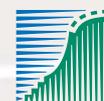


Waterbirds around the world

A global overview of the conservation,
management and research of the
world's waterbird flyways

Edited by G.C. Boere, C.A. Galbraith and D.A. Stroud

*Assisted by L.K. Bridge, I. Colquhoun, D.A. Scott,
D.B.A. Thompson and L.G. Underhill*



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Effects of the North Atlantic Oscillation and El Niño-Southern Oscillation on return rates, body mass and timing of migration of Common Terns *Sterna hirundo* breeding in Germany

Marco Favero¹ & Peter H. Becker²

¹Biology Department, University of Mar del Plata – CONICET, Funes 3250 (B7602AYJ), Mar del Plata, Argentina.

²Institut für Vogelforschung "Vogelwarte Helgoland", An der Vogelwarte 21, D-26386, Germany.

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ABSTRACT

Environmental variability at breeding and wintering areas may have complex effects on populations of migratory seabirds. Here, we report on the correlation of climate variability in the winter quarters and at migration stopover sites with return rates, individual condition and migration strategy of Common Terns *Sterna hirundo* breeding in northern Germany. Climate variability was defined by the North Atlantic Oscillation Index (NAOI) and Southern Oscillation Index (SOI, a measure of the El Niño-Southern Oscillation). Data on Common Terns were obtained over the last ten years at a breeding colony in the Banter See (northern Germany) by systematically marking adults and fledged chicks with transponders. The return rate of breeders was negatively correlated with the NAOI in the previous year, but for two-year-old sub-adults was positively correlated with the lagged SOI, indicating possible dependence for survival on food availability at migration stopover sites and in the wintering areas, respectively. Sub-adults also arrived later at the breeding colony after years of high NAO, suggesting that conditions at the wintering sites and during spring migration strongly influence the survival and behaviour of prospecting terns. The sub-adults appear to be more dependent on climatic conditions at wintering and migration stopover sites than adults, possibly as a result of different migratory behaviour, or foraging experience and the breeding requirements of adults. Studies on the wintering and migration strategies of the species are required to confirm the mechanisms linking migration and climate variability.

INTRODUCTION

There is much evidence of biological responses to climate variability in marine and terrestrial ecosystems (Holmgren *et al.* 2001, Beaugrand & Reid 2003). Studies on bird species have demonstrated impacts of climate change and oscillations in climate on many aspects of their life history, including survival, recruitment, reproductive output, population dynamics and timing of migration. Many species of migratory birds now arrive considerably earlier in spring than just a few decades ago, and several studies have shown that fluctuations observed in populations are regulated by climate change (Sillert *et al.* 2000, Moss *et al.* 2001, Møller 2002, Both *et al.* 2004, Hüppop & Hüppop 2002, Saino *et al.* 2004). For seabirds, the impact of climate change and oscillations has been observed predominantly at breeding colonies (e.g. Thompson & Ollason 2001, Croxall *et al.* 2002, Simeone *et al.* 2002). Therefore, an understanding of the dynamic consequences of climate oscillations and environmental conditions operating in the winter quarters and along the migration routes is required for these marine predators.

The Common Tern *Sterna hirundo* is one of the most cosmopolitan tern species, breeding mostly in the Northern Hemisphere and wintering in the tropics and temperate regions of the Southern Hemisphere (Nisbet 2002, Becker & Ludwigs 2004). Common Terns breeding in Europe spend the winter along the coast of Africa, from north-west Africa to Cape Town, and migrate along the East Atlantic coast. The Common Terns from breeding colonies in the Banter See in northern Germany winter predominantly in West Africa between the equator and 20°N (Becker & Ludwigs 2004). Most of the 47 recaptures of birds ringed in the Banter Sea have been in West Africa, although some birds have been recovered as far south as 10°S (P.H. Becker unpubl. data). In general, sub-adult Common Terns remain in their winter quarters throughout their first two years, returning to the breeding colonies as prospectors when they are two years old. The age of first breeding ranges from two to five, but is most commonly three (Becker *et al.* 2001, Ludwigs & Becker 2002, Dittmann & Becker 2003).

