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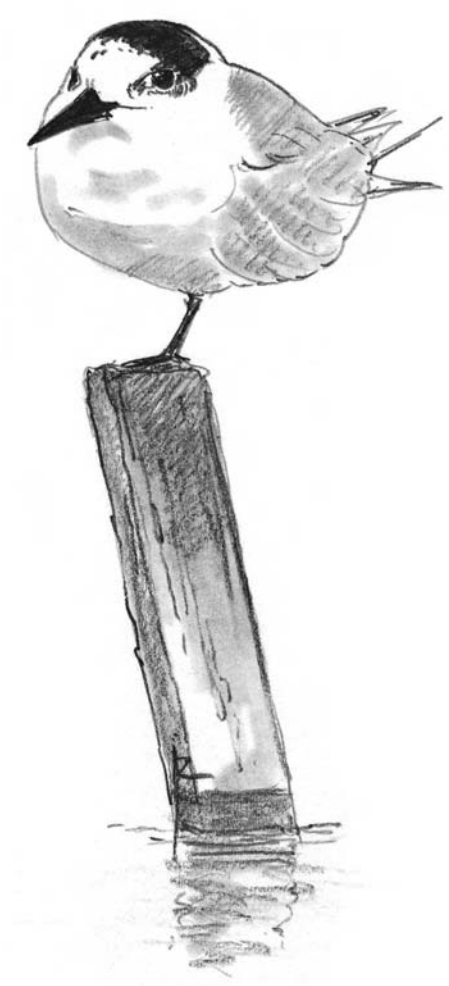
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Immature survival and age at first breeding of Damara Terns: conservation from a non-breeding perspective

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Braby J., Braby S.J., Braby R.J. & Altwegg R. Immature survival and age at first breeding of Damara Terns: conservation from a non-breeding perspective. Ardea 99: 185–190.

Protecting breeding sites should not be the only conservation measure for seabirds that exhibit delayed maturity and spend extended periods of time in their non-breeding areas. We investigated age at first breeding and immature survival of Damara Terns *Sterna balaenarum* which breed in southern Africa and migrate c. 4000 km to their non-breeding grounds in West Africa. Using multi-state capture–mark–recapture models adult annual survival was estimated to be 0.87 (95% confidence interval: 0.73–0.94). Mean annual immature survival of Damara Terns from nest stage to breeding was estimated to be 0.59 (95% confidence interval: 0.48–0.68). Immature survival contained an element of pre-fledging mortality since most individuals were ringed before fledging. Furthermore, our estimate could be biased low due to permanent emigration from the study area. The age at first breeding was three years (probability of 0.27), and all terns were breeding at four years. This is comparable to other plunge-diving migratory terns which have extended periods of post-fledging dependence. In the light of this we suggest that consideration be given regarding the protection of the species in its non-breeding countries in addition to the protection of current breeding sites.

Key words: immature survival, age at first breeding, seabirds, Damara Tern, post-fledging dependence

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To assess and ensure the long-term viability of any population requires an understanding of its life-history. Immature survival and the age at which a bird first breeds are important parameters in the life-history of seabirds (Lack 1967, Crespin *et al.* 2006, Jenouvrier *et al.* 2008, Aubry *et al.* 2009). However, long-term studies are required to attain these parameters. Such studies of seabirds were rare in the past (Breton *et al.* 2006), but have been steadily increasing (e.g. Cam *et al.* 2005, Crespin *et al.* 2006, Jenouvrier *et al.* 2008, Le Bohec *et al.* 2008, Aubry *et al.* 2009, Gauthier *et al.* 2010). Because some seabirds migrate to isolated or inaccessible areas during non-breeding seasons, taking their fledged offspring with them, there are often periods of 'unobservability' following fledging. However, with the advancement of statistical modelling, there is a growing literature which estimates juvenile survival in seabirds with reasonable precision (e.g. Cam *et al.* 2005, Crespin *et al.* 2006, Jenouvrier *et al.* 2008, Le Bohec *et al.* 2008, Aubry *et al.* 2009, Gauthier *et al.* 2010).

Age of first breeding has been reported for several species of terns (reviewed by Mundkur 1992, Becker & Wendeln 1997, Becker *et al.* 2001). Age at first breeding may be influenced by a number of factors, such as physiological maturity, non-breeding migration, learning of food availability and predation risks at breeding grounds, and acquiring skills sufficient to feed offspring (Chabrzyk & Coulson 1976, Mundkur 1992, Jenouvrier *et al.* 2008, Aubry *et al.* 2009). With the exception of

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river terns (e.g. Indian River Tern *Sterna aurantia*) which tend not to migrate and generally have permanent and reliable access to food resources (Mundkur 1992), terns exhibit delayed or deferred maturity and initiate breeding at the age of two to three years (Mundkur 1992), and up to five years for some species (Harrington 1974).

