alternatively, late-nesting pairs may need to maintain high levels of aggression through the period of hatching, because their own small chicks are usually surrounded by larger chicks and are at high risk of kleptoparasitism (Oswald et al. 2005). In either case, the increased territorial aggression displayed by younger males at the time of hatching would distract them from chick-feeding at the critical time when the males are required to bring food to the newly-hatched chicks (Galbraith et al. 1999). Additional studies (observational or experimental) are desirable to distinguish between the effects of age, laying date and experience in determining the trade-offs between territorial defense and parental care. It would also be interesting to investigate the hormonal basis of the changes in aggressive behavior.

Our observations are consistent with the ‘dear enemy’ hypothesis (Fisher 1954), in that the birds that we studied were much more aggressive towards the ‘unfamiliar intruder’ they saw in the mirror than they usually are to their established neighbors. However, this aggression was elicited only at very short ranges (40 cm), when the ‘unfamiliar intruder’ would have been perceived as within the owner’s territory. Moreover, the ‘unfamiliar intruders’ responded aggressively when threatened, whereas neighbors usually

retreat once territorial boundaries have been established early in the season. We suggest that the 'dear enemy' phenomenon in Common Terns may arise more from the behavior of the neighbors, who generally respect territorial boundaries and retreat when threatened, than from targeted reduction in aggression towards familiar individuals.

In conclusion, the results of our study conform to and extend the results of several other studies which show that Common Tern colonies are finely structured by age and laying date. Older and earlier-laying Common Terns are superior to younger and later-laying birds in many aspects of breeding performance. Our study suggests that nest defense behavior is one of the elements that contribute to parental performance: specifically, that older birds fine-tune their aggressive behavior so that it is high when territorial defense is most needed, and is reduced when the birds need to switch to chick-feeding; younger birds do the opposite.

References

- Apanius V and Nisbet ICT (2005) Serum immunoglobulin G levels are positively related to reproductive performance in a long-lived seabird, the common tern *Sterna hirundo*. *Oecologia* (published online Oct. 2005)
- Arnold JM, Hatch JJ and Nisbet ICT (2004) Seasonal declines in reproductive success of the Common Tern: timing or parental quality? *J Avian Biol* 35: 33–45
- Becker PH and Ludwigs, J-D (2004). *Sterna hirundo* common tern. *BWP Updat* 6: 91–137
- Bridge ES and Nisbet ICT (2004) Wing-molt and assortative mating in Common Terns: a test of the molt-signaling hypothesis. *Condor* 106: 336–343
- Burger J (1983) Competition between two species of nesting gulls: On the importance of timing. *Behav Neurosci* 97(3): 492–501
- Butler RG and James-Butler S (1982) Territoriality and behavioral correlates of reproductive success of Great Black-backed Gulls. *Auk* 99: 58–66
- Coulson JC (1968) Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature* 217: 478–479
- Coulson JC and Thomas CS (1985) Differences in the breeding performance of individual Kittiwake Gulls (*Rissa tridactyla*). In: Sibly RM and Smith RH (eds) *Behavioural Ecology*, pp. 489–503. Blackwell Scientific Publications, Oxford
- Dulude A-M, Baron G and McNeil R (1989) Influence of the type of territorial intruder on the aggressive response of Ring-billed Gulls. *Can J Zool* 67: 1249–1256
- Fisher J (1954) Evolution of bird sociality. In: Huxley J, Hardy AC and Ford EB (eds) *Evolution as a Process*, 367 pp. Allen & Unwin, London
- Galbraith H, Hatch JJ, Nisbet ICT, and Kunz TW (1999) Age-specific reproductive efficiency among Common Terns: measurement of energy expenditure using doubly-labelled water. *J Avian Biol* 30: 85–96
- González-Solís J, Wendeln H and Becker PH (1999) Within and between nest-site and mate fidelity in Common Terns (*Sterna hirundo*). *J Ornithol* 140: 491–498
- González-Solís J, Becker PH, Jover L and Ruiz, X (2004) Individual changes underlie age-specific pattern of laying date and egg-size in female Common Terns (*Sterna hirundo*). *J Ornithol* 145: 129–136
- Hamer KC and Furness RW (1991) Age-specific breeding performance and reproductive effort in Great Skuas *Catharacta skua*. *J Anim Ecol* 60: 693–704
- Haussmann MF, Winkler DW, O'Reilly KM, Huntington CE, Nisbet ICT and Vleck CM (2003) Telomeres shorten more slowly in long-lived birds and mammals than in short-lived ones. *Proc R Soc Lond B* 270: 1387–1392
- Hays H (1978) Timing and breeding success in three- to seven-year-old Common Terns. *Ibis* 120: 127–129
- Ludwigs J-D and Becker PH (2002) The hurdle of recruitment: influences of arrival date, colony experience and sex in the Common Tern *Sterna hirundo*. *Ardea* 90: 389–399
- Meehan TD and Nisbet ICT (2002) Nest tenacity in Common Terns (*Sterna hirundo*) threatened by a model predator. *Waterbirds* 25: 278–284
- Nisbet ICT (2001) Detecting and measuring senescence in wild birds: experience with long-lived seabirds. *Exp Gerontol* 36: 833–834
- Nisbet ICT (2002) Common Tern *Sterna hirundo*. In: Poole A and Gill F (eds) *The Birds of North America*, No 618. The Birds of North America, Inc., Philadelphia, PA
- Nisbet ICT and Welton M (1984) Seasonal variations in breeding success of Common Terns: consequences of predation. *Colon Waterbirds* 86: 53–60
- Nisbet ICT, Winchell JM and Heise AE (1984) Influence of age on the breeding biology of Common Terns. *Colon Waterbirds* 7: 117–126
- Nisbet ICT, Apanius V and Friar MS (2002) Breeding performance of very old Common Terns. *J Field Ornithol* 73: 117–124
- Oswald SA, Arnold JM, Hatch JJ and Nisbet ICT (2005) Effect of intraspecific interactions on seasonal decline in productivity of Common Terns *Sterna hirundo*. *Bird Study* 50: 80–87
- Pierotti R (1981) Male and female parental roles in the Western Gull under different environmental conditions. *Auk* 98: 532–549
- Pugesek BH (1983) The relationship between parental age and reproductive effort in the California Gull (*Larus californicus*). *Behav Ecol Sociobiol* 13: 161–171
- SAS Institute (1996) *SAS® User's Guide: Statistics*. Version 6.2 Edition. SAS Institute, Inc., Cary, NC
- StatSoft, Inc. (2001) *STATISTICA™* for Windows. StatSoft, Inc., Tulsa, OK
- Temeles EJ (1990) Northern harriers on feeding territories respond more aggressively to neighbors than to floaters. *Behav Ecol Sociobiol* 26: 57–63
- Temeles EJ (1994) The role of neighbours in territorial systems: when are they 'dear enemies'? *Anim Behav* 47: 339–350

- Tims J, Nisbet ICT, Friar MS, Mostello C and Hatch JJ (2004) Characteristics and performance of Common Terns in old and newly-established colonies. *Waterbirds* 27: 321–332
- Wendeln H (1997) Body mass of female Common Terns (*Sterna hirundo*) during courtship: relationships to mate quality, egg mass, diet, laying date and age. *Colon Waterbirds* 20: 235– 243
- Wendeln H and Becker PH (1999) Effects of parental quality and effort on the reproduction of Common Terns. *J Anim Ecol* 68: 205–214
- Wunderle JM Jr (1978) Differential response of territorial yellow-throats to the songs of neighbors and non-neighbors. *Auk* 95: 389–395