

Breeding biology of Masked Boobies (*Sula dactylatra tasmani*) on Lord Howe Island, Australia

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Abstract. The breeding biology and reproductive output of a colony of Masked Boobies on Mutton Bird Point, Lord Howe Island, Australia, were studied during the 2001–02 breeding season. The colony produced a total of 200 clutches. Eggs were laid between 31 May and 15 September 2001, with 80% of clutches begun before 21 July. More than 90% of clutches consisted of two eggs, laid, on average, 5.3 days apart. Mean incubation period was 45 days. Where both eggs hatched, the later-hatched chick had to compete with an aggressive elder sibling of greater mass; consequently, it seldom survived longer than 1 week. Hatching success was 38% for single-egg clutches, 81% for two-egg clutches and 78% overall. For two-egg clutches, 13% of successful chicks hatched from the second egg. In keeping with the comparative mass of adults, eggs and chicks from Lord Howe Island were larger than those from any other Masked Booby population where measurements have been made. Chick mass increased steadily to reach a maximum of 2235 ± 292 g (equivalent to mean adult mass) at 11 weeks of age. Overall, fledging success was 65%, but was greatest for eggs laid early in the breeding season. There was no difference in fledging success between chicks that were handled weekly and those that were handled only once. Overall breeding success was 51%. Rats were not a significant predator of eggs or chicks, and no other predators or land-based threats were identified. Clutch-size indicated that, at the time of laying, the Masked Booby population on Lord Howe Island was well nourished, but decreasing rates of hatching and fledging success, and less than optimal growth rates of chicks, suggested food availability declined during the nesting period. Regurgitations indicated that flying fish were the main prey.

Introduction

The Masked Booby (*Sula dactylatra*) has an extensive distribution in tropical and subtropical parts of the Indian, Pacific and Atlantic Oceans, breeding on oceanic islands between $\sim 30^{\circ}\text{S}$ and $\sim 30^{\circ}\text{N}$ (Marchant and Higgins 1990; Pitman and Jehl 1998). Lord Howe Island is the southernmost breeding location of the species.

The Masked Booby is polytypic. The subspecies that breeds on Lord Howe was described by O'Brien and Davies (1990) as *Sula dactylatra fullagari*. The greater body mass, longer wing and the brown (not yellow) colour of the iris are the main distinguishing features of this subspecies, which also breeds on Norfolk and Kermadec Islands (O'Brien and Davies 1990; Fricson and Anderson 1997). Earlier, another subspecies, known as the 'extinct' Tasman Booby (*Sula tasmani*), was described from subfossil material on Lord Howe (van Tets *et al.* 1988). It is now thought that this subfossil material was of individuals at the upper size range of *Sula dactylatra fullagari* (Holdaway and Anderson 2001). Recognising that *S. tasmani* and *S. d. fullagari* are the same taxon, we follow the recommendation of Holdaway *et al.*

(2001) that the birds currently, and formerly, on Lord Howe Island be known as *Sula dactylatra tasmani*.

When Lord Howe was discovered in 1788, Masked Boobies bred there in large congregations of thousands of birds (Hindwood 1940), but such densities have long since disappeared, presumably the result of persecution by man (McKean and Hindwood 1965). Nowadays, probably fewer than 500 pairs breed within the Lord Howe Group, mostly on small islets. Breeding on the main island is restricted to two small headlands where access by land is difficult. The situation is similar on Norfolk and Kermadec Islands, where populations now number ~ 350 and ~ 100 pairs respectively (Garnett and Crowley 2000). *Sula dactylatra tasmani* is currently classified as threatened (IUCN 1994; Garnett and Crowley 2000).

Suspected threats to the Masked Booby population on Lord Howe include predation by Black Rats (*Rattus rattus*), which were introduced in 1918. They quickly spread over the island and devastated the bird and invertebrate life (Hutton 1991). Two species of seabird that no longer occur on the main island of Lord Howe - the Kermadec Petrel

(*Pterodroma neglecta*) and the White-bellied Storm-Petrel (*Fregettagallaria*) - were probably extirpated by rats. The current impact of rats on Masked Booby populations is not known. An advanced Masked Booby chick found bleeding from a large hole in its neck raised concerns that rats may be attacking Masked Booby chicks, thereby reducing breeding success.

This paper reports on the first detailed study of the breeding biology of Masked Boobies on Lord Howe Island. The study examined population size, clutch-size, hatching success, fledging success and growth of chicks. The status of the population was investigated by comparing data from Lord Howe Island with similar data from two other populations of Masked Booby: *Sula dactylatra personata* on Kure Atoll, in the Hawaiian Leeward Islands (Kepler 1969; Woodward 1972) and *Sula dactylatra dactylatra* on Ascension Island (Dorward 1962a, 1962b). Threats to the population on Lord Howe are identified and discussed.

Methods

Study area

Lord Howe (31°30'S, 159°04'E) is a small (1455 ha) volcanic island in the South Pacific Ocean, ~570 km east of the Australian mainland (Fig. 1). Norfolk Island lies ~900 km to the north-east. The island is ~11 km long and 2.8 km at its widest point.

Masked Boobies breed on the main island of Lord Howe at Mutton Bird Point and King Point, as well as on Roach, South, Sugarloaf, Gower and Mutton Bird Islands, and Sail Rock (Fig. 1). A small colony also breeds on Balls Pyramid, 31 km to the south-east. The size of each colony is not known, but the largest congregations probably occur on Roach Island and Mutton Bird Point. The colony on Mutton Bird Point was the subject of this study. Mutton Bird Point is an oval-shaped plateau (up to 39 m above sea level), ~250 m in length and 150 m wide, covered almost entirely by introduced Kikuyu Grass (*Pennisetum clandestinum*). It is joined to the main island by a steep, narrow neck which can be traversed, with difficulty, in all but the most extreme sea conditions. Access to all other colonies within the Lord Howe Group is restricted to times when sea conditions are calm. No attempt was made to estimate the size of the total population within the Lord Howe Group.

