

Annual survival and breeding dispersal of a seabird adapted to a stable environment: implications for conservation

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Abstract Understanding the spatial dynamics of populations is essential for conservation of species at the landscape level. Species that have adapted to stable environments may not move from their breeding areas even if these have become sub-optimal due to anthropogenic disturbances. Instead, they may breed unsuccessfully or choose not to breed at all. Damara Terns *Sternula balaenarum* feed off the highly productive Benguela Upwelling System. They breed on the coastal desert mainland of Namibia where development and off-road driving is threatening breeding areas. We report annual survival and breeding dispersal probabilities of 214 breeding adult Damara Terns through capture–mark–recapture at two colonies for 9 years (2001–2009) in central Namibia. Using multi-state models in program MARK, model selection

based on AICc favoured a model that suggests local annual survival of Damara Terns for the dataset was 0.88 (95% CI, 0.73–0.96) and the annual dispersal probability was 0.06 (0.03–0.12). High survival and low dispersal probabilities are consistent with other seabirds adapted to stable environments. These estimates contribute to the first baseline demographic information for the Damara Tern. Low dispersal probabilities indicate that current protection of breeding sites is an important management approach for protecting the species.

Keywords Breeding dispersal · Fidelity · Survival · Conservation · *Sternula balaenarum* · Damara Tern

Zusammenfassung

Jährliche Überlebensrate und Brutortstreue bei einem an stabile Umweltbedingungen angepassten Seevogel: Auswirkung auf Schutzmaßnahmen

Um Arten auf Landschaftsebene zu schützen ist es wichtig, die räumliche Dynamik der Populationen zu verstehen. Es ist möglich, dass Arten, die an eine stabile Umwelt angepasst sind, ihre Brutgebiete nicht verändern können, selbst wenn diese infolge anthropogener Veränderungen nicht mehr optimal sind. Stattdessen könnten sie dort erfolglos zu brüten versuchen oder gar nicht mehr brüten. Damara-Seeschwalben *S. balaenarum* ernähren sich im hochproduktiven Benguela Auftriebsgebiet. Sie brüten an der Küste der Namibwüste, wo Überbauungen und Fahren im Gelände ihre Brutgebiete gefährdet. Wir präsentieren jährliche Überlebensraten und Dispersionswahrscheinlichkeiten basierend auf 214 brütenden adulten Damara-Seeschwalben, ermittelt durch Fang-Wiederfang Methoden über neun Jahre (2001–2009) in zwei Kolonien Zentralnamibias. Multi-state

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Modelle in Programm MARK zeigten für diese Daten, dass die jährliche lokale Überlebensrate von Damara-Seeschwalben 0.88 (95% Vertrauensbereich 0.73–0.96) war und die jährliche Dispersionswahrscheinlichkeit zwischen den Kolonien betrug 0.06 (0.03–0.12). Die hohe Überlebensrate und niedrige Dispersionswahrscheinlichkeit sind vergleichbar mit anderen an stabile Umwelten angepassten Seevögeln. Diese Schätzungen sind ein erster Beitrag zum Verständnis der Demographie von Damara-Seeschwalben. Die niedere Dispersionswahrscheinlichkeiten legen nahe, dass der Schutz der Brutgebiete, wie er momentan betrieben wird, eine tatsächlich wichtige Maßnahme zum Schutz dieser Art ist.

