Prey capture success and chick diet of Damara terns Sterna balaenarum in Namibia

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Feeding terns are affected by a variety of environmental conditions. We studied prey capture success of Damara terns *Sterna balaenarum* in relation to six variables at two breeding colonies in southern Namibia: tidal phase, wind speed, water clarity, cloud cover, water depth and locality. Damara terns dived most successfully at high tide and least successfully at low tide. Prey capture success improved whereas total dive rate decreased with increasing wind speed. Prey capture success was highest in the least turbid water, but was not significantly affected by cloud cover or water depth, and there was no significant difference in dive success between localities. The diet of Damara tern chicks were studied throughout Namibia. Of 55 prey items collected, Cape silverside *Atherina breviceps*, southern mullet *Liza richardsonii* and Cape anchovy *Engraulis encrasicolus* were among the most abundant prey species. At least nine prey species were found in the diet of Damara tern chicks that had not been previously reported from Namibian waters

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Introduction

The success of foraging seabirds is influenced by prey availability, which is a function of both prey abundance and prey accessibility (Henkel 2006). Especially for seabird species feeding close to the coastline, prey accessibility may be influenced by a number of environmental factors. For example, tidal phase and wind speed can have an affect on the feeding ecology of terns (Hulsman et al. 1989, Becker and Specht 1991, Frank 1992, Becker et al. 1993, Brenninkmeijer et al. 2002, Peste et al. 2004, Paiva et al. 2008). Prey capture success or chick provisioning has generally been found to increase at low or receding tides (Brenninkmeijer et al. 2002, Peste et al. 2004, Paiva et al. 2006), and increased success at high tide has been shown (Hulsman 1976, Burger 1982). Taylor (1983) found a decreasing capture rate at higher wind speeds, but Dunn (1972, 1973) indicated that capture rates improved with increasing wind speed.

Water clarity has an effect on the distribution and ecology of feeding seabirds (e.g. Abrahams and Kattenfield 1997, Holm and Burger 2002, Day et al. 2003, Henkel 2006). Baptist and Leopold (2010) found a non-linear relationship between prey capture success and water turbidity, with the least success in either clear or very turbid waters, and greatest for moderate levels of turbidity.

Hawksley (1957) and Lemmetyinen (1972) showed that Arctic tern *Sterna paradisaea* chicks gained weight on clear days (low cloud cover) and generally lost weight on foggy days, but neither study considered prey capture success directly. Factors affecting prey capture success are important as they can influence various aspects of breeding success (Peste et al. 2004).

Damara terns *Sterna balaenarum* feed mainly by plunge-diving (Simmons and Braine 1994). Feeding terns are found in sheltered bays, lagoons, estuaries and in the surf zone along the open coast (Frost and Shaughnessy 1976, Clinning 1978, Williams and Myer 1986, Braby et al. 1992, Simmons 2005a). Small samples of prey items collected from chick regurgitations (Clinning 1978, Simmons and Braine 1994) have been found to be similar to those of related species, such as Peruvian terns *Sterna lorata* (Zavalaga et al. 2008) and little terns *Sterna albifrons* (Bogliani et al. 1994, Catry et al. 2006, Paiva et al. 2006).

The main aim of this study was to investigate the prey capture success of Damara terns *Sterna balaenarum* breeding at two localities in southern Namibia as a function of six variables: wind speed, tidal phase, water clarity, cloud cover, water depth and locality. New information on the diet of Damara tern chicks is also presented.

