

Slow life history traits in an endangered tropical island bird, the Ma'oma'o

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Summary

An effective conservation strategy for a species requires knowledge of its biology and life history. This applies to the endangered Ma'oma'o *Gymnomyza samoensis*, a honeyeater endemic to the Samoan archipelago. Now locally extinct in American Samoa, this species is currently found only in declining numbers on the islands of Upolu and Savai'i in Samoa. Despite being endangered, the life history and breeding behaviour of the Ma'oma'o has not been documented previously. Here we examine Ma'oma'o nesting and breeding biology, which are unique among studied honeyeaters and unusual for passerines in general. Ma'oma'o lay only a single egg per clutch and have an extended breeding season that occurs outside the rainy season and peaks during budburst. Allometric analysis of the length of the nesting period of different honeyeaters versus adult body weight showed that Ma'oma'o remain in the nest for a longer period than expected for their body size. The post-fledging dependency period of 2.5–3 months was also extended compared to other honeyeater species. No Ma'oma'o were observed re-nesting after successfully raising a chick, though pairs attempted to re-nest following breeding failure. Despite the extended breeding season, the maximum annual reproductive capacity of Ma'oma'o is limited by their one-egg clutch and failure to nest again after fledging one chick. We discuss how these slow life history traits can influence conservation strategies, affect monitoring and limit recovery.

Introduction

Basic information about the biology and life history of any species is essential for estimating population growth rates and predicting the response of species to future environmental change (Hau 2001, Jetz *et al.* 2008, Hau *et al.* 2010, Williams *et al.* 2010). For endangered species, such information is also required for identifying conservation priorities, making accurate IUCN threat assessments, designing protected areas, and other conservation management strategies. This information is particularly important for the large number of threatened birds in the tropical South Pacific, yet few data are available on the breeding biology of most South Pacific passerine species.

In this study, we investigated the breeding biology and life history strategies of the Ma'oma'o *Gymnomyza samoensis*. The Ma'oma'o is an endangered honeyeater endemic to the Samoan archipelago (BirdLife International 2012). Ma'oma'o are found both in native forest habitat and at the forest edge where tall trees still remain. The Ma'oma'o is a large honeyeater approximately 28–31 cm long, with dark plumage varying from blackish on the head and breast to olive-green on the wings, tail and body. It has an olive-green stripe under the eye. The bill is long, curved and black in adults. Little is known about the breeding ecology of the species and, to our knowledge, no published information exists on the breeding biology of the two other *Gymnomyza* species. Though the Ma'oma'o previously occurred on Tutuila Island in American Samoa, it is now

presumed to be extinct there since no birds have been observed in the last 50 years. It is currently found only on Samoa's two largest islands, Upolu and Savai'i, where its numbers are declining (MNRE 2006). In Samoa, forest loss and invasive mammals, such as rats, are assumed to be impacting populations (MNRE 2006). Basic biological information is needed to clarify which conservation management strategies may be effective. Here, we provide data on the breeding biology of the Ma'oma'o, including courtship behaviour and territory defence, nest site selection, egg characteristics, clutch size, length of incubation and nestling period, and the time from fledgling to independence. We also analyse the seasonality of breeding and relate it both to rainfall and to the phenology of plants used for foraging. We compare the breeding biology of the Ma'oma'o with that of other honeyeaters and discuss how slow life history strategies such as that of the Ma'oma'o affect conservation management options.

Methods

Study area

Samoa is dominated by two large volcanic islands, Savai'i and Upolu, which lie in the South Pacific. Both islands are over 1,000 km² and are mountainous with a maximum elevation of 1,900 m (Whistler 1992, 2004). The main wet season is December to March (Morrissey *et al.* 1995).

We monitored Ma'oma'o at two study sites on Upolu. The first site was 3 km from Magiagi village in the Vaisigano water catchment (Upolu Island, 13°54.5'S, 171°44.3'W). It comprised steep ridges and steep slopes (average slope 18°) reaching up to 300 m asl and dissected by many creeks. At high elevations, parts of this site were planted with banana and taro crops, but large primary and secondary forest patches dominated by maota *Dysoxylum huntii* still remained. Some of the area was grazed by cattle resulting in a mosaic of open habitat, especially on the flats, and dense native forest, particularly on the slopes. The habitat also consisted of a high density of introduced tamaligi *Falcataria moluccana* containing native mistletoe *Loranthus samoensis*; several introduced tree species, such as the African tulip *Spathodea campanulata*; and a large variety of native forest species.

The second study site was near Lake Lanoto'o at 13°54.6'S, 171°49.6'W at an elevation of 700–800 m. This site had gentle slopes covered in a dense native forest dominated by maota and a large variety of other native forest species. Non-native tree species such as African tulip and tamaligi were present though they were not as abundant as at the first site.

Observational methods

We monitored focal pairs of Ma'oma'o from June 2010 to January 2013. In the territories of known pairs, the female was followed to locate the nest. Spatial use and interactions between adjacent pairs were noted for both males and females. For six breeding pairs we recorded conspecific territorial defence for five breeding phases of: 1) nest building, 2) while a chick was present in the nest, 3) while a fledgling was present in the territory and being fed, 4) following nest failure when no previous nest had been successful and 5) when a chick had been fledged successfully and was no longer present in the territory. We recorded territorial behaviour such as territorial boundary song, chasing and physical contact for 30-minute blocks until five hours of monitoring was completed for each breeding phase per individual.

Some adults and juveniles were captured using a high canopy mist-net combined with playback of recordings of conspecific adult or chick calls. Conspecific calls were played through speakers placed within 5 m of the mist-net. When possible, mist-nets were placed close to known nest sites. Birds were largely unresponsive, however, unless a chick close to fledging was nearby. Captured birds were banded with coloured split bands and butt-ended Y-sized metal bands (New Zealand banding scheme). Colour bands were glued shut using super glue. The following measurements were taken: wing length (maximum length; flattened and stretched), bill length (culmen length from bill tip to skull), head to beak length (from the back of the skull to the tip of the beak), tarsus

length, and tail length. All means are expressed as \pm SD unless otherwise stated. All measurements are in mm unless otherwise stated. Birds were weighed to the closest 0.1 g using a Pesola spring balance. Three feathers were plucked under the wing coverts to enable DNA sexing of the birds. All DNA sexing analyses were conducted by the Equine Parentage and Animal Genetic Services Centre at the Institute of Veterinary Animal and Biomedical Sciences, Massey University, New Zealand using methods as per Norris-Caneda and Elliott (1998). Additional measurements (not including weight) of Ma'oma'o were taken from 10 adult male specimens from the American Museum of Natural History, New York to increase the sample size. Museum birds had been sexed during specimen preparation and sex was indicated on museum labels, so DNA sexing was not undertaken on these samples. Birds from American Samoa were not included in the sample because they are larger than the Samoan birds (Stirnemann unpubl. data).

Active nests were monitored every 1–4 days by observing parental behaviour from a distance. When possible, a nest camera was placed above each active nest to monitor it continuously. Some nests were inaccessible for camera placement. In these cases we made direct observations at the nest. Observations of breeding behaviour were made on all nest sites during incubation and the nestling phase. When possible, chicks were individually banded, either prior to fledging or 1–2 days after fledging, in the same way as adults, i.e. with metal and coloured split plastic bands. At both study sites, newly fledged chicks were observed for up to 1 hour every 3–7 days until the fledging left the natal territory. Adults with a chick were located by listening for the continuous begging calls of the chick. After fledging or nest failure, we measured nest characteristics (e.g. nest diameter, nesting material), and nest site characteristics, including height from the ground, percentage nest cover and tree species.

Phenology of key resource plants

Key resource plant species, utilized for food by the Ma'oma'o in the study site (Stirnemann unpubl. data), were identified by following the Ma'oma'o pairs. Because Ma'oma'o feed on invertebrates, fruit and nectar, we monitored fruiting, flowering and budburst phenology. We monitored the 10 most frequently used resource plant species within the birds' home ranges at the two study sites. Individual plants were randomly selected which occurred in both study sites and were within the territories of the monitored breeding pairs. Of the 10 species, eight were trees: malili *Terminalia richii*, albisia/tamaligi, coral tree/gatae *Erythrina variegata*, tufaso *Dysoxylum samoense*, moso'oi *Cananga odorata*, mamalava *Planchonella torricellensis*, heliconia/tutuila *Heliconia laufao*, pua-lulu *Fagraea berteriana*. We also monitored two non-tree species: mistletoe and ginger *Etlingera cevuga*. For each species, 10 individual plants were selected and their phenology monitored. Individual trees were tagged and each month we collected phenology data including timing of budburst, fruiting and flowering. Because phenological patterns were similar over both years and there was little variation, within-species data were pooled across years. Monthly rainfall data were provided by the Samoan Meteorology Division from the Afiamalu weather station (13°54.0'S, 171°46.12'W; elevation: 688 m) for the years 2011–2012. A 10-year average (2004–2014) of the Afiamalu weather station showed monthly rainfall patterns similar to those in our two-year study.

Comparative analysis of the breeding biology of other honeyeaters

Data were compiled from published accounts of the breeding biology of other species of honeyeaters for comparison with our data on the Ma'oma'o. Little research has been undertaken on the breeding biology of honeyeaters in the Pacific Islands so we were limited to comparisons with predominantly Australian and New Zealand honeyeaters. Data for adult body weights, maximum clutch size and the number of clutches a species can produce, irrespective of survival, were obtained from Higgins *et al.* (2001) and del Hoyo *et al.* (2014). We then calculated the maximum annual reproductive capacity of each species by multiplying its maximum clutch size by the maximum number of broods a species can fledge per year.

We were also interested in whether the length of incubation, nestling, and time-to-independence periods were purely due to the large size of the Ma'oma'o or whether, even with its size taken into account, these development times were extended compared to other honeyeaters. To this end we fitted a linear regression of log-transformed female body weight of honeyeater species where data were available (without Ma'oma'o) against the log-transformed length of each development period (incubation, nestling, and post-fledgling care) to assess whether they show an allometric relationship to body mass. Where a relationship existed between the log of body weight and the log of length of development at each stage, we used the linear equation to obtain predicted development periods for the Ma'oma'o. We then calculated the deviation of observed values from those predicted as a proportion of the observed values by substituting the adult weight of the Ma'oma'o into the linear equation obtained from the regression.

We used paired *t*-tests to assess whether territorial defence by either males or females in breeding pairs was reduced significantly following the successful fledging and rearing of a chick compared to the amount of territorial defence observed in pairs following a failed nesting attempt. We calculated the number of defensive acts per individual per unit of time summed over 30-minute periods. All statistical analyses were carried out with R statistical software (R Development Core Team 2011).

Results

Over the two years of the study we observed 10 nests at which eggs were laid. Three of the 10 nests resulted in fledglings. The timing of 16 further breeding efforts was determined based on finding fledged young. No pair initiated a second brood within the same year it successfully raised a chick. At least three pairs, however, initiated 2–3 further nesting attempts on 3 occasions after failure.

The breeding season

Ma'oma'o have a protracted breeding season which can occur over 9–10 months of the year although a peak in egg-laying appears to occur from late May through to October (Fig. 1a). Nesting was uncommon during the period when rainfall was highest (December–March) and only a single (unsuccessful) nest was found during this period. Incubation, chick rearing and post-fledgling care of a single chick takes c.100–120 days (see below).

Seasonality of plants

The phenology of budburst, flowering and fruiting of plants used for food by Ma'oma'o showed clear seasonal patterns (Figure 1b). For the large and medium-sized forest trees, budburst occurred in the dry season from July to September/October, with a peak of flowering between August and December. Mistletoe showed two peaks in flowering. The main peak occurred between August and September with a smaller peak early in the dry season in March and April. Seasonal fruit production occurred from October to December during the early rainy season. The timing of the peak in Ma'oma'o nesting occurred immediately before and during the period when the majority of Ma'oma'o foraging trees experience budburst, which did not coincide with the period of highest rainfall in our study sites (Figure 1a&b).

Breeding behaviour

Territorial defence was effected through song, chasing and occasional physical contact. Both sexes exhibited territorial defence prior to and during breeding although males displayed more intense defence, especially during nest building. Over different years, male-singing displays occurred consistently in the same trees; these are subsequently referred to as