Introduction

When habitat becomes unsuitable for a species, it is of great conservation interest to know if and how far the individuals will move to resettle in other suitable areas. Knowledge of dispersal is therefore vital when considering wildlife management at the landscape scale. The level to which a species displays fidelity or dispersal depends on the environmental conditions it has evolved in (McPeck and Holt 1992; Clobert et al. 2001). We expect such a life-history strategy is dependent on various environmental conditions, such as food availability, predation rates, and how much habitat is available. Generally seabirds are long-lived and faithful to their breeding areas (Beadell et al. 2003), but species living in highly variable environments are nomadic and may suffer higher rates of mortality (Renken and Smith 1995a, b; Robinson and Oring 1997). The tendency for individuals to return to areas where they were hatched (natal philopatry), and/or previously bred (breeding philopatry), has been well documented for a variety of seabirds, including gulls (Coulson and White 1958; Southern 1977; Southern and Southern 1980; Blockpoel and Courtney 1980; Stenhouse and Robertson 2005) and terns (Austin 1940, 1949; Atwood and Massey 1988; Becker and Wendeln 1997; Spindel et al. 1995, 2008, 2010; Becker et al. 2001; Lebreton et al. 2003; Ezard et al. 2006; Devlin et al. 2008). Because prior knowledge exists on available nesting sites, food resources and predation pressures, it is often considered a safer strategy for birds to return to a previous breeding site or natal territory than to move to a new area with unknown resources and/or risks (Renken and Smith 1995b). Factors such as predation, low reproductive success and changes in habitat have been implicated in causing breakdowns in fidelity (McNicholl 1975; Erwin 1977; Conover and Miller 1978; Oro et al. 1999). However, in spite of the obvious negative impacts of these factors, continued re-use of adversely affected sites

has been reported for several seabird species (Austin 1940, 1949; Southern and Southern 1979, 1982; Peterson 1980). The level to which species display fidelity to their breeding sites is important in understanding the management and protection of these species.

Damara Terns *Sternula balaenarum* breed predominantly on the coastline where the harsh Namib Desert meets the cold and dynamic Benguela current (Simmons and Braine 1994). Damara Terns feed primarily inshore where physical fluctuations result in biological patchiness and high variability (Branch et al. 1987). Recruitment of prey species like Anchovy *Engraulis encrasicolus* in the northern Benguela system shows high inter-annual variability (Boyer et al. 2001). However, the Benguela system is not as variable as, say, the Humboldt system, and seabirds here are generally adapted to a more stable supply of food (Crawford et al. 2006). We would expect that Damara Terns have adapted to this stable food supply by displaying high annual survival and fidelity to their breeding sites. In addition, although there is ample available undisturbed habitat along the coastline of Namibia, Damara Terns are found breeding in specific areas (Clinning 1978). However, predation rates are high and predation has been considered the major driving force in the evolution of the unique one-egg clutch trait of this tern (Frost and Shaughnessy 1976; Clinning 1978). High or fluctuating predation has resulted in lower fidelity in some other tern species (e.g. Spindel et al. 2002), and even caused mass periodic dispersal in other species of gulls (e.g. Oro et al. 1999).

The Damara Tern is globally near-threatened (IUCN 2009) and it is the only small tern that predominantly lays just one egg (Simmons and Braine 1994; de Villiers and Simmons 1997). During the non-breeding season (May–September), Damara Terns migrate to West African countries such as Gabon, Cameroon and Nigeria (Williams et al. 2004). The age at first breeding is estimated at 3 years, and immature survival is estimated at 0.59 (Braby et al. 2011). The Benguela Upwelling System is currently undergoing changes due to over-fishing and climate change (Clark 2006). In addition, Damara Tern breeding grounds are threatened by off-road driving and coastal development (Braby et al. 2001, 2009; Braby, unpublished data). It is thus becoming increasingly important to understand the life-history adopted by the species. Few demographic parameters exist for the Damara Tern and these are necessary to test whether the current management approach of protecting specific breeding sites is appropriate. The objective of this paper is to provide estimates of (1) adult survival and (2) dispersal probabilities of Damara Terns based on 9 years of capture–mark–recapture data of adult Damara Terns breeding at two close-proximity colonies along the central coastline of Namibia.

Methods

Study area

The Horses Graves colony contained 30–60 pairs, was located 4 km south of Swakopmund, on the central Namibian coast (22°42'S, 14°33'E; Fig. 1), and comprised approximately 3.5 km². Over the course of 1 or 2 years, the size of the area would increase only slightly (up to a maximum of 500 m to the north-west), but this increase did not reduce the distance between Horses Graves and Caution Reef. The study area comprised a series of barchan, linear, and crescent dunes separated by gravel plains in which the terns bred (Braby et al. 2001). The area was situated just south of a disused railway line, 3 km east of the sea, and ran parallel to the coast. The areas used by the breeding terns were devoid of vegetation.

