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Breeding biology of Brown Noddies *Anous stolidus* at their southern-most breeding site, Gough Island, in comparison to other sites

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We investigated the breeding biology of the Brown Noddy *Anous stolidus* at its southern-most breeding locality, cold-temperate Gough Island (40°S) in the South Atlantic Ocean. We monitored 19 nests over three seasons for breeding schedules, and measured the growth of eight chicks and six fledglings during the 2005/06 breeding season. Across all seasons, egg-laying occurred between 2–12 December, mean incubation was 37 days and median hatch date was 15 January. Three late hatch dates suggest that replacement clutches can be laid if failure occurs early in the season. Chicks fledged after a mean of 46 days, but remained in the vicinity of the nest and were provisioned by adults for up to 11 days. Hatching success was 88%, fledging success 92% and breeding success 81%, which is higher than at most other sites. The size, chick growth-rates and pre-fledging fast displayed by Gough's Brown Noddies are similar to that of Brown Noddies breeding at other mid-latitude Atlantic locations. These similarities of these migratory noddy populations, as well as mirrored breeding schedules suggest a single mid-latitude Atlantic meta-population.

Key words: Atlantic Ocean, breeding success, chick growth rates, Tristan da Cunha, tropical seabird

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The Brown Noddy *Anous stolidus* is a widespread tern species, ranging over tropical and subtropical parts of the Pacific, Atlantic and Indian oceans (del Hoyo *et al.* 1996). Although predominantly a tropical breeder, they also breed at temperate localities including the Tristan da Cunha archipelago (Richardson 1984). Gough Island, ca. 400 km south-southeast of Tristan, is the southern-most and only Brown Noddy breeding location outside the sub-tropical convergence (Swales 1965, Cooper & Ryan 1989).

The breeding biology of the Brown Noddy is relatively well documented from tropical and subtropical islands (Megyesi & Griffin 1996, and references therein), but virtually nothing is known about populations occurring at cold-temperate localities, with previously published accounts confined to general descriptions of the timing and location of breeding (Elliott 1953, Elliott 1970, Richardson 1984, Fraser *et al.* 1988, Cuthbert & Sommer 2004, Ryan 2006). Here we present the first data on Brown Noddy breeding biology at Gough Island. We compare our results to those from other Brown Noddy populations.

Methods

Approximately 200 pairs of Brown Noddies annually breed in the lowlands of Gough Island Island (40°21'S,

9°53'W), characterised by coastal tussock vegetation and fernbush (Wace 1961). Apart from a weather station, there are no other permanent human occupants or structures on the island (Cooper & Ryan 1994).

Nests found in 1988/89, 2003/04 and 2005/06 were checked every 4–7 days (less regularly during incubation), and laying, hatching and fledging dates recorded. When eggs were found after laying, the laying date was estimated using hatching date and the median incubation period estimated from this study. Hatching success is defined as the proportion of eggs that produced a chick, fledging success as the proportion of chicks that fledged and breeding success as the proportion of eggs laid that produced a fledgling. Fledging is defined by the date when chicks that completed moulting into sub-adult plumage were first observed to fly, even though they may remain on or near the nest and be provisioned for some time after first flying (Megyesi & Griffin 1996).

We also took eggs and morphometric measurements of chicks and adults during the 2005/06 season. Lengths and breadths of fresh (<7 days old) eggs were measured to the nearest 0.1 mm using vernier callipers, and weighed to the nearest gram using a 100 g Pesola spring balance. Body mass was taken to the nearest 2.5 g using a 200 g Pesola spring balance, wing length measured to an accuracy of 1 mm with a stopped wing-ruler, and bill and tarsus length measured to an accuracy of 0.1 mm with vernier callipers. Measurements of chicks were taken on the first day they were found and thereafter every 2–6 days until fledging. Measurements were also taken from a single post-fledging chick. To eliminate potential bias resulting from time since last feeding (see Cuthbert & Davis 2002), we estimated maximum mass and age at maximum mass of chicks using the best-fit quadratic curve. We calculated growth constants using linear models (or logistic for tarsus growth) fitted to mass and morphometric measurements (hatching to peak mass) for all chicks of known age that survived to fledge. Evidence of diet was obtained from chicks that occasionally regurgitated while being handled, and from spilled food beneath nests. All statistics were conducted using R (R Development Core Team 2008).