Nest monitoring

On Lord Howe, Masked Boobies breed between May and March, with most eggs laid between June and November (Hutton 1991). Breeding activity on Mutton Bird Point was monitored weekly from the start of laying (7 June 2001) until all chicks either fledged or died (2 February 2002). Each week the entire plateau was searched for nests, and the contents of each nest recorded. The interval between the first and second visit was 9 days, thereafter it was 7 days.

Masked Boobies nest on the ground. The nest, a flattened, circular area of grass up to 1 m across, is easily recognisable. Each new nest containing at least one egg was marked with a numbered plastic tag attached to a 1-m tall aluminium stake. Prepared nests without eggs were neither marked nor counted. New eggs were weighed to the nearest gram using a 100-g spring balance, measured (length and maximum breadth) to the nearest 0.1 mm with vernier calipers, and marked with the nest number and, where known, laying order using a graphite pencil.

Chicks from odd-numbered nests were weighed and measured weekly. Chicks of mass <300 g were weighed to the nearest gram using a 300-g spring balance; those >300 g were weighed to the nearest 10 g

using a 2.5-kg spring balance. Measurements of head-bill length, culmen length and tarsus length were taken to the nearest 0.1 mm using vernier calipers. Tail length was measured to the nearest millimetre using a butt-end ruler. See Lowe (1989) for a description of measurement techniques. Growth curves were plotted for all measurements. Growth curves for mass and culmen length were then compared with those from other populations. Comparable growth curves for other measurements were not available.

At about 5 weeks of age, chicks were banded with individually numbered, stainless-steel bands supplied by the Australian Bird and Bat Banding Scheme (ABBBS, Canberra). At the same time, nesting adults were captured and banded. Chicks that wandered short distances from the nest before they were banded were identified on the basis of current size in relation to previous measurements. Chicks from even-numbered nests were handled only once, to band. To test whether frequent (i.e. weekly) handling of chicks affected their survival, fledging success was compared between odd and even numbered nests. Nests from the two groups were spatially mixed.

Hatching success, fledging success and breeding success

Masked Boobies are an obligate siblicide species (Dorward 1962b). Each clutch usually contains two eggs that hatch asynchronously (Kepler 1969; Woodward 1972). The later-hatched chick is usually attacked by its larger, elder sibling and so rarely survives for more than a few days. Thus, a clutch was deemed to have been successful if at least one chick hatched. Hatching success, therefore, was calculated as the number of clutches that hatched a chick as a proportion of the total

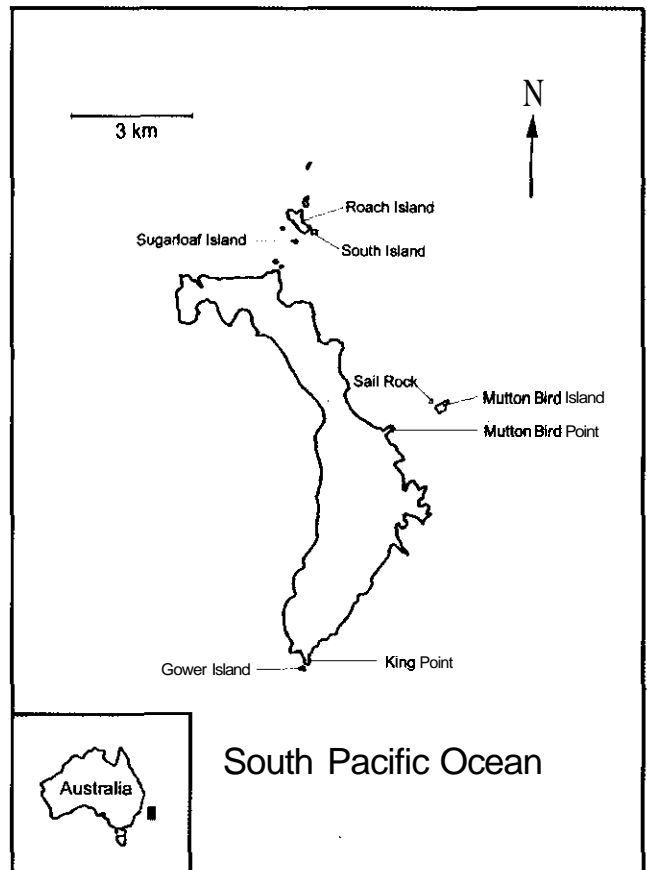


Fig. 1. Location of Masked Booby colonies within the Lord Howe Group.