The Caution Reef colony contained 60–100 pairs, was situated 8 km from Swakopmund and 3.7 km SSW of the Horses Graves colony (22°44'S, 14°32'E; Fig. 1) and comprised approximately 2.5 km². The size of this colony did not vary between seasons. The main road to Walvis Bay cut across the breeding area, with the area west of the road being 2 km parallel to and 1 km from the sea, and east of the road up to 600 m towards the high dunes (Braby et al. 2001). 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). The next closest colonies of similar size were 280 km away.

Both Caution Reef and Horses Graves are fenced off from the public to ensure minimal disturbance from off-road driving. These two areas are protected from coastal development. There were three additional colonies within a 30-km radius of Horses Graves and Caution Reef. One (approximately 30 pairs) has been extinct since 2005 due to coastal development. Fewer than 20 pairs are found breeding at each of the other colonies.

Data collection

Incubating adults were trapped on their nests using a netted snap-trap controlled remotely by a trigger from a distance of up to 200 m. Individually numbered SAFRING (South African Bird Ringing Unit, University of Cape Town) metal rings and a unique combination of colour rings pertaining to the breeding season were placed on each leg. Damara Terns were trapped between October and February, when they are breeding during the austral summer months. We used data collected on 214 adult terns between October 2001 and December 2009 (Table 1), defining the survival intervals to run from 1 October until 30 September of the following year.

We used multi-state capture–mark–recapture models (Spindelov et al. 1995) to estimate adult survival rates at

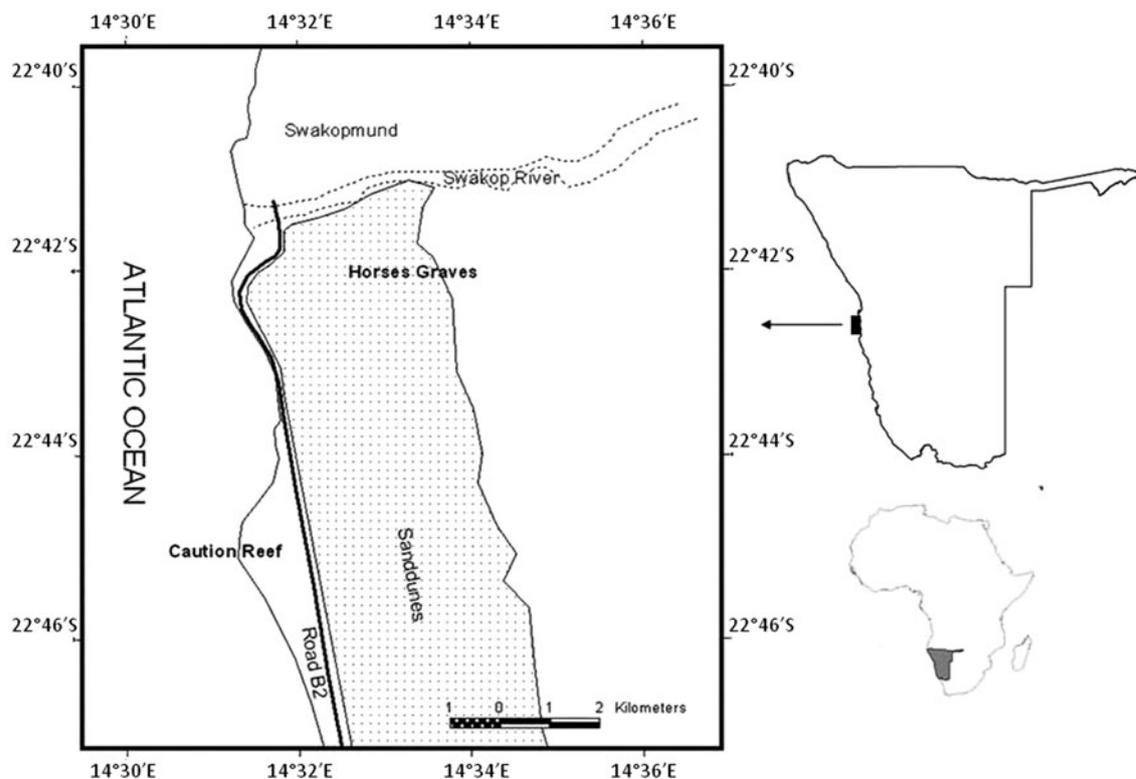


Fig. 1 Location of two Damara Tern *Sternula balaenarum* breeding colonies, Caution Reef and Horses Graves, in central Namibia