Damara Terns *Sterna balaenarum* breed along the desert mainland of southern Africa during the austral summer and migrate to West Africa for the non-breeding season (Simmons 2005). Successful breeding attempts result in one fledged chick per pair and fledging dependency extends for up to two and a half months (Williams & Myer 1986). Two-egg clutches are extremely rare (0.002%, Braby 2011). Damara Terns breed in harsh desert environments with high risks of predation and the probability of a breeding attempt being successful is 0.356 (Braby 2011). Like most terns, Damara Terns feed by plunge-diving for prey; this skill requires considerable time to perfect and explains the extended post-fledging dependency (Ashmole 1971, Heidinger *et al.* 2006, Braasch *et al.* 2009, Bluso-Demers *et al.* 2010, Jaquemet 2010).

In the light of these factors we predict that Damara Terns share the life-history traits of most terns by displaying delayed (or deferred) maturity and thus relatively high annual immature survival (Ricklefs 2000). Breeding Damara Terns are threatened by habitat loss due to coastal development (Braby, unpubl. data) and disturbance caused by off-road driving (Braby *et al.* 2001, Williams *et al.* 2004, Braby *et al.* 2009). In addition, non-breeding and immature Damara Terns are harvested in their non-breeding grounds. However, how many individuals are killed, and the impact of this mortality on the global population is unknown (Braby 2010). It is thus important to estimate life-history parameters from information pertaining to the non-breeding grounds to find a holistic approach to the conservation of the species.

The objectives of this study are two-fold: to report (a) estimates of immature survival, and (b) age at first breeding of Damara Terns.

METHODS

This study is based on 10 years of capture–mark–recapture data at two breeding colonies on the coastline of central Namibia, south of the town of Swakopmund (22°44'S, 14°32'E): Caution Reef (22°44'S, 14°32'E), 8 km from town (60–100 breeding pairs), and Horses Graves (22°42.5'S, 14°32.3'E), 4 km south of Swakopmund (30–60 breeding pairs). The habitat at Caution Reef consisted mainly of open and sparsely vegetated sandy plains with a raised gravel ridge through the centre (Braby *et al.* 2001). Horses Graves comprised a series of barchan, linear, and crescent dunes separated by gravel plains in which the terns bred (Braby *et al.* 2001). The next closest colony of similar size was 280 km away.

Incubating adults were trapped on their nests using a netted snap-trap controlled by remote trigger from a distance of up to 200 m. Adults and chicks were trapped during the breeding seasons (October– February) from 2000/01 to 2009/10. Chicks were ringed when first found with a 2.3 mm SAFRING stainless steel ring on the right leg and one breeding-season-specific colour ring on the left leg. Adults received the same combination along with an additional colour ring on the left leg specific to breeding site. SAFRING rings are numbered and individual-specific.

We used multi-state capture–mark–recapture models to estimate the age at first breeding (Clobert *et al.* 1994, Lebreton *et al.* 2003). For this analysis we used data on Damara Terns ringed either as chicks (678 individuals) or adults (174 individuals). Immatures (other than those fledged during that season) were never recorded at breeding grounds. We included the data on adult terns to estimate breeder recapture probabilities. We defined two states, immature and breeder. All birds ringed as chicks, i.e. age 0, were initially assigned to the immature state. The age-specific transition probability from the immature state to the breeder state was then used as an estimate of the probabilities of first breeding at a given age. In this analysis, the maximum age at which all individuals will start to breed needs to be assumed (Lebreton *et al.* 2003). We considered values for this parameter up to a maximum of 6 years.

We were only able to trap breeding birds, and the recapture probability in the immature stage was therefore set to zero. As a result, we did not estimate yearly age-specific survival for immature birds, but obtained an average estimate of annual survival during that life stage.

An added complication is that chicks were ringed at variable ages, ranging from the day of hatching until shortly before fledging. The immature survival rate thus contains a component of pre-fledging mortality. To account for the resulting heterogeneity, we used the age when a chick was last seen (ranging from 0.5 to 23 days) as an individual covariate in the analysis. Our estimate of juvenile survival corresponds to an individual with mean age when last seen in the nest; this was 4.7 days.