Results

Most Brown Noddies arrived and commenced prebreeding activities in mid to late October, with the earliest sighting on 29 September, and all had left Gough island by early May. Nests were built from *Phylica arborea* twigs and lined with grasses and fruticose lichens (*Usnea* spp.). While some Brown Noddy pairs at Gough Island occupied cliff sites in previous years, during this study breeding occurred exclusively in the sub-canopy of *Phylica arborea* trees in small, dispersed colonies, but we never recorded more than one nest per tree. Nests were situated 1–2 m from the ground, typically over or near a stream. Three nests from a previous season were reused in 2005/06. From regular nest checks and measuring adults, it was evident that both parents incubated eggs and fed chicks a diet comprised predominantly of regurgitated small fish.

All clutches comprised a single white egg with varying degrees of brown and black speckling (n = 16 nests). Mean egg length was 50.8 mm (range 48.3–52.2 mm, n = 7), mean breadth was 34.6 mm (34.1–36.0 mm, n = 7) and mean weight 31 g (range 26–33 g, n = 7). Most eggs were laid between 2–12 December (median: 9 December, n = 9). Incubation lasted 33–38 days (median: 37 days, n = 5), with eggs hatching between 9–19 January (median: 15 January, n = 9), though during 2003/2004 and 2005/06 we also found three nests that respectively hatched on 1, 7 and 8 February. Although chicks were observed flying when they were on average 46 days old (range: 39–47 days), they remained in the vicinity of the nests and continued to be provisioned by adults for up to 11 days, until an average age of 54 days (n = 5, range: 51–56 days) when chicks were not seen near the nest anymore. The last chicks fledged on 20 March 2004 and 29 March 2006. Over the three seasons, mean hatching success was 88% (n = 14), fledging success was 93% (n = 13) and breeding success 81% (n = 13).

Mean body measurements of breeding Brown Noddies and fledglings are presented in Table 1. The mass of chicks from hatching to fledging was well described by a quadratic curve (r^2 = 0.862, Fig. 1). From age 1–28 days, chicks gained weight at an average of 6.6 ± 0.4 g/day (r^2 = 0.890). Mean maximum chick mass, attained at a mean age of 29 days (n = 8, range 26–35 days), was 181 g (n = 8, range 170–198 g). Thereafter chicks lost mass at approximately 2.6 ± 0.4 g/day (r^2 = 0.741).

Throughout the chick period, the average increase in culmen length was logistic at 0.42 ± 0.01 mm/day (r^2 = 0.90), reaching adult length at fledging (Fig. 1). The egg tooth was lost at 4–5 days, while feathers started growing at approximately 7 days; the first primaries broke their sheath at a mean age of 15 days. Wing growth rate was linear at 5.11 ± 0.1 mm/day (r^2 = 0.96), reaching adult length at fledging (Fig. 1). Tarsus growth was also linear at 0.49 ± 0.1 mm/day, r^2 = 0.68) up until chicks were 19 days old, when tarsus length reached adult length (Fig. 1).

Table 1. Mean morphometrics (with SD and range) of Brown Noddy adults (n = 8), and fledglings (n = 6, taken as last measurement before chick fledged) at Gough Island during the 2005/06 breeding season.

	Adults			Fledglings		
	Mean	SD	Range	Mean	SD	Range
Body mass (g)	153.1	24.3	118.0–185.0	149.7	20.9	141.0–173.0
Bill length (mm)	33.0	4.3	28.2–43.0	31.5	1.6	28.2–32.4
Tarsus length (mm)	25.2	0.7	24.0–26.0	25.0	0.6	24.0–25.5
Wing length (mm)	222.1	22.6	179.0–257.0	215.6	18.1	179.0–225.0