Table 1 The number of adult breeding Damara Terns *Sternula balaeenarum* captured at two colonies in central Namibia compared with the number of nests found per year from 2001 to 2009

Year	No. of nests		Adults captured	
	Caution Reef	Horses Graves	Caution Reef	Horses Graves
2001	92	58	2	2
2002	122	57	6	1
2003	40	89	19	39
2004	60	97	21	49
2005	13	32	6	6
2006	92	69	21	12
2007	52	56	3	6
2008	71	54	24	41
2009	108	45	8	10

the two colonies, and the annual movement probabilities between them. These models are extensions of classical capture–mark–recapture models (Lebreton et al. 1992) and provide estimates of survival and movement while accounting for the recapture probabilities at the two colonies.

The models consist of three components. The first estimates local survival, which is the probability of surviving from 1 year to the next, and staying in the study area. We cannot distinguish between mortality and permanent emigration to sites not studied here, and our survival estimates will therefore tend to be biased slightly low. The second component estimates recapture, which is the probability of capturing an individual given that it is alive and in the study area. The third component estimates movement between the colonies. The most general model that could fit to our data allowed all components to differ between the colonies and the recapture rates to vary over the years. We then considered simplified versions of this model and used the sample-size adjusted Akaike's Information Criterion (AICc) to evaluate model performance, following standard methodology (Burnham and Anderson 2002). All models were fitted in program MARK 6.0 (White and Burnham 1999).

Results

The models we used make the assumption that individuals have similar survival, recapture, and movement probabilities. We tested this assumption for our most general model using the median- \hat{c} procedure in program MARK. This test showed little sign of over dispersion ($\hat{c} = 1.19$, $SE = 0.03$), and thus suggested that this model captured the structure in our data well. Transients were not an issue

in this data set (in contrast to capture–mark–recapture studies on other terns; Ratcliffe et al. 2008). Adding a parameter to account for such a potential constant transients effect (following Pradel et al. 1997) led to a less well supported model (Model 3, Table 2).

Model selection based on AICc favoured a model that kept the annual survival rate constant across colonies, assumed that the recapture rate was a linear function of effort (number of hours spent trapping per season), and that movement probabilities were equal in both directions (Model 1, Table 2). According to this model, annual local survival was 0.88 (95% confidence interval CI 0.73–0.96). The annual movement probability was 0.06 (0.03–0.12), and the recapture probabilities were positively related to effort and ranged from 0.041 (0.023–0.076) to 0.18 (0.10–0.30).

Discussion

Our results show that Damara Terns have high survival rates and are faithful to their breeding sites, life-history traits typical of seabirds adapted to stable environments (Beadell et al. 2003). Despite variability of prey in the near-shore ecosystem where Damara Terns feed, the Benguela Upwelling System is abundant in prey species such as Anchovy (Crawford et al. 2006). The most similar upwelling system, in the Humboldt Current, experiences more frequent El Niño perturbations and seabirds feeding on the same species of prey there have a demography that enables them to recover more rapidly from population decreases due to these perturbations (Crawford et al. 2006). No comparative demographic parameters exist for the Peruvian Tern *Sternula lorata*, an ecological equivalent which is adapted to a more variable environment than the Damara Tern (Crawford et al. 2006). Such a comparison would be necessary to determine how similar species have adapted to different environments. However, our results conform with the suggestion by Crawford et al. (2006) that seabirds reliant on the Benguela system are adapted to a more stable supply of food.