A major source of inter-annual variability in the atmospheric circulation of the Northern Hemisphere is the North Atlantic Oscillation (NAO), which is associated with changes in the surface westerly winds across the North Atlantic into Europe. Whereas warm, wet and stormy winters in the north-east Atlantic and northern Europe are associated with a high North Atlantic Oscillation Index (NAOI), these conditions are associated with a low NAOI in southern Europe (Hurrell 1995). However, unlike the tropical Pacific, seasonal climate variability in the tropical Atlantic is not dominated by any single process (Sutton *et al.* 2000). This region is subject to multiple competing forces among which El Niño-Southern Oscillation (ENSO) teleconnections have been linked to important environmental processes such as enhanced upwelling phenomena in equatorial West Africa (Roy & Reason 2001). These large-scale climatic factors may affect ecological patterns and processes in both marine and terrestrial systems, changing the relative amount of resources and habitats available in the breeding grounds, and consequently affecting the life history, demography and population dynamics of the species (Alerstam & Hedenström 1998, Stenseth *et al.* 2002). Hemispheric systems, such as the NAO or ENSO, may potentially influence migrants beyond their breeding ranges – during migration as well as in the wintering areas. Variability in arrival mass and date of arrival for individual migration strategies could be an expression of phenotypic plasticity (Saino *et al.* 2004), and ecological conditions during winter may affect the energetic balance, individual condition and moult of birds, and therefore the timing of departure and migration strategy (Marra *et al.* 1998), with significant consequences for life history.

Table 1. Multiple regression and partial correlation analyses of arrival date, return rate and arrival mass of Common Terns *Sterna hirundo* breeding in Germany, with North Atlantic Oscillation (NAOI) and Southern Oscillation (SOI) indices as independent variables.

	Breeders			Prospectors		
	Date of arrival	Arrival mass	Return rate	Date of arrival	Arrival mass	Return rate
Multiple R	0.554	0.284	0.689	0.798	0.306	0.833
Multiple R ²	0.307	0.081	0.475	0.638	0.094	0.694
F ^{2,7}	1.553	0.307	3.171	6.175	0.361	7.938
(p)	(0.277)	(0.745)	(0.105)	(0.028)	(0.709)	(0.016)
Partial correlations						
Lag NAOI β	0.173	0.267	-0.684	0.658	-0.302	-0.489
(p)	(0.599)	(0.486)	(0.041)	(0.023)	(0.429)	(0.049)
Lag SOI β	-0.537	-0.114	-0.053	-0.496	0.069	0.699
(p)	(0.132)	(0.763)	(0.852)	(0.066)	(0.855)	(0.012)