Material and methods

Study area and foraging observations

The prey capture success of Damara terns was measured during two consecutive breeding seasons (2007/2008 and 2008/2009) at two localities in southern Namibia: Grosse Bucht (26°43′ S, 15°40′ E) and Elizabeth Bay (26°55′ S, 15°14′ E; Figure 1). Elizabeth Bay is about 4 km wide: Elizabeth Point, a rocky promontory, forms the western arm of the bay and rocky shores backed by sand dunes form the eastern shoreline (Pulfrich et al. 2003). There is a valley directly north-east of Elizabeth Bay, which is comprised of salt pans and gravel plains, most of which have been disturbed by diamond mining operations. South-east of Elizabeth Bay is an extensive area of sand dunes and gravel plains, which reach the shoreline on the eastern side of the bay. Damara terns breed within this area, about 4 km from the sea. Grosse Bucht is a bay about 2.5 km wide within the recreational area on the Lüderitz Peninsula. Small rocky promontories extend on either side of the bay. Damara terns breed on a salt pan directly north of the bay about 800 m from the sea. Both bays are influenced by winds that may exceed 50 km h^{-1}.

Observations on foraging by terns were made throughout the two breeding seasons, during daylight hours and either from a vehicle or the beach. Once a Damara tern was recorded foraging, it was watched continuously using 8×42 binoculars. Its activities were timed (to the nearest second) until it flew back to the colony, landed or flew out of sight. A single foraging bout consisted of a bird looking down while flying or hovering 1–5 m above the sea surface. The numbers of successful and unsuccessful dives were recorded for each foraging bout.

Five environmental conditions were recorded during each foraging bout: tidal phase, wind speed, water clarity, cloud cover and feeding location. Four tidal phases were categorised: high tide (HT; 90 minutes before HT until 90 minutes after HT), receding tide (RT; the following three hours), low tide (LT; 90 minutes before LT until 90 minutes after LT) and incoming tide (IT; the following three hours).

Wind speed was estimated in the field and allocated to four categories: 1 — calm to gentle breeze, 2 — moderate breeze, 3 — wind and 4 — strong wind. When the observed descriptions of wind speeds were checked against the measured wind speeds at the weather station at Diaz Point (26°38′ S, 15°05′ E), the mean wind speeds in the four categories were approximately 10, 20, 30 and 45 km h^{-1} respectively. Using the midpoints between these values (15, 25 and 37.5 km h^{-1}) as boundary points, there were only eight occasions (out of 119 observations) when the assigned category differed from the measurement. For all except one of these, the wind speed at Diaz Point was greater than in the study area. Diaz Point is particularly exposed to winds, and is 11 km north of Grosse Bucht and 33 km north of Elizabeth Bay (Figure 1). Wind conditions can vary considerably between these areas, depending on its direction.

Water clarity was classified on a three-point scale at Elizabeth Bay, where clarity was affected by sediments deposited into the bay as a result of the diamond mining extraction process (Clark 1998, Simmons 2005b). Water colour was used to estimate water clarity: a gradient from 1 to 3 was adopted, where 1 was the least turbid water (blue water) and 3 the most turbid water (brown water). It should be noted that least turbid water at Elizabeth Bay is still relatively turbid on account of sediment deposits into the bay and the high winds and natural turbidity of the area.

Cloud cover was estimated in the field on a scale of 0 for no cloud to 4 for completely overcast. Adults observed foraging were assigned to water depth: the shallows, in the surf zone, or behind the breakers

A generalised linear model (GLM) with a binomial distribution and a logistic link function was used to relate the number of successful dives in a foraging bout, i.e. dives that resulted in prey capture to the five explanatory variables observed at the time of the bout. For each variable, the first level was set as the baseline level in the GLM. Analyses were performed in GenStat 12 (GenStat Committee 2009). Because water clarity was only gauged at Elizabeth Bay, the dataset for all explanatory variables (including water clarity) was analysed separately when investigating the influence of water clarity on prey capture success. A GLM with a Poisson distribution and logarithmic link function was used to relate the number of dives during the observation period to wind speed. The modelled probabilities of prey capture success were calculated using the inverse of the logistic transformation from the parameter coefficients that were determined from the GLMs.

During each observation, the total number of adults actively foraging in Elizabeth Bay was counted. Single-factor ANOVA was performed on the numbers of Damara terns counted foraging during observations with respect to three environmental variables: tidal phase, wind speed and cloud cover. Because terns moved as they foraged, it was not possible to count terns in each category of water depth during each observation.