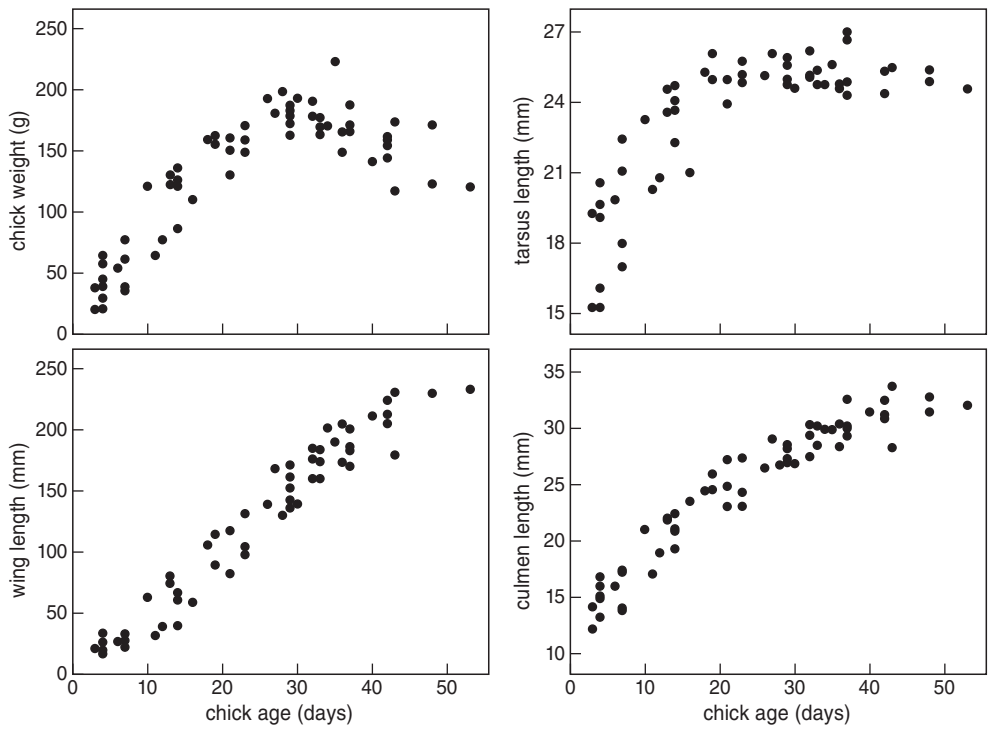

Figure 1. Growth rates of eight Brown Noddy chicks on Gough Island, South Atlantic Ocean, during the 2005/06 breeding season.

Discussion

The incubation period of 37 days for Brown Noddies at Gough Island corresponds closely to incubation periods recorded elsewhere (see Megyesi & Griffin 1996 for summary). Fledging ages however vary between localities, ranging from 40 days (Dry Tortugas, Ricklefs & White-Schuler 1978) to 48 days (Hawaii, Megyesi & Griffin 1996). That fledging ages of 42 days (Manana Island, Brown 1976) and 48 days (Tern Island, Megyesi & Griffin 1996) reported from different islands of Hawaii suggest that differences in fledging periods may be the result of observer bias in determining fledging ages as the time when chicks can fly vs. when they leave the nest (see also Megyesi & Griffin 1996). The range of fledging ages shows much overlap between localities, including Gough Island, and we therefore conclude that noddy chicks on Gough fledge at a similar age to chicks elsewhere. There is however a striking difference in the amount of time chicks spent near the nest and being provisioned by parents after fledgling at Gough (up to 11 days; this study) compared to elsewhere, e.g. up to 100 days at Hawaii (Brown 1973) and French Polynesia (MHB, pers. obs.).

Mass gains of Brown Noddy chicks also show much variability between localities. Chicks at Gough Island gain mass faster (6.7 g/day) than chicks at tropical localities such as the Seychelles (4.0 g/day, Ramos *et al.* 2006) and Hawaii (5.3 g/day, Megyesi & Griffin

1996). Furthermore, unlike chicks from tropical localities (e.g. Seychelles: Ramos *et al.* 2006, but see Brown 1976), noddy chicks from Gough Island (this study) and other Atlantic Ocean breeding localities such as the Dry Tortugas (Ricklefs & White-Schuler 1978) and Ascension Island (Dorward & Ashmole 1963) undergo a pre-fledging fast/weight loss after the mass gain phase. Given that tropical non-migratory noddy populations do not display pre-fledgling breeding fasts, and the short period Gough's noddy chicks remain near nests after fledging, the Atlantic Ocean noddies' pre-fledging fast may be an adaptive strategy in light of time constraints in preparation for migration, as parents stop feeding chicks at an early stage, forcing them to sea in search of food.

While hatchling body masses of Gough's noddies match those reported elsewhere (see e.g. Ricklefs & White-Schuler 1978, Megyesi & Griffin 1996, Dorward & Ashmole 1963), fledgling and adult body masses differ widely between locations. Such differences are likely the result of varied growth rates displayed by noddies at different breeding localities as well as different nutritional status of the respective feeding grounds. For example, fledgling and adult body masses at Gough Island are similar to mean masses reported for similarly aged noddies from the Dry Tortugas (~160 g, and 159.2 g, respectively; Ricklefs & White-Schuler 1978). Adults and fledglings at these high- and mid-latitude Atlantic Ocean localities are however lighter than similarly-aged noddies from Tern Island (Hawaii) (200.4 g and 195.8 g, Megyesi & Griffin 1996) and Ascension Island (~190 g and ~210 g, Dorward & Ashmole 1963), both tropical islands.