Our annual survival estimate of 0.88, albeit with wide confidence intervals owing to a relatively small dataset, is consistent with published estimates of adult annual survival in other terns and gulls, among which survival estimates are typically high (Table 3). Our estimated annual survival probability is probably lower than the true value because we could not distinguish between mortality and permanent emigration from our study area. To determine the relative importance of permanent emigration will require a study of inter-colony movement between all major colony sites. No large colonies exist in the vicinity of our study area, but it is possible that three small colonies (<30 pairs) within

Table 2 Summary of model selection analysis for survival and movement of Damara Terns in Namibia

Model	AICc	Δ AICc	AICc weights	<i>K</i>	Deviance
1 Sh() = Sc()Ph(effort) = Pc(effort) $\Psi_{hc}()$ = $\Psi_{ch}()$	484.675	0.000	0.475	4	156.475
2 Sh()Sc()Ph(effort) = Pc(effort) $\Psi_{hc}()$ = $\Psi_{ch}()$	486.383	1.708	0.202	5	156.103
3 Sh(trans) = Sc(trans)Ph(effort) = Pc(effort) $\Psi_{hc}()$ = $\Psi_{ch}()$	486.719	2.044	0.171	5	156.438
4 Sh()Sc()Ph(effort) = Pc(effort) $\Psi_{hc}()$ $\Psi_{ch}()$	488.136	3.461	0.084	6	155.758
5 Sh()Sc()Ph(effort)Pc(effort) $\Psi_{hc}()$ $\Psi_{ch}()$	489.924	5.249	0.034	7	155.432
6 Sh() = Sc()Ph(year) = Pc(year) $\Psi_{hc}()$ = $\Psi_{ch}()$	490.310	5.635	0.028	10	149.372
7 Sh()Sc()Ph(year) = Pc(year) $\Psi_{hc}()$ $\Psi_{ch}()$	494.670	9.995	0.003	12	149.345
8 Sh() = Sc()Ph() = Pc() $\Psi_{hc}()$ = $\Psi_{ch}()$	497.103	12.428	0.001	3	170.967
9 Sh()Sc()Ph(year)Pc(year) $\Psi_{hc}()$ $\Psi_{ch}()$	505.763	21.088	0.000	20	142.148

The model components were survival (*Sh* at Horses Graves colony, and *Sc* at Caution Reef colony), recapture probability (*Ph* and *Pc* at the two colonies, respectively), movement from Horses Graves to Caution Reef (Ψ_{hc}), and movement in the opposite direction (Ψ_{ch}). We considered variable recapture rates over the years (*year*), or as a linear function of effort (*effort*; number of hours spent trapping). We also fitted a model accounting for transients (*trans*) following Pradel et al. (1997). *K* is the number of estimated parameters

Table 3 Estimates of annual survival rates of gulls and terns

	Survival rate	References
Sternidae		
Damara Tern <i>S. balaenarum</i>	0.880 (0.730–0.960)	This study
Least Tern <i>S. antillarum</i>	0.850 (SE = 0.060)	Renken and Smith (1995a)
Common Tern <i>S. hirundo</i>	0.880 (SE = 0.040)	Nisbet and Cam (2002)
	0.910 (0.870–0.970)	Becker et al. (2001)
	0.923 (fem); 0.835 (mal)	Ezard et al. (2006)
Arctic Tern <i>S. paradisaea</i>	0.704–0.960	Devlin et al. (2008)
Roseate Tern <i>S. dougallii</i>	0.740–0.840	Spendelov et al. (1995)
	0.850	Lebreton et al. (2003)
	0.835 (SE = 0.006)	Spendelov et al. (2008)
	0.850 (wintering, not breeding)	O’Neill et al. (2008)
	0.71–0.90 (range)	Nisbet and Ratcliffe (2008)
Sooty Tern <i>O. fuscatus</i>	0.910 (SE = 0.010)	Feare and Doherty (2004)
Royal Tern <i>T. maximus</i>	0.950	Collins and Doherty (2006)
Caspian Tern <i>H. caspia</i>	0.820 (SE = 0.030)	Collins et al. (2010)
Laridae		
Kelp Gull <i>L. dominicanus</i>	0.840	Altwegg et al. (2007)
Audouin’s Gull <i>L. audouinii</i>	0.910 (0.890–0.920)	Oro et al. (1999)
Herring Gull <i>L. argentatus</i>	0.826–0.975	Pons and Migot (1995)
Sabine’s Gull <i>X. sabini</i>	0.890 (SE = 0.030)	Stenhouse and Robertson (2005)
Ivory Gull <i>P. eburnea</i>	0.860 (SE = 0.040)	Stenhouse et al. (2004)
Black-legged Kittiwake <i>R. tridactyla</i>	0.880 (SE = 0.020)	Harris et al. (2000)
	0.800 (SE = 0.030)	Oro and Furness (2002)
Black-headed Gull <i>C. ridibundus</i>	0.900 (0.860–0.920)	Prévoit-Julliard et al. (1998)