Table 1. Dimensions and mass of Masked Booby eggs from various locations

Data are in order of decreasing length. Macauley Island is in the Kermadec Group, Willis Island is in the Coral Sea, and Bedout Island is in north-western Western Australia

Location	Length (mm)		Breadth (mm)		N	Mass (g)		N	Source
	Mean	Range	Mean	Range		Mean	Range		
Lord Howe Island	67.2	58.1–74.7	46.6	41.0–50.7	289	79.3	56.0–100.0	289	This study
Kermadec Island	67.0	64.5–70.0	47.0	46.0–49.3	5				Merton (1970)
Pacific islands	67.0	60.0–77.0	46.0	40.0–48.5	67				Bent (1922)
Macauley Island	66.3	61.7–71.1	46.5	45.1–47.9	12	75.1	68.0–85.0	12	Marchant and Higgins (1990)
Willis Island, Coral Sea	64.8	62.8–73.5	46.1	44.4–47.8	8	77.5	70.0–85.0	6	Serventy (1959)
Bedout Island, WA	63.2	55.9–68.4	45.5	39.5–57.4	15				Kolichis (1977)
Coral Sea islands	63.0	61.0–68.5	45.9	43.0–49.0	6				Hindwood <i>et al.</i> (1963)
Ascension Island	60.4	57.4–70.6	44.4	40.6–46.6	12	67.3	52.0–X2.5	12	Dorward (1962 <i>b</i>)

number of clutches. Fledging success was calculated as the number of fledglings produced as a proportion of the number of clutches with eggs that hatched. Age-specific survival of chicks was calculated as the number of individuals known to have survived to x weeks of age expressed as a proportion of the number of chicks surviving to $x-1$ weeks of age, excluding younger siblings.

Masked Boobies begin flying from ~15 weeks of age (Kepler 1969; Woodward 1972) and although flying juveniles may remain in the colony for a further 3–4 weeks and continue to be fed by their parents (Kepler 1969), they do not always return to the nest. Therefore, a chick was deemed to have fledged when it reached 14 weeks of age. Breeding success (the multiple of hatching success and fledging success) was calculated as the number of fledglings produced as a proportion of the number of clutches. Hatching, fledging and breeding success on Lord Howe Island were compared with other populations for which data were available.

Diet

Care was taken to avoid causing adults and chicks to regurgitate food while being approached or handled. Where these precautions failed, the regurgitant was examined and weighed, and then offered back to the bird that expelled it.

Results

Clutches and nests

During the 2001–02 breeding season, a total of 200 clutches was recorded. Three nest-sites were used twice. One reused nest contained a single egg that, 1 week later, had been ejected from the nest and replaced with a new egg. Two other nest-sites were reused after the first clutch failed to hatch. The time elapsed between these first and second clutches was 28 and 63 days respectively. As the first clutches were abandoned before the adult birds were banded, it is not known whether these second clutches were laid by the same pair of birds re-nesting at the same site or by another pair using the same nest.

Eggs

The 200 clutches contained a total of 387 eggs, giving a mean clutch-size of 1.9 eggs ($n = 200$), which is similar to that recorded for populations of Masked Booby on Kure Atoll (1.9 eggs, $n = 105$, Kepler 1969; 1.9 eggs, $n = 192$, Woodward 1972) and Vostok Island in the Line Islands (1.8

eggs, $n = 97$, Clapp and Sibley 1971), but greater than that on Ascension Island (1.3 eggs, $n = 96$, Dorward 1962*b*). Sixteen clutches were a single egg, 181 clutches had two eggs, and three clutches had three eggs. We do not know whether nests containing three eggs were laid by more than one female or whether the bird rolled an extra egg into the clutch, as has been reported by Dorward (1962*b*).

Eggs measured 67.2 ± 2.2 mm long (mean \pm s.d.), 46.6 ± 1.2 mm wide and weighed 79.3 ± 5.5 g. These eggs were among the largest of any population of Masked Booby for which data are available (Table 1). Where it was clear as to the order that the individual eggs within a clutch of two were laid (i.e. the two eggs were first recorded in different visits), the size and mass of the eggs were compared (Table 2). In comparison to the first egg laid, the second egg was shorter (paired t -test, $t = 4.228$, d.f. = 84, $P < 0.001$), narrower ($t = 2.765$, d.f. = 84, $P < 0.007$) and weighed less ($t = 5.499$, d.f. = 90, $P < 0.001$).

Laying dates

On the basis of hatching dates and incubation length (see below), several nests contained eggs that were 1 week old during the first search on 7 June 2001. Thus, laying started during the week ending 31 May 2001. The last egg of the season was laid in the week ending 15 September 2001. Laying was concentrated in the early part of the season, with 80% of clutches begun before 21 July 2001 (Fig. 2).

Single-egg clutches (Fig. 2) were more common later in the season (21% of clutches laid after 4 August 2001 compared to 8% overall). The mean interval between laying was

Table 2. Comparison of mean size and mass of first and second eggs of a clutch

Measurements and weights are for eggs up to 7 days old; P significance of paired t -test

	Length (mm)	N	Breadth (mm)	N	Mass (g)	N
First egg	67.7	85	46.9	85	81.1	91
Second egg	66.5	85	46.5	85	78.1	91
P	0.001		0.007		0.001	

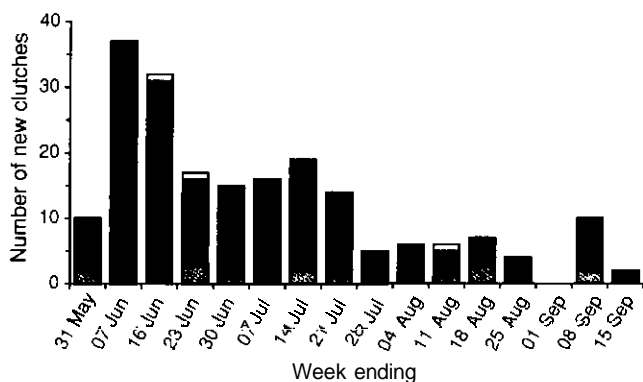


Fig. 2. Number of new clutches laid on Mutton Bird Point each week. Laying date of each clutch was taken as the date when the first egg was laid. Light shading, single-egg clutches; solid shading, two-egg clutches; no shading, three-egg clutches.

estimated to be 53 days. This is similar to the mean laying interval reported in other populations of this species; 5.3 days (Woodward 1972) and 5.6 days (Kepler 1969).