Collection of prey items

Chick regurgitations and prey items dropped by adults while provisioning their chicks were collected at the following localities and time periods: Ogden Rocks (21°06′ S, 13°34′ E) on 19 December 1992; Durissa Bay Pans (21°15′ S, 13°41′ E) and White Stones (21°39′ S, 13°56′ E) during December 2009–March 2010; Caution Reef (22°44′ S, 14°32′ E) during October 1994–March 1995; Hottentots Bay (26°14′ S, 14°59′ E), Grosse Bucht, Elizabeth Bay and Marmora Pan (27°45′ S, 15°34′ E) during October 2007–April 2008 and October 2008–April 2009 (Figure 1).

Energetic content of fish

In order to estimate the energetic content of the fish species fed to chicks, fresh specimens were collected using a small net from foraging areas at Grosse Bucht. These specimens were measured (standard length), washed with fresh water and frozen. To determine the energetic content, specimens were thawed and dried in an oven at 60 °C until no further weight loss occurred (c. 7 days). Each dried specimen was crushed to dust in a mortar. This was converted into discs in a press and used to determine the calorific content in the Cal 2k bomb calorimeter. The energetic content was given by the calorimeter in kilojoules per gramme of dry mass.
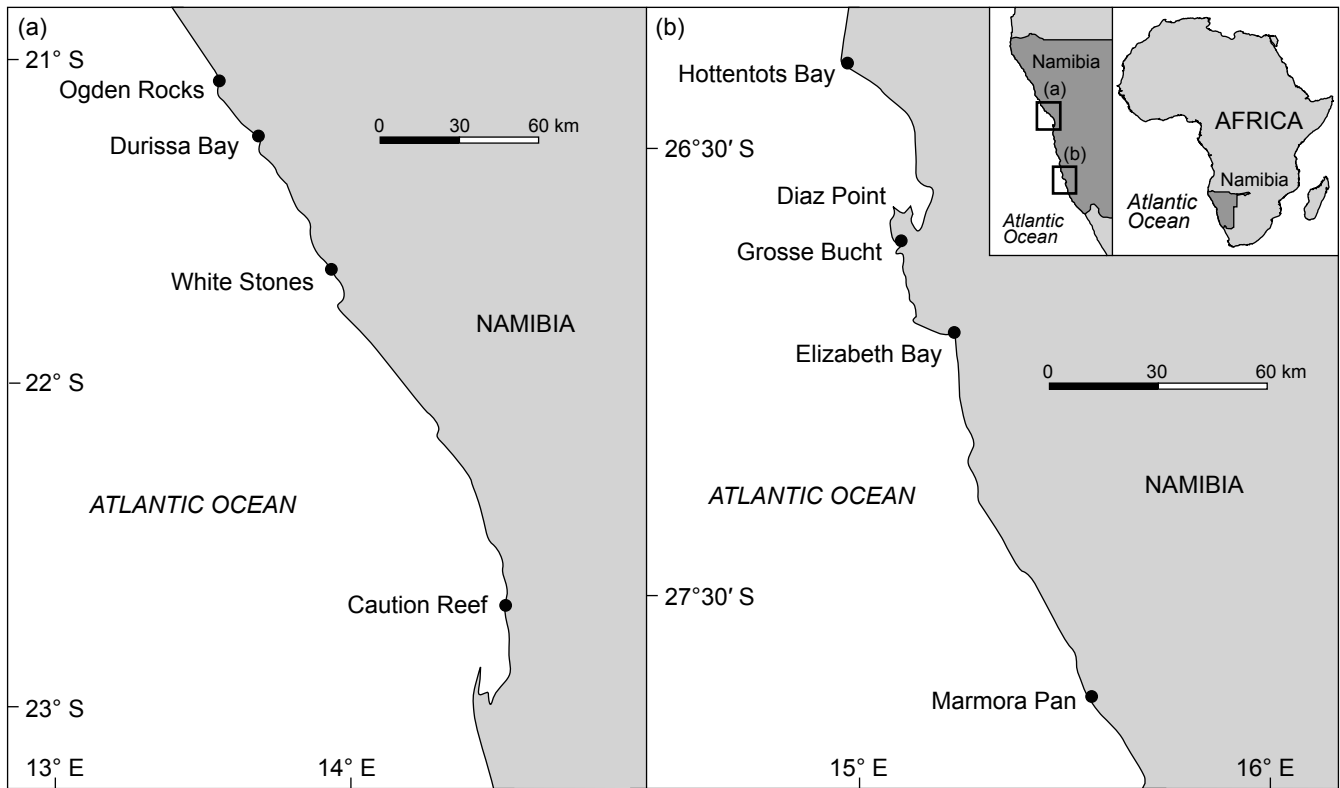
Figure 1: (a) Map of Namibia showing the breeding localities where prey items of Damara tern chicks were collected; (b) map showing Elizabeth Bay and Grosse Bucht in southern Namibia where prey capture success of Damara terns was measured. Wind speed measurements were obtained from Diaz Point
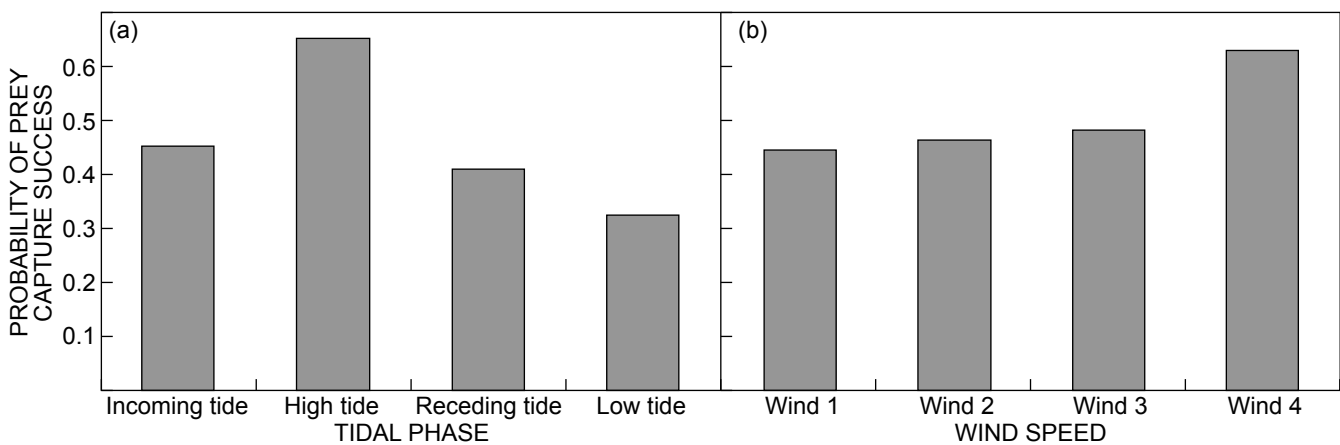