Growth of skeletal features of Gough Island's noddies appears similar to that of noddies elsewhere. For example, chicks from Gough Island (this study), Hawaii (Brown 1976), the Seychelles (Megyesi & Griffin 1996), the Dry Tortugas (Ricklefs & White-Schuler 1978) and Ascension Island (Dorward & Ashmole 1963) display rapid, linear tarsus growth that reaches an asymptote at 25–30 days, and linear bill and wing development until fledging. Mean bill length of Gough's hatchlings and fledglings are similar to mean bill lengths reported from the Dry Tortugas (Ricklefs & White-Schuler 1978), which is smaller than reported for hatchlings and fledglings from tropical localities such as the Seychelles (Ramos *et al.* 2006), Hawaii (Megyesi & Griffin 1996, but see Brown 1976) and Ascension Island (Dorward & Ashmole 1963).

Gough Island's Brown Noddies have a high breeding success compared to noddies breeding elsewhere (e.g. Megyesi & Griffin 1996,). Predatory seabirds are a major cause of brood losses elsewhere (Megyesi & Griffin 1996). Though we were unable to ascertain the cause of the few brood failures of Gough Island's noddies, predation events appear to be relatively minor on Gough Island. This is probably due to the well protected nesting sites of Gough Island noddies (subcanopy of *Phylica* trees; also on cliff ledges at other Tristan archipelago islands (P.G. Ryan pers. comm.)) compared to the unprotected nesting sites at tropical breeding localities (e.g. Megyesi & Griffin 1996, Ramos *et al.* 2006). In addition, noddies at Gough Island defend their young from predators such as Subantarctic Skuas *Catharacta antarctica* by forming cooperative mobbing groups that includes non-breeding birds (JW & MHB pers. obs.). Mice are known to prey on seabird chicks on Gough Island (Wanless *et al.* 2007); however, Brown Noddies, are able to defend themselves against mice (see Heatwole 1985). We found three eggs that hatched in early February, suggesting a laying date of late December or early January, assuming a 37-day incubation period, (this study). While late breeders may have laid these eggs, it was more likely replacement clutches laid after early egg failure. Brown Noddies elsewhere do lay replacement clutches (Diamond & Prys-Jones 1986, Megyesi & Griffin 1996), but because of the relatively short breeding season of Gough's noddies, such a strategy may only be possible in the event of early egg failure.

Brown Noddies at Gough Island and elsewhere in the Tristan archipelago have a similar breeding schedule to birds from Ascension Island (November–May, Dorward & Ashmole 1963). This schedule closely mirrors the breeding season (April–September) of noddies from northern hemisphere, west Atlantic islands, notably the Dry Tortugas and Puerto Rico (Sprunt 1948, Morris & Chardine 1992). By contrast, Noddies breeding on tropical islands elsewhere are typically resident with asynchronous breeding and variable periodicity (Megyesi & Griffin 1996, and references therein). Some authors have postulated that Brown Noddies breeding at subtropical south Atlantic islands spend their non-breeding periods at sea (Murphy 1936, Dorward & Ashmole 1963). Nevertheless, two indirect lines of evidence, namely the timing of breeding and the very similar body sizes and growth rates of Brown Noddies at various Atlantic Ocean localities, makes the possibility of a single meta-population for high-latitude breeders and trans-equatorial migrations intriguingly possible. Genetic studies would confirm the relatedness of the different populations, while stable light isotope analysis (see Cherel *et al.* 2006) could potentially reveal major geographic migrations.

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Samenvatting

De Noddy *Anous stolidus* is een zeevogel die vooral in tropische gebieden broedt. De meest zuidelijk plek waar deze soort – zij het in kleine aantallen – broedt, is het eiland Gough, gelegen in de gematigde klimaatzone van de zuidelijke Atlantische Oceaan. Hier werd de broedbiologie van de soort onderzocht om een vergelijking te kunnen maken met soortgenoten die in de tropen broeden. In drie seizoenen werd het broedverloop van in totaal 19 nesten geregistreerd. In één seizoen werd de groei van acht kuikens en zes uitgevlogen jongen vastgelegd. De eieren werden tussen 2 en 12 december gelegd, de broedduur was gemiddeld 37 dagen en de eieren kwamen rond 15 januari (mediane datum) uit. Drie nesten kwamen erg laat uit, wat er op wijst dat het in deze gevallen ging om vervolglegsels na een mislukte broedpoging. De jongen waren na 46 dagen vliegvlug en werden erna nog 11 dagen in de buurt van het nest door hun ouders verzorgd. Van de eieren kwam 88% uit en van de jongen vloog 92% uit. Het broedsucces kwam hiermee op 81%, wat hoger is dan elders is vastgesteld. De grootte en groeisnelheid van de jongen van de Noddy op Gough zijn vergelijkbaar met die van soortgenoten op andere plekken in de gematigde zone van de Atlantische Oceaan. Ook is het tijdstip en duur van broeden vergelijkbaar met vogels van het noordelijk halfrond, behalve dat de Noddies van Gough tijdens onze wintermaanden broeden. (JP)

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