Incubation

The period of incubation (measured as the number of days between when the egg was first recorded and when the chick was first seen) was generally 42–49 days (mean \pm s.d. = 45.0 ± 4.1 days, $n = 137$). This was comparable with the mean incubation period recorded in other populations of this species: ~44 days for first eggs (range 40–49 days) and ~43 days for second eggs (range 38–47 days) (Kepler 1969; Woodward 1972) and 42–46 days (Dorward 1962b).

For 19 clutches the apparent incubation period was only 35–37 days. These abnormally short incubation periods were presumed to be the result of the nest not having been recorded in the first week it was present.

Hatching success

One or more chicks hatched from 156 of the 200 clutches. Overall hatching success (clutches that hatched at least one chick) was 78% (Table 3). Hatching success of solids is generally 70–90% (Nelson 1978). Hatch rates on Lord Howe were similar to hatch rates on Kure Atoll (76.4%) where food was plentiful (Woodward 1972) but better than those on Ascension Island (38.8%) where a large number of eggs were abandoned owing to an acute shortage of food (Dorward 1962b). The causes of egg failure on Lord Howe were not determined, but at least 18% of the clutches that failed were abandoned only after the normal period of incubation had elapsed.

Hatching success was lower for single-egg clutches (38%) than for clutches of two or three (81% and 100% respectively, Table 3). Similar comparative hatching rates occurred on Kure: 32% for one-egg clutches and 66% for two-egg clutches (Woodward 1972). Overall, for clutches of two, 13% of successful chicks hatched from the second egg.

One-third of all two-egg clutches hatched two chicks, with many more second chicks likely to have been killed by their sibling before being recorded. When first observed, second chicks weighed significantly less than their elder siblings (62.5 ± 2.8 g cf. 131.5 ± 5.5 g; paired t -test, $t = 10.451$, d.f. = 23, $P < 0.001$). Three younger siblings were dead when first found, 47 survived less than 1 week and seven survived for 1 week only. Injuries sustained by these chicks were consistent with them having been attacked by their larger sibling. Three younger siblings survived for 5, 6 and 9 weeks. One of these long-lived sibling pairs came from a clutch of three, the other two both came from clutches of two. We do not know whether broods of two were fed by more than one set of parents, as has been reported elsewhere (Kepler 1969). The siblings that survived in the same nest for 6 weeks were of similar size and mass during the first 5 weeks, despite one hatching later than the other.

Fledging success

A total of 101 chicks fledged successfully. Overall fledging success (the number of young that fledged as a proportion of those clutches of eggs that hatched) was 65% (Table 3). This was less than the fledging rate on Kure (81%, $n = 73$ clutches; $\chi^2 = 5.367$, $P < 0.025$; Kepler 1969) but greater than on Ascension (25%, $n = 272$; $\chi^2 = 63.884$, $P < 0.001$) during an El Niño (Dorward 1962b). Age-specific survival of chicks was relatively constant throughout the entire nestling period (mean = 0.97, range = 0.94–0.98).

Breeding success

Overall breeding success (the proportion of clutches that produced fledglings) was 51% (Table 3), less than that reported from all other colonies other than Ascension (Table 4). Breeding success was lower for single-egg clutches (31%) than from clutches of two or three eggs (52% and 67%, respectively).

Table 3. Hatching, fledging and breeding success as a function of clutch size

Hatching success was calculated as the proportion of clutches that hatched at least one chick. Fledging success was calculated as the proportion of hatched clutches that produced fledglings. Breeding success (the multiple of hatching success and fledging success) was calculated as the number of fledglings produced as a proportion of the number of clutches

	Clutch size			Total
	1	2	3	
Clutches	16	181	3	200
Chicks ^A	6	147	3	156
Fledglings	5	94	2	101
Hatching success	0.38	0.81	—	0.78
Fledging success	0.83	0.64	0.67	0.65
Breeding success	0.31	0.52	0.67	0.51

^AOnly one chick from each clutch was counted.

Table 4. Breeding success of Masked Boobies from various locations

Breeding success was calculated as the proportion of clutches that produced fledglings

Location	Breeding success	N (years)	Source
Lord Howe Island	0.51	1	This study
Kure Atoll	0.52-0.64	2	Kepler (1969)
Kure Atoll (North)	0.57-0.86	6	Woodward (1972)
Kure Atoll (South)	0.34-0.74	6	Woodward (1972)
Ascension Island	0.1	1	Dorward (1962b)

Clutches were grouped according to the week the first egg was laid, and hatching, fledging and breeding success calculated for each week (Fig. 3). There was a significant negative relationship between breeding success (transformed by arcsine) and the week of laying (linear regression analysis, $r^2 = 0.7707$, $F = 43.6822$, $P < 0.0001$). This decline in breeding success was attributable to a decline in both hatching success and fledging success (arcsine transformed, linear regression analysis, $r^2 = 0.8025$, $F = 48.7683$, $P < 0.0001$; $r^2 = 0.8594$, $F = 79.5045$, $P < 0.0001$, respectively). Late in the season chick mortality was high. None of the 29 clutches laid after 4 August 2001 successfully produced fledglings.

Impact of handling

To get access to eggs and small chicks, the parent in attendance was gently pushed off the nest. In most instances the parent would remain a few metres away and come back to the nest immediately after the nest area was vacated. Breeding outcomes were compared between nests where chicks were handled, weighed and measured weekly ($n = 99$) and nests where chicks were handled only once ($n = 98$). Three nests where chicks were inadvertently handled more than once, but less than weekly were excluded from the analysis. There

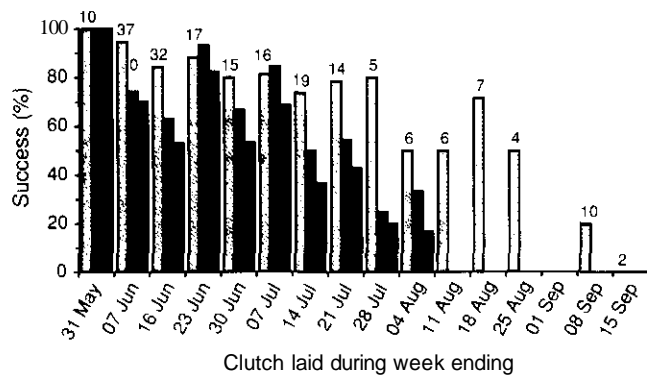


Fig. 3. Hatching, fledging and breeding success for clutches, grouped according to the week that the clutch was laid. Laying date of each clutch was taken as the date that the first egg was laid. Light shading, hatching success; medium shading, fledging success; solid shading, breeding success. Numbers above the first column indicate sample sizes, i.e. the number of clutches laid in that week.

was no difference between treatments in either hatching success (0.74 cf. 0.82; $\chi^2 = 1.334$, $P > 0.10$), fledging success (0.66 cf. 0.65; $\chi^2 = 0.005$, $P > 0.90$) or breeding success (0.48 cf. 0.53; $\chi^2 = 0.182$, $P > 0.50$). Although this assessment does not take into account possible stress-induced effects caused by researchers entering the colony, it demonstrates that repeated handling, at least, had no discernible adverse effect on survival of chicks.

Chick growth curves

The mean mass of adult males is 2000 ± 122 g (range = 1900-2200) and females 2533 ± 125 g (range = 2400-2700) (ABBBS data in Marchant and Ilgins 1990). Chick mass (Fig. 4) increased steadily to reach a mean asymptotic mass of 2235 ± 292 g at 11 weeks, and thereafter declined. Mean mass of chicks at 17 weeks was 2052 ± 176 g ($n = 21$). Of the chicks that died before fledging, more than 90% had a lower than average body weight in the week before their death (Fig. 4).

Culmen length (Fig. 5a) increased sharply until chicks were 8 weeks old, at which time it measured 99 ± 4 mm. Thereafter, it increased at a slower rate to reach a maximum of 108 ± 3 mm at 17 weeks. Tarsus length (Fig. 5b) increased early in the chick stage, reaching a maximum of 62 mm at 7 weeks. Head-bill length (Fig. 5c) increased rapidly until 7 weeks (171 ± 15 mm) and thereafter increased more slowly to reach a maximum of 184 ± 9 mm at 17 weeks. Tail length (Fig. 5d) increased from 0 mm at 5 weeks to 203 ± 13 mm at 17 weeks.

Comparative growth curves

Figure 6 compares the growth by mass of chicks on Lord Howe with those at Kure (Kepler 1969) and Ascension (Dorward 1962b). It shows that, in keeping with the comparative sizes of adults, chicks on Lord Howe were heavier at fledging than those from each of the other two locations. The growth curve for Booby chicks is similar to that for many other seabirds: a steady increase to a maximum asymptotic mass, followed by a decline in mass to fledging (Brooke

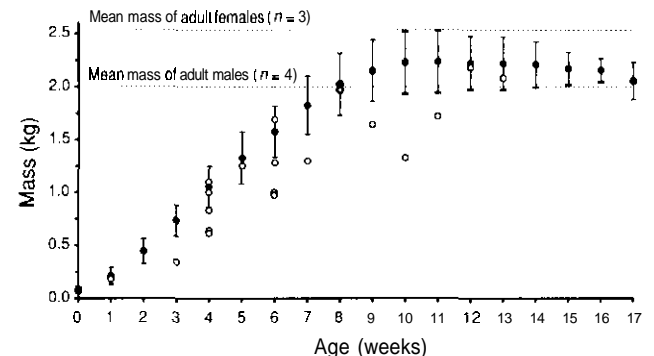


Fig. 4. Growth in body mass of Masked Booby chicks on Lord Howe Island. Data are means \pm s.d. Open circles indicate the body mass of dead chicks in the week before their death. Broken lines indicate mean mass of adult males and females (data from the ABBBS).

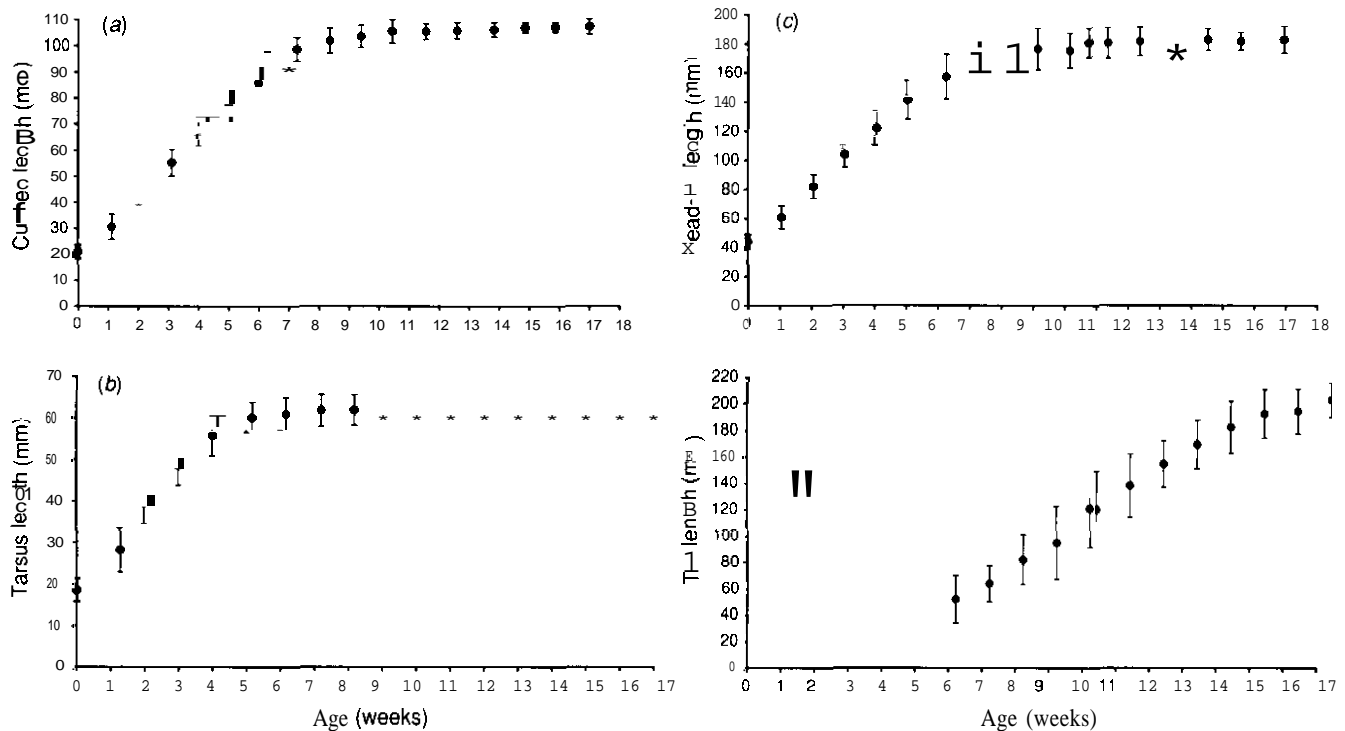


Fig. 5. Growth curves for Masked Booby chicks on Lord Howe Island: (a) culmen; (b) tarsus; (c) head bill; and (d) tail. Data are means \pm s.d.

2004). In contrast, chicks on Ascension during El Niño years when food was in short supply (Dorward 1962*b*) failed to reach a high asymptotic mass. The shape of the growth curve for chicks on Lord Howe closely resembled that from Ascension. Maximum mass exceeded fledging mass by less than 9%. We conclude that the growth in body mass on Lord Howe Island during the 2001–02 breeding season indicates that food resources were less than optimal.

Figure 7 compares the growth of the culmen of Masked Booby chicks on Lord Howe with those from other locations. Fledglings from Lord Howe had marginally longer culmen than fledglings from Kure and Ascension but the rate of growth was similar in all locations.

Diet

In all, 21 samples of regurgitant were examined. Eighteen contained only fish, principally flying fish (*Cheilopgon* spp.). Adults generally regurgitated one, sometimes two, large fish (each up to 430 g). Chicks regurgitated fish weighing 160–400 g. In December 2001, three of the four regurgitations collected also contained squid (1–4 individuals, weighing 30–45 g each). Whereas adults readily ate any regurgitant returned to them, chicks invariably ignored it.

Discussion

Breeding cycle and strategy

The nesting period on Lord Howe during the 2001–02 breeding season extended from May 2001 to February 2002. Eggs

were laid between late May and mid-September, although most were laid in June and July. Further study is required to determine the degree of variation between years. In some years laying may extend into December (Hutton 1991) and a freshly hatched chick seen on Roach Island in March 1971 (Fullagar *et al.* 1974) suggests that a few birds may breed at times of the year other than during spring.

As is typical for boobies, Masked Boobies on Lord Howe Island reared only one young from each clutch, owing to siblicidal brood reduction affecting the later-hatched chick. Although the second chick to hatch often did not survive long there was significant advantage in laying a clutch of

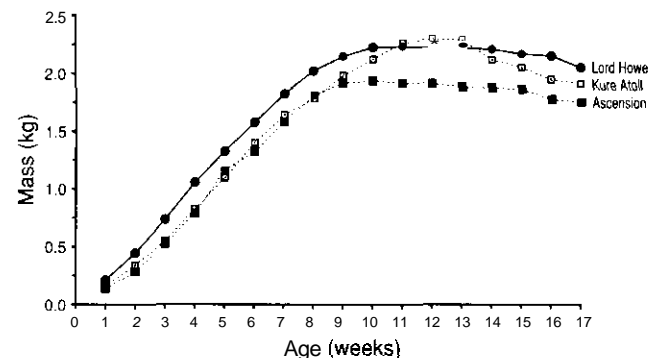


Fig. 7. Mean growth in body mass of Masked Booby chicks on Lord Howe Island compared with that of chicks on Kure Atoll and Ascension Island. Figure adapted from compilation in Nelson (1978) using data from this study, Dorward (1962*b*) and Kepler (1969).

two. Breeding success was substantially greater for two-egg clutches (52%) than for single-egg clutches (31%). Some of this difference was attributable to a high proportion of single-egg clutches being laid late in the season when hatching success was lowest. The second egg in this obligate brood-reducing species may function as an insurance egg (Dorward 1962b) in the event that the first egg fails to hatch or the first chick dies within its first few days of life. The production of insurance offspring is an adaptive parental strategy (Evans 1996), the benefits of which have been documented by comparative studies of boobies (Anderson 1990) and demonstrated experimentally for the American White Pelican (*Pelecanus erythrorhynchos*, Cash and Evans 1986) and the Nazca Booby (*Sula granti*, Clifford and Anderson 2001). Later-hatched Masked Booby chicks on Lord Howe Island replaced their failed sibling in 13% of nests. This insurance value falls within the range of 0–32% reported in previous studies of this species (Kepler 1969; Woodward 1972).

Diet

The Masked Booby feeds principally on flying fish (Exocoetidae), its distribution being largely correlated with the distribution of this particular prey (Murphy 1936). Prey taken by Masked Boobies on Lord Howe Island includes flying fish, kingfish (*Regificola grandis*), mullet (*Mugil* spp.) and unidentified cephalopods (McKean and Hindwood 1965). In this study, regurgitations were mostly flying fish, although garfish and squid were also recorded. Squid appeared in the diet only during December, a time when breeding failures suggested food may have been scarce.

Threats

Rats are regular predators of birds' eggs (Booth *et al.* 1996; Innes 2001). The presence of fresh rat faeces on Mutton Bird Point indicated that rats were present throughout the study, and many abandoned eggs had parallel scratch marks on them, the spacing matching that of rat incisors. However,

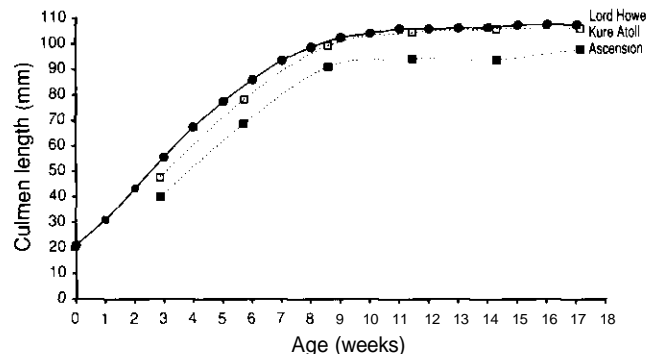


Fig. 7. Mean growth in culmen of Masked Booby chicks on Lord Howe Island compared with that of chicks on Kure Atoll and Ascension Island. Figure adapted from compilation in Nelson (1978) using data from this study, Dorward (1962b) and Kepler (1969).

there was no evidence that rats took eggs from underneath incubating birds, and eggs still being incubated were free of scratches. Similarly, there was no definitive evidence of rats attacking Masked Booby chicks. Several dead chicks were partially eaten by rats, but the damage was consistent with these individuals having been scavenged after they died. One chick (10 weeks old) was found alive with a wound to its neck that could have been caused by rats, but could equally have resulted from intraspecific aggression. One observation suggested that Masked Boobies were able to defend their nest from attack by rats. A dead rat with wounds to its body was found on the side of a nest. When we attempted to retrieve the rat, the adult Booby at the nest attacked it savagely. From the evidence available, it appears that rats were not a significant predator of Masked Booby eggs or chicks, essentially feeding only on broken or abandoned eggs and dead chicks. No other predators were identified.

A juvenile Masked Booby, banded on Mutton Bird Point in October 2001, was caught and killed 9 months later on a longline at sea (~20°S, 163°E) a few kilometres north-west of New Caledonia, and ~1340 km from Lord Howe Island. The extent of mortality of Masked Boobies in longline fisheries is unknown. Hindwood (1940) and local fishers report Masked Boobies, particularly juveniles, taking lures trolled behind boats. Further research is needed to determine the extent of interaction between Masked Boobies and fishers, both commercial and recreational.

Size of the colony

In all, 200 clutches were laid during the 2001–02 breeding season. Assuming each clutch represented a single breeding pair, the size of the colony on Mutton Bird Point was ~200 breeding pairs. The exact number may differ slightly, depending on the number of clutches that were lost before they were recorded and the number of birds that laid a replacement clutch after the first failed. The incidence of replacement laying in Masked Boobies varies greatly. No replacement laying was observed on Ascension (Dorward 1962b), but the proportion of fledglings produced from re-laying pairs on Kure sometimes exceeded 20% (Kepler 1969). Nelson (1978) suggested that the lack of recorded replacement laying at some sites is because they are impoverished. The incidence of replacement laying on Lord Howe is a topic worthy of further investigation.

Conclusions

This study provides the first detailed assessment of the size of the Masked Booby colony on Mutton Bird Point. Fullagar *et al.* (1974) counted more than 80 individuals nesting or roosting there in the early 1970s, but made no estimate of population size. The current population estimate provides an important benchmark from which future population trends can be assessed. Until such trends are known, the health of the population can be judged only by comparing our data

from one breeding season with data from studies of other populations. Breeding success in boobies is highly responsive to environmental conditions and varies considerably among locations and among years according to the availability of food resources (Dorward 1962*b*; Kepler 1969; Nelson 1978; Schreiber and Schreiber 1984). For seabirds, breeding success may also be affected by the age or experience of the parents (Brooke 1978; Ollason and Dunnet 1986). However, evidence from Kure suggests that, for Masked Booby populations, marked fluctuations in the availability of prey can overshadow any effects of age. In some years, early nesters on Kure were more successful, but in other years the reverse was true (Kepler 1969). In one particular year, re-nesting was proportionally more successful than initial nesting.

The high proportion of two-egg clutches on Lord Howe in 2001-02 suggested that, early in the breeding season, the Masked Booby population on Lord Howe Island was well nourished. Early hatched chicks did well, but chicks that hatched later in the season fared poorly, with none of the eggs laid after early August successfully producing a flying young. Mediocre fledging success, less than optimal chick growth rates, and lower than average body weight of chicks in the week before their death were all strongly suggestive of a shortage of food. We conclude that food availability was high at first but declined, presumably owing to some oceanographic perturbation, to levels that could no longer sustain breeding. Further research into the diet of Masked Boobies on Lord Howe Island is needed to enhance our understanding of the relationship between temporal fluctuations in prey abundance and breeding success.

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References

- Anderson, D. J. (1990). Evolution of obligate siblicide in boobies. I. A test of the insurance-egg hypothesis. *American Naturalist* 135, 334-350. doi:10.1086/285049
- Bent, A. C. (1922). 'Life Histories of North American Petrels and Pelicans and Their Allies.' Bulletin 121 of the United States National Museum. (Government Printing Office: Washington, DC.)
- Booth, A. M., Minot, E. O., Fordham, R. A., and Innes, J. G. (1996). Kiore (*Rattus exulans*) predation of the eggs of the Little Shearwater (*Puffinuassimilis haurakiensis*). *Notornis* 43, 147-153.
- Brooke, M. (2004). 'Albatrosses and Petrels Across the World.' (Oxford University Press: New York.)
- Brooke, M. de L. (1978). Some factors affecting the laying date, incubation and breeding success of the Manx shearwater, *Puffinu puffinus*. *Journal of Animal Ecology* 47, 477-495.
- Cash, K. J., and Evans, R. M. (1986). Brood reduction in the American White Pelican (*Pelecanus erythrorhynchos*). *Behavioral Ecology and Sociobiology* 18, 413-418. doi:10.1007/BF00300515
- Clapp, R. B., and Sibley, F. C. (1971). The vascular flora and terrestrial vertebrates of Vostok Island, South-central Pacific. *Atoll Research Bulletin* 145, 1-10.
- Clifford, L. D., and Anderson, D. J. (2001). Experimental demonstration of the insurance value of extra eggs in an obligately siblicidal seabird. *Behavioral Ecology* 12, 340-347. doi:10.1093/beheco/12.3.340
- Dorward, D. K. (1962*a*). Behaviour of boobies, *Sula* spp. *Ibis* 103*b*, 174-220.
- Dorward, D. F. (1962*b*). Comparative biology of the white booby and the brown booby, *Sula* spp., at Ascension. *Ibis* 103*b*, 221-234.
- Evans, R. M. (1996). Hatching asynchrony and survival of insurance offspring in an obligate brood reducing species, the American White Pelican. *Behavioral Ecology and Sociobiology* 39, 203-209. doi:10.1007/s002650050282
- Friesen, V. L., and Anderson, D. J. (1997). Phylogeny and evolution of the Sulidae (Aves: Pelecaniformes): a test of alternative modes of speciation. *Molecular Phylogenetics and Evolution* 7, 252-260. doi:10.1006/mpev.1996.0397
- Fullagar, P. J., McKean, J. L., and van Tets, C. K. (1974). Appendix K Report on the birds. In 'Environmental Survey of Lord Howe Island'. (Eds H. F. Recher and S. S. Clark.) pp. 55-72. (New South Wales Government Printer: Sydney.)
- Garnett, S., and Crowley, G. M. (2000). The Action Plan for Australian Birds 2000. (Environment Australia: Canberra.)
- Hindwood, K. A. (1940). The birds of Lord Howe Island. *Emu* 40, 1-86.
- Hindwood, K. A., Keith, K., and Serventy, D. L. (1963). 'Birds of the South-west Coral Sea.' Division of Wildlife Research Technical Paper No. 3. (Commonwealth Scientific and Industrial Research Organisation: Melbourne.)
- Holdaway, R. N., and Anderson, A. (2001). Avifauna from the Emily Bay Settlement Site, Norfolk Island: a preliminary account. *Records of the Australian Museum Supplement* 27, 85-100.
- Holdaway, R. N., Worthy, T. H., and Tennyson, A. J. D. (2001). A working list of breeding bird species of the New Zealand region at first human contact. *New Zealand Journal of Zoology* 28, 119-187.
- Hutton, I. (1991). 'Birds of Lord Howe Island: Past and Present.' (Ian Hutton: Coffs Harbour, NSW.)
- Innes, J. (2001). Advances in New Zealand mammalogy 1990-2000: European rats. *Journal of the Royal Society of New Zealand* 31, 111-125.
- IUCN (1994). 'IUCN Red List Categories.' (IUCN: Gland, Switzerland.)
- Kepler, C. B. (1969). Breeding biology of the blue-faced booby *Sula dactylatra personata* on Green Island, Kure Atoll. *Publications of the Nuttall Ornithological Club* 8, 1-97.
- Kolichis, N. (1977). Birds of Bedout Island - a visit in May 1975. *Western Australian Naturalist* 13, 191-194.
- Lowc, K. W. (1989). 'The Australian Bird Bander's Manual.' (Australian Bird and Bat Banding Schemes, Australian National Parks and Wildlife Service: Canberra.)
- Marchant, S., and Higgins, P. J. (1990). 'Handbook of Australian, New Zealand and Antarctic Birds. Vol. 1: Ratites to Ducks.' (Oxford University Press: Melbourne.)
- McKean, J. L., and Hindwood, K. A. (1965). Additional notes on the birds of Lord Howe Island. *Emu* 64, 79-97.
- Merton, D. V. (1970). Kermadec Islands Expedition reports: a general account of birdlife. *Notornis* 17, 147-199.
- Murphy, R. C. (1936). 'Oceanic Birds of South America.' (MacMillan: New York.)