Figure 2: Modelled probabilities of prey capture success of Damara terns in southern Namibia. In each plot, all (except one) explanatory variables are held constant. Prey capture success probability is shown in relation to (a) tidal phase, with wind set to category 4 and (b) wind speed, with tidal phase set to high tide. A similar pattern was obtained for other combinations of the explanatory variables (not shown)

Results

Prey capture success

Damara terns were always observed foraging at sea. During 105 hours of observations for foraging terns, there were 389 bouts of feeding, lasting a total of 16.6 hours. During these bouts, there were 865 dives of which 305 were successful (30.5%; SD 3.1). The mean time spent foraging during a feeding bout was 153 seconds (SD 124 , n = 389). The mean number of terns counted foraging per observation was two. The numbers of terns foraging were not significantly affected by tidal phase ($F_{3,126}$ = 0.51, p > 0.25), wind speed ($F_{3,126}$ = 0.47, p > 0.25) or cloud cover ($F_{3,102}$ = 0.67, p > 0.25).

Modelled probability of prey capture success was highest (0.65) at high tide (Figure 2a). Capture success at

incoming (0.45), receding (0.41) and low (0.33) tides was significantly lower than at high tide (Table 1).

There was a tendency for capture success to increase with increasing wind speed. For wind level 1 (the baseline level of the model), it was 0.45 and increased to 0.47 at wind level 2, to 0.49 at wind level 3 and to 0.63 at wind level 4 (Figure 2b). For wind level 4, capture success was significantly different from wind level 1 ($p = 0.001$), but not for wind levels 3 ($p = 0.487$) and 2 ($p = 0.769$). However, the dive rate (dives per minute) decreased with increasing wind speed (Table 2). The product of the dive rate and the modelled prey capture success provided an estimate of prey capture rate (successful dives per minute) and this decreased with increasing wind speed (Table 2).

At Elizabeth Bay, water clarity was a significant explanatory variable in predicting prey capture success (Table 3).

In relation to water clarity 1 (least turbid water, success of 0.37; Figure 3) the capture success (0.12) was significantly lower in water clarity 3 (most turbid water, $p < 0.001$). The capture success in water clarity 2 (0.24) also was significantly lower than in water clarity 1 ($p = 0.008$; Figure 3).

Cloud cover, water depth and locality were not significant explanatory variables in predicting prey capture success. Neither were interactions between explanatory variables significant.

Diet composition

In total, 55 prey items were collected at seven localities along the Namibian coast over a period of 18 years (1992–2010; Table 4). Five prey categories could not be identified to species level. The 50 identifiable prey categories represented 15 fish species in 12 families, of which Cape

Table 1: Results of the generalised linear model with binomial distribution and logistic link function relating the prey capture success of Damara terns at two breeding areas in southern Namibia to two explanatory variables, tidal phase and wind speed. Both variables are categorical, with baseline categories, for which the estimated regression coefficients are set to zero

Explanatory variable	Coefficient	SE	$t_{388,2}$	p-value
Constant	−0.209	0.283	−0.74	0.460
Tide high	0	0	0	−
Tide receding	−0.906	0.285	−3.18	0.001
Tide low	−1.270	0.303	−4.19	<0.001
Tide incoming	−0.735	0.275	−2.67	0.008
Wind 1 (calm breeze)	0	0	0	−
Wind 2 (moderate breeze)	0.071	0.241	0.29	0.769
Wind 3 (wind)	0.147	0.211	0.69	0.487
Wind 4 (strong wind)	0.754	0.232	3.25	0.001

Table 2: Percentage of successful dives, dive rate (dives per minute) and prey capture rate (number of prey captured per minute) in relation to wind speed for foraging Damara terns in southern Namibia

Wind category	Successful dives (%)	Dive rate	Prey capture rate
Wind 1 (calm breeze)	24.0	1.366	0.612
Wind 2 (moderate breeze)	27.9	0.935	0.436
Wind 3 (wind)	28.4	0.814	0.395
Wind 4 (strong wind)	45.8	0.598	0.379

Table 3: Results of the generalised linear model with a binomial distribution and a logistic link function showing modelled prey capture success of Damara terns at Elizabeth Bay in southern Namibia in relation to three explanatory variables: tidal phase, wind speed and water clarity. Because water clarity was only measured at Elizabeth Bay (due to turbidity increase as a result of diamond mining processes), a separate analysis was performed for Elizabeth Bay. All three variables are categorical, with baseline categories, for which the estimated regression coefficients are set to zero