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In this analysis, we considered models where the breeders' recapture probability was constant, year-dependent, or a linear function of effort (number of hours spent trapping each year). Breeder survival was kept constant and we did not distinguish between the two colonies.

We examined the fit of our most general model without individual covariates (with year specific recapture probabilities) using the median-ĉ procedure in program MARK (White & Burnham 1999). This test showed little sign of overdispersion (ĉ = 1.23, SE 0.02), and including the individual covariate should account for some remaining heterogeneity. A further goodness-of-fit test for multi-state models conducted in program U-CARE (Choquet *et al.* 2009) also revealed no evidence of significant lack of fit (χ^2 = 11.6, *df* = 23, *P* = 0.96).

The standard optimization routine used in program MARK, based on a Newton–Raphson algorithm, did not always appear to converge properly. We therefore fitted most models using the alternative optimization based on simulated annealing, also provided in program MARK. All analyses were conducted in program MARK 6.0 (White & Burnham 1999), and we used the sample-size adjusted Akaike's Information Criterion for model selection.

RESULTS

Model selection favoured a model which assumed that the maximum age at first breeding was four years (Model 1, Table 1), that immature survival was positively related to the age when a chick was last seen, and that the recapture rate was positively related to field effort. This model averaged (over the top two models) probability of starting to breed was zero for 1-year old birds, 0.06 (95% confidence interval = 0.007–0.36) for 2-year old birds, 0.27 (0.03–0.79) for 3-year old birds, and that all birds breed at 4-years old. Data sparseness has partly affected this result, and we interpret it as showing that most Damara Terns started breeding either at 3 or 4 years of age.

Average annual survival of immature terns was 0.59 (95% confidence interval = 0.48–0.69), and adult survival was 0.88 (0.72–0.96). Our estimate of immature survival contains an element of pre-fledging mortality because it is mean annual survival from mean ringing age (4.7 days old chick) to breeding. We included chick age as a linear covariate into our models, mainly to account for heterogeneity in observed survival caused by variable age at ringing. The best-fitting linear relationship, on the logit scale, was logit(Φ) = 0.009 [SE 0.263] + 0.072 [SE 0.029] × age [in days]. We can use this relationship to estimate expected survival for individuals that reach fledging age (23 days). Based on that relationship our best estimate for immature survival would be 0.84 (0.64–0.94), much closer to adult survival.

DISCUSSION

Our results show that, as with many seabirds, Damara Terns show lower immature survival than adult survival; and delayed maturity. These are the first estimates of immature survival and age at first breeding of the species.

Table 1. Summary of model selection for age at first breeding (*Ψ*) and survival of Damara Terns in Namibia. We examined models that assumed the maximum age to start breeding was 3, 4, 5, or 6 years. Annual survival during the immature period (*S*j) was either kept constant (), or assumed to be a linear function of the age when last seen in the nest (nage). Annual adult survival (*S*a) was assumed to be constant in all models. Immature birds could not be trapped, and we examined models where adult recapture probability (*P*a) was either constant (), varied over the years (year), or a linear function of yearly effort (effort). K is the number of estimated parameters.

Model	AICc	Δ AICc	Weight	K	Deviance
*S*j(nage)*S*a()*P*a(effort) *Ψ*(age4)	680.82	0.00	0.618	7	666.69
*S*j(nage)*S*a()*P*a(year) *Ψ*(age4)	682.28	1.46	0.299	14	653.76
*S*j()Sa()*P*a(year) *Ψ*(age3)	686.00	5.18	0.046	11	663.68
*S*j()Sa()*P*a(year) *Ψ*(age4)	687.69	6.87	0.020	13	661.24
*S*j()Sa()*P*a(year) *Ψ*(age5)	688.79	7.97	0.012	14	660.28
*S*j()Sa()*P*a(year) *Ψ*(age6)	690.51	9.69	0.005	15	659.93
*S*j(nage)*S*a()*P*a() *Ψ*(age4)	695.99	15.17	0.000	6	683.89

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The estimated immature survival rate of 0.59 was lower than the adult survival rate of 0.88. However, it was higher than those of other tern species (Spendelow 1991, Becker *et al.* 2001, Spendelow *et al.* 2002, Limmer & Becker 2010). Our estimate of immature survival contained an element of pre-fledging mortality because it is mean annual survival from mean ringing age (4.7 days old chick) to breeding. The calculation required for the immature survival of 0.84 relied on the assumption that survival during the chick stage is constant, due to the linear relationship used. Since chick survival probably improves with chick age, and we had few individuals ringed close to fledging age, this estimate of immature survival is likely to be too high because we were attributing some immature mortality to the chick stage. Nevertheless, it may be a realistic upper bound. In a study of Atlantic Puffins *Fratercula arctica*, where only juveniles that had fledged were considered, survival rates of immatures were not depressed in relation to adults (Sandvik *et al.* 2008). We predict that our estimate of 0.59 may have been higher if only immatures that had fledged were considered, especially when taking into account the high risk of predation during pre-fledging. Our estimates of immature survival should be considered as apparent survival rates and may therefore be biased by permanent migration.