95% confidence intervals, or standard errors (SE) are given in parentheses

30 km of the study site may have absorbed a small number of emigrants. Reed and Oring (1993) found that expanding their study site gave a more accurate picture of site fidelity and dispersal in Spotted Sandpipers *Actitis macularius*. However, previous multi-site studies on breeding terns showed that terns nesting on colonies closer together

experience higher rates of movement than those further apart (Spendelov et al. 1995; Devlin et al. 2008). The two colonies in our study were extremely close together (c. 4 km), and very little movement was observed between the two sites. Due to this low movement probability, we assume that there is little emigration of Damara Terns from

colonies, but a multi-site study would be required to test this assumption. Spendelov et al. (2010) found that a small sample of Roseate Terns *Sterna dougallii*, even after breeding in one region for many years, may move up to 400 km to another region to breed.

The low local dispersal probability of 0.06 indicated that Damara Terns show fidelity to the same breeding area. Low dispersal probabilities may have evolved in the species as a result of previous knowledge of breeding sites, like associated predation risk factors and prey availability. Damara Terns suffer high predation rates, even at the study areas in question (Braby et al. 2001, 2009; Braby 2011). Generally, increased predation rates at tern colonies result in low site fidelity, or mass movement from breeding areas (Spendelov et al. 2002). It thus comes as a surprise that Damara Terns display little dispersal from their study sites. This tern may have evolved with high rates of predation, and thus shows fidelity to sites due to learned and acquired knowledge of predation risks at these sites. In addition, protection of colonies from disturbance by ORVs may also be playing a role in colony-site fidelity. Little or no change to habitat occurs at either breeding sites (Horses Graves and Caution Reef, Braby, personal observation) and unpredictable breeding habitat usually yields little fidelity (Robinson and Oring 1997). For instance, California Least Terns *Sternula antillarum browni*, which are confined to several secure breeding sites, display a 79% rate of return to the same breeding site yearly (Atwood and Massey 1988), but interior Least Terns *Sternula antillarum athalassos*, which breed on sandbars and islands in rivers (a habitat that is continuously changing), display yearly return rates of only 42% (Renken and Smith 1995b). Species which are not accustomed to changing habitats are generally more site faithful and they may fail to move if their breeding habitats are impacted by humans, which would therefore reduce their ability to breed successfully (Southern and Southern 1982).

Prior to this study no details of the demography of Damara Terns were known, which in the past has (1) prevented basic population modeling, and (2) prevented meaningful comparisons with other terns. Such comparisons could help determine whether or not species considered closely related share important demographic characteristics and would better our understanding of similar life-history strategies (Stenhouse and Robertson 2005). Demographic parameters also help us find appropriate conservation approaches to ensure the species survival. Damara Terns migrate c. 8,000 km each year and breed in harsh desert environments with high rates of predation, but feed in highly productive waters where food is abundant (Crawford et al. 2006). Low breeding success (probability of less than 0.4 of nests surviving predation per season per pair; Braby 2011), high annual survival and fidelity to breeding sites may have

evolved as a response to these conditions. In light of this, the most important management approach for the population viability for seabirds such as the Damara Tern, which display high rates of fidelity, may be long-term maintenance and protection of current colony sites.

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