Explanatory variable	Coefficient	SE	$t_{176,2}$	p-value
Constant	0.279	0.385	0.72	0.469
Tide high	0	0	0	−
Tide receding	−1.120	0.403	−2.78	0.005
Tide low	−1.893	0.470	−4.03	<0.001
Tide incoming	−0.825	0.421	−1.96	0.05
Wind 1 (calm breeze)	0	0	0	−
Wind 2 (moderate breeze)	0.790	0.479	1.65	0.099
Wind 3 (wind)	0.631	0.359	1.76	0.078
Wind 4 (strong wind)	0.987	0.353	2.80	0.005
Water clarity 1 (least turbid)	0	0	0	−
Water clarity 2	−0.605	0.286	−2.11	0.035
Water clarity 3 (most turbid)	−1.434	0.327	−4.38	<0.001

silverside *Atherina breviceps* was the most abundant (18%, *n* = 10). This species was, however, not represented in any of the prey items found in the breeding colonies of southern Namibia. Species from the family Blennidae (14.2%, *n* = 8), southern mullet *Liza richardsonii* (12.5%, *n* = 7), and

Cape anchovy *Engraulis encrasicolus* (10.7%, *n* = 6), were among the most abundant prey species. The mean length of 27 whole prey items was 5.67 cm (SD 2.56 cm, range = 2.27–10.84 cm). Fresh weight of three items were obtained: two Cape anchovy weighed 4 g (length = 7.48 cm) and 3.48 g (length = 9.26 cm) and a needlefish (Belonidae) weighed 2.7 g (length = 9.20 cm).

Energetic content
The mean energetic content of four fresh southern mullet prey (mean length = 5 cm) that were foraged at Grosse Bucht was 14.84 kJ g dry mass^{-1} (Table 5).

Discussion

Prey capture success
Tidal phase, wind speed and water clarity significantly affected the prey capture success of foraging Damara terns, but cloud cover, water depth and feeding locality did not. The data showed that Damara terns had an overall prey capture success of 30.5%. Simmons and Braine (1994) found a successful capture rate of only 14% from 35 attempts by Damara terns foraging in northern Namibia. This lower prey capture success may have resulted from a smaller sample size in their study or a lower availability of prey.

This study found that Damara terns dived most success-fully at high tide. In six other studies, no consistent trend in prey capture success was found with the tidal cycle. For little terns. Peste et al. (2004) found a higher prey capture
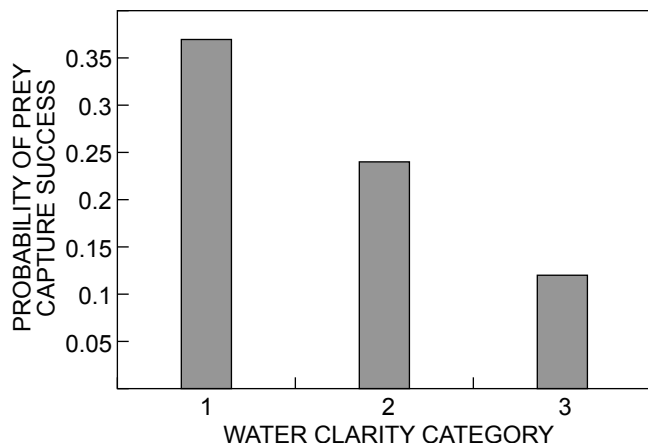

Figure 3: Modelled probabilities of prey capture success of Damara terns at Elizabeth Bay in relation to water clarity (1 = least turbid, 3 = most turbid). Other explanatory variables were held constant, wind at category 4 and tide at high. A similar pattern was obtained for other combinations of wind categories and tidal phase (not shown)

Table 4: Damara tern chick diet composition in Namibia as determined from chick regurgitations and food dropped by adults (1992–2010)