Of the six small terns closely related to the Damara Tern, the only other species for which age at first breeding is known is the California Least Tern *Sterna antillarum browni*, which breeds at age three years, and rarely at age two years (Massey & Atwood 1981). The age at first breeding of three to four years of Damara Terns is similar. It is also typical of most plunge-diving terns where an extended period is needed to learn this skill, and immatures are much less efficient at foraging than adults (Dunn 1972, Ainley *et al.* 1986). The difficulty that adults face in bringing sufficient and adequate food to their young is therefore an important factor in delayed maturity (Lack 1968, Ashmole 1971). Like many seabirds, Damara Terns migrate thousands of kilometers to non-breeding areas and immatures probably stay there for at least two years before they return to their breeding grounds (Ashmole 1971, Harrison 1983, Cramp 1985).

In some species it has been found that within-species variation exists in the age of breeding with different populations of birds (Mundkur 1992). Recent studies have found that high variability exists in recruitment age even within the same population of birds (Aubry *et al.* 2009, Rebke *et al.* 2010). The age of breeding is decreased when more food is available and competition for nest sites is reduced in some seabird species (Lack 1968). In other seabird species, recruitment has been linked to population size (Crespin *et al.* 2006) and predation risk (Finney *et al.* 2003). Since Damara Terns do not breed in dense colonies and breeding habitat is not a constraining factor in the immense desert coastline, recruitment is unlikely to be affected by reduced competition for nest sites (Braby 2011). It is uncertain whether Damara Terns which breed in areas with lower predation risks may breed at a younger age and this may need to be explored in further studies.

Because Damara Terns exhibit delayed maturity, high immature survival and lay only one egg with low probabilities of success (Simmons & Braine 1994, Braby, unpubl. data), we expect that the generational turn-over rate of the species is low. Extended periods are taken by immature Damara Terns in non-breeding grounds in West Africa, and breeding Damara Terns migrate along c. 4000 km of West African coastline twice a year. Migratory seabirds like the Damara Tern are trapped and sold for food in these migratory countries (Braby 2010, de Wit, pers. comm.). In light of these factors, special consideration should be given to species like the Damara Tern toward the protection of populations in their non-breeding countries in addition to the conservation management of breeding areas. We suggest that further studies look at building a population model to investigate the turn-over rate of the two colonies. This would be particularly useful when proposing conservation measures for the species.

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SAMENVATTING

De Damarastern *Sterna balaenarum* broedt in zuidelijk Afrika (vooral in Namibië) en overwintert 4000 km noordelijker langs de kust van West-Afrika. De soort wordt bedreigd door habitatvernietiging en verstoring van de broedplaatsen. Door vogels op het nest te vangen en vervolgens te ringen kon de jaarlijkse overleving worden vastgesteld. De overleving van oude vogels was 0,87 (95% betrouwbaarheidsinterval 0,73–0,94). Voor vogels die als nestjong waren geringd, lag de jaarlijkse overleving tot het moment van broeden op 0,59 (0,48–0,68). Deze schatting is inclusief de periode dat de vogels nog niet vliegvlug waren, omdat de vogels geringd werden op een gemiddelde leeftijd van 4,7 dagen. De schatting houdt geen rekening met vogels die in andere broedkolonies zijn gaan broeden. De werkelijke overleving moet dus hoger zijn geweest. Na het uitvliegen lieten de sterns zich twee jaar of langer niet zien. Vermoedelijk bleven de jonge vogels in het overwinteringsgebied tot het jaar waarin ze begonnen te broeden. In overeenstemming met andere soorten broedden de eerste vogels pas na drie jaar (27% van de vogels die toen nog in leven waren). Na vier jaar broedden alle nog in leven zijnde vogels. Om de Damarastern adequaat te beschermen is dus ook bescherming in het overwinteringsgebied noodzakelijk. (ND)

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