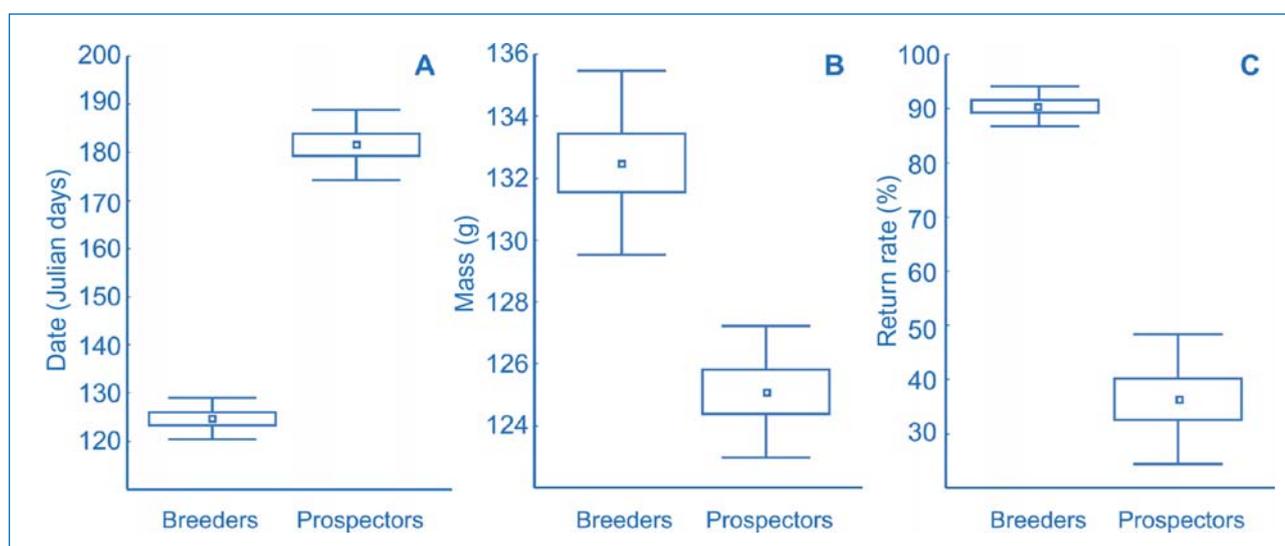


Fig. 1. Date of arrival (A), arrival mass (B), and return rate (C) of breeding and prospecting Common Terns *Sterna hirundo* throughout the study period. Means – dots; standard errors – boxes; standard deviations – error bars.

This study aimed to analyse the long-term variability observed in migration schedule, body mass at arrival and return rate of prospecting and breeding Common Terns in relation to oscillations in climate operating across the species' distribution, hypothesising a significant effect of climate on body mass, timing of migration and return rates.

METHODS

Common Tern data were collected at a breeding colony located at Banter See, Wilhelmshaven, Northern Germany. Between 1992 and 2001, complete cohorts of fledged Common Terns ($n = 2\,081$) and 101 adults were implanted with transponders. The migration schedule (date of arrival), individual arrival mass and return rates of breeders (individuals older than four years) and prospectors (two-year-old sub-adults; 91% of the sub-adults return at the age of two years; Dittmann & Becker 2003) were automatically recorded every season over a 10 year study period (1994 to 2003), using antennas and electronic balances located at resting sites throughout the breeding colony (for details, see Wendeln & Becker 1996, Becker & Wendeln 1997, Becker *et al.* 2001).

Environmental variability was defined in this study by the North Atlantic Oscillation Index (NAOI) and El-Niño-Southern Oscillation (ENSO; indicated by the Southern Oscillation Index, SOI). High positive values of SOI indicate La Niña conditions, and low, negative values indicate El Niño conditions. For all analyses, we used annual mean monthly values of the standardized NAOI and SOI for each calendar year. The NAOI data set was obtained from the Climate Prediction Centre website, and the SOI data set from the Commonwealth Bureau of Meteorology website. Temporal auto-correlation in the NAOI and SOI during the study period was found to be non-significant ($F_{1,9} = 0.01$, $r^2 = 0.001$, $P = 0.939$, and $F_{1,9} = 0.48$, $r^2 = 0.056$, $P = 0.510$, respectively).

We measured the effects of the NAO and ENSO on the return rates, timing of migration and individual condition of prospecting and breeding Common Terns. Mean index values from the year before were correlated to parameter values collected for Common Terns (i.e. average indices of the year i paired with parameters from the breeding season for the year $i+1$). The annual schedule of Common Terns from the study site was assumed as follows: breeding season from May to late

August, autumn migration from September to November, winter season from December to March, and spring migration from late February to May. For each breeding season of the ten-year study period, average arrival mass, date of arrival and return rate were calculated. The arrival mass was the mean body mass during the first three days after arriving at the colony. The return rate for breeders was the percentage of birds breeding in the previous year that were recorded, and for prospectors was the percentage of successful fledglings from two years previously. The ranges of annual sample sizes were as follows: date of arrival of adults, 56-388 (total N = 1 785); date of arrival of prospectors, 14-228 (total N = 808); return rate of adults, 53-273 (total N = 1 466); return rate of prospectors, 103-502 (total N = 2 078); arrival mass of adults, 40-160 (total N = 947), arrival mass of prospectors, 9-113 (total N = 406). Multiple regression and partial correlation analyses of all three parameters were performed with NAOI and SOI as independent variables.