Family	Common name	Scientific name	Prey items (*n*)	Place and season
Atherinidae	Cape silverside	*Atherina breviceps*	10	Caution Reef (1994/95, *n* = 5), White Stones (2009/10, *n* = 1), Durissa Bay Pans (1992/93, *n* = 2; 2009/10, *n* = 2)
Belonidae	Needlefish sp.	*	2	Durissa Bay Pans (1992/93, *n* = 1), Ogden Rocks (1992/93, *n* = 1)
Blennidae	Larval blenny sp.	*	2	Caution Reef (1994/95, *n* = 2)
	Horned blenny	*Parablennius cornutus*	6	Caution Reef (1994/95, *n* = 6)
Clinidae	Klipfish sp.	*	2	Caution Reef (1994/95, *n* = 2)
	Super klipfish	*Clinus superciliosus*	1	Caution Reef (1994/95, *n* = 1)
Engraulidae	Cape anchovy	*Engraulis encrasicolus*	6	Hottentots Bay (2008/09, *n* = 4), Caution Reef (2009/10, *n* = 1), Durissa Bay (1992/93, *n* = 1)
Gobidae	Goby sp.	*	1	Caution Reef (1994/95, *n* = 1)
Gonorhynchidae	Beaked sandfish	*Gonorhynchus gonorhynchus*	1	Hottentots Bay (2008/09, *n* = 1)
Merlucciidae	Hake sp.	*	3	Hottentots Bay (2008/09, *n* = 1), Marmora Pan (2007/08, *n* = 2)
Mugilidae	Southern mullet	*Liza richardsonii*	6	Marmora Pan (2007/08, *n* = 2), Grosse Bucht (2008/09, *n* = 2), Hottentots Bay (2007/08, *n* = 1), Caution Reef (1994/95, *n* = 1)
Scomberesocidae	Saury	*Scomberesox saurus scomberoides*	2	Hottentots Bay (2008/09, *n* = 2)
Serranidae	Comber	*Serranus cabrilla*	4	Marmora Pan (2007/08, *n* = 4)
Sparidae	Seabream sp.	*	1	Grosse Bucht (2008/09, *n* = 1)
	Blacktail	*Diplodus sargus capensis*	3	Caution Reef (1994/95, *n* = 3)
Unidentified sp.	*	*	5	Hottentots Bay (2007/08, *n* = 2; 2008/09, *n* = 3)

* Denotes species (or families) that could not be accurately identified

Table 5: The energetic content of southern mullet specimens collected at Grosse Bucht in southern Namibia

Southern mullet specimen number	Standard length (cm)	Energetic content (kJ g^{-1} dry mass)
1	4.7	14.25
2	6.2	14.04
3	–	Sample too small
4	–	15.78
5	7.8	15.32

success during the receding tide, and Davies (1981) observed chicks of this species being fed mostly in the last hours of the receding and incoming tide. Brenninkmeijer et al. (2002) estimated a better food intake rate for little terns during the receding tide. Because these studies were mainly conducted at lagoons, estuaries and salinas, the narrow channels of water connecting them to the ocean would be greatly affected by the tide. Possibly during the receding tide, fish become more grouped and conspicuous in these channels and easier to catch (Peste et al. 2004). Paiva et al. (2006) found that the number of foraging little terns was higher during low tide. However, this was not the case in our study where the number of Damara terns was similar across all four tidal phases. Common terns *Sterna hirundo* in Jamaica fed primarily during high tides (Burger 1982). Hulsman (1976) had similar observations with black-naped terns *Sterna sumatrana*. However, Erwin (1977) found no effect of tides on common terns feeding in Maryland. Burger (1982) postulated that during low tides, many areas of a bay may be exposed, thus decreasing feeding habitat, and fish may move back into the shallow areas of the bay with an incoming tide. Damara terns frequently dived in shallow waters but water depth did not significantly impact prey capture success. Both Elizabeth Bay and Grosse Bucht have areas exposed at low tides and these areas are relatively shallow at high tide. Perhaps during high tide there is more feeding habitat, thus reducing competition between terns within the feeding grounds in the bays studied.