RESULTS

Significant differences were found between breeders and prospectors in the three parameters under consideration. Breeders arrived at the colony significantly earlier than sub-adults ($T_{18} = 21.41$, $P < 0.0001$, Fig. 1a). Breeders were about 5% heavier than sub-adults when they arrived at the colony ($T_{18} = 6.53$, $P < 0.0001$, Fig. 1b), and the proportion of breeders returning to the colony was almost three times higher than the proportion of sub-adults returning after two years ($T_{18} = 13.68$, $P < 0.0001$, Fig. 1c).

The return rate in breeders was negatively correlated with the lagged NAOI, while in prospectors it was positively correlated with the lagged SOI (Table 1, Fig. 2a). Prospectors arrived later following high NAO years, and both prospectors and

breeders showed similar but non-significant trends following low SOI years (Fig. 2b). All significant correlations explained nearly 40% of the variability in the parameters under consideration. The arrival masses of breeders and prospectors were not correlated with the NAOI or SOI.

Multiple regression models with both lagged NAOI and SOI as independent variables explained significant proportions of the variability in the prospectors' date of arrival (64%) and return rate (69%) (Table 1). Post-hoc partial correlations indicated that the NAOI explained nearly 66% of the variability in the prospectors' date of arrival, 50% in the prospectors' return rate and 68% in the breeders' return rate; the SOI explained 70% of the variability in the prospectors' return rate (Table 1).

DISCUSSION

Higher adult survival and earlier arrival of prospectors following low NAO years were most likely attributable to favourable foraging conditions during the spring migration. Higher abundance of marine fish, including Herring *Clupea harengus* (a key prey for Common Terns in Europe; Greenstreet *et al.* 1999) in estuarine areas (Attrill & Power 2002), as well as higher copepod abundance in the North Atlantic (Heath 1999) have been observed following winters characterized by low NAOI values. Consequently low NAOI values should indicate better feeding conditions in breeding areas and along the migration routes between north-west Africa and Europe.

While the return rates in adults were not correlated with the SOI (an index of ENSO conditions), the return rates of prospecting terns were significantly explained by variability in the SOI, being higher after cold La Niña events (i.e. high SOI). The impact of La Niña on local climate and the intensification of Atlantic trade winds cause concomitant upwellings in coastal West Africa (Roy

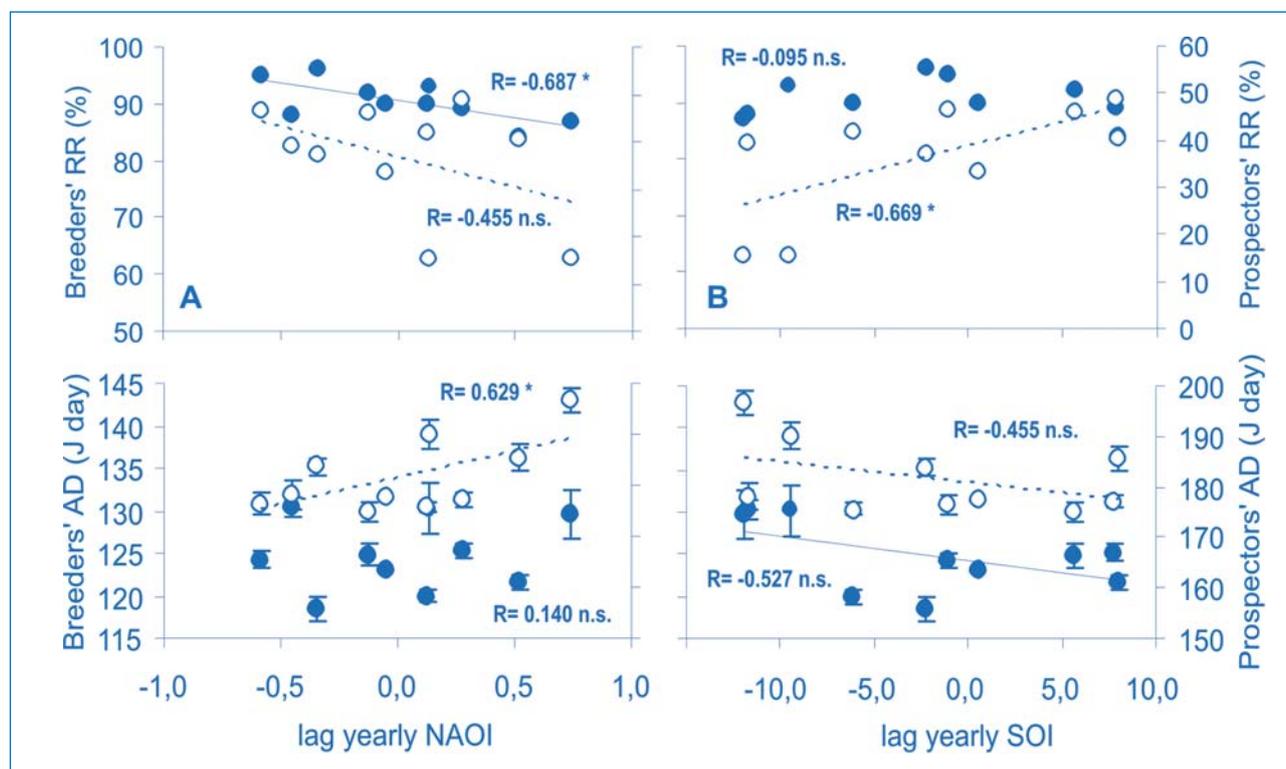


Fig. 2. Correlation between return rate (RR) and date of arrival (AD) of breeding Common Terns *Sterna hirundo* (filled circles, continuous lines) and prospectors (open circles, dashed lines), and one year lagged (A) North Atlantic Oscillation (NAOI) and (B) Southern Oscillation (SOI) indices for 1994-2003 ($n = 10$ years). * = $P < 0.05$; n.s. = non-significant correlation.

& Reason 2001), which are likely followed by increases in food availability. Subsequent increases in rainfall (Nicholson & Selato 2000, Holmgren *et al.* 2001) might increase river runoff in the vicinity of wintering areas, enhancing local productivity and food availability for Common Terns, as has been observed in the winter quarters off southern South America (Favero *et al.* 2001, Acha *et al.* 2004). Individuals departing in better physical condition from the wintering areas should therefore arrive earlier at the breeding grounds than those departing in poor condition (Forchhammer *et al.* 2002), as observed for prospecting sub-adults (Fig. 2b).

Prospectors showed higher variability in all three parameters than did adult terns, and their parameters followed more closely fluctuations observed in the NAO and ENSO. This may be because adults have to return to the breeding colonies earlier than prospecting sub-adults in order to breed, irrespective of climatic conditions. Multiple regression models explained more than 80% of the variability in timing of migration and return rate of prospectors, showing the differential responses of age classes to climate and environmental variability (Alerstam & Hedenström 1998). The absence of an effect of large-scale climate variability on body mass at arrival could be related to the fact that local food availability (affected by short-term processes) may immediately influence body mass in small seabirds, such as terns, that possess low energetic reserves (Greenstreet *et al.* 1999). The lower variability observed in adult terns could be related to the fact that more experienced individuals might be able to cope better with fluctuations in environmental conditions, as the increase in body mass with age shows (Dittmann & Becker 2003, Limmer & Becker unpubl. data). The stronger effects of variability in the ENSO on the survival of sub-adults (expressed as the observed return rates over a two-year period) could also be related to the fact that the birds spend their first two winter seasons in West Africa (Becker & Ludwigs 2004), where ENSO teleconnections have a strong influence.

Higher adult return rates and earlier arrival of prospectors were observed after low NAO years, while higher return rates of prospectors corresponded with cold ENSO events. For the moment, the reasons for these parallel trends between climate variability and return rates, body mass and timing of migration in the Common Tern are rather speculative. Further analyses and experimental studies examining local weather and environmental manifestations of climate (e.g. sea surface temperature, productivity) at wintering, staging and breeding areas are required for a better understanding of the effects of climate on variability in the migration and survival of Common Terns.

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Common Terns *Sterna hirundo* at the southern terminus of their migration, at Dyer Island, South Africa. Photo: Dieter Oschadleus.