As in this study, for sandwich terns *Sterna sandvicensis*, Dunn (1972, 1973) found that prey capture success increased with increasing wind speed. This could be explained by visibility of the predator to prey organisms, which may be influenced by more vigorous hovering action at low wind speed and by the visibility of the predator afforded by the properties of a smooth sea surface (Dunn 1973). Dive rates and prey capture rates increased with decreasing wind speeds. Prey visibility is probably better during calm conditions and Damara terns may dive more frequently in these conditions because of this greater visibility. Taylor (1983) also found that dive rates decreased significantly with increasing wind speed in common and sandwich terns, but prey capture success showed no significant relationship to wind speed. Paiva et al. (2006) found that wind speed affected delivery rate of prey to little tern chicks. Stienen et al. (2000) reported an increased chick provisioning rate for sandwich terns in the Wadden Sea at wind speeds of around 30 km h^{-1} compared to lighter winds, but found a rapid decline at speeds over 50 km h^{-1}. However, Dunn

(1975) postulated that, under most wind conditions, the fishing success of adult terns is not altered sufficiently to influence tern chicks' daily intake of food. Wind conditions may affect flight speed to and from the breeding area, as well as foraging success.

Prey capture success was highest in least turbid water at Elizabeth Bay. Based on only 10 foraging bouts during 24.5 minutes of continuous foraging in murky water, Simmons (2005a) suggested that Damara terns avoid murky, sediment-filled water. Henkel (2006) suggested that plunge-divers should be associated with clear waters, where prey can be located visually from a distance, but noted studies that showed some species including terns prefer more turbid water (Haney and Stone 1988, Safina and Burger 1988). Prey may avoid the surface layers in clear waters to escape from plunge-diving predators. Hence, plunge-divers like terns may prefer moderated turbid waters, where prey may concentrate near the surface. The strongest upwelling in the Benguela system occurs near Lüdertiz (Shannon 1989) and natural water turbidity is generally quite high around Grosse Bucht and Elizabeth Bay, both of which are close to Lüderitz. Water turbidity at Elizabeth Bay is also increased due to the discharging of fines into the bay as part of the diamond mining process (Clark 1998, Simmons 2005b). The Damara terns under study dived for prey more successfully in the least turbid water, which arguably is still quite murky. Prey capture success may decrease if the water was very clear. Such a non-linear relationship was found in a study of sandwich terns in the North Sea (Baptist and Leopold 2010).

Chick diet and energy content

At least nine prey species were found in the diet of Damara tern chicks that had not been reported in two previous feeding studies in Namibian waters (Clinning 1978, Simmons and Braine 1994). Prey commonly found in all three studies included larval blenny, mullet, anchovy and needlefish. The diet of the Damara tern chicks under study was similar to that described by Catry et al. (2006) for fish fed to little tern chicks (e.g. *Artherina* sp., *Mugil* sp., Blennidae, Gobidae), by Elliot et al. (2007) for the diet of the California least tern *Sterna antillarum browni* (e.g. *Atherina* sp., Gobidae, *Engraulis* sp.), and by Zavalaga et al. (2008) for the diet of the Peruvian tern (e.g. *Atherina* sp., *Engraulis* sp., *Scomberesox* sp.). This emphasises the ecological similarities between these small terns.

Cape silverside occurs all along the coastline of south-western Africa (Smith and Heemstra 1986), but none were collected from chick regurgitations in southern Namibia. This absence of Cape silverside in the diet may be attributable to a small sample size. Most of the Cape silverside specimens were collected from the central coastline where Damara terns feed predominantly around the Swakop River Estuary (JB pers. obs.). A possible reason for this is that the Cape silverside is one of the few marine fish species that can withstand the reduction in salinity within the estuarine environment (Smith and Heemstra 1986) and thus may be important prey of Damara terns feeding in estuarine environments. The energy content of southern mullet specimens (14.84 kJ g^{-1} dry mass) was lower than that for Mugilidae species fed to little tern chicks in Portugal (20.35 kJ g^{-1} dry

mass; Paiva et al. 2006). A lower energy content of food may have implications for chick growth and other aspects of their breeding biology.

This study confirms the importance of environmental conditions on the feeding success of plunge-divers. Environmental conditions affecting feeding success are likely to be linked to numbers of Damara terns breeding and reproductive success in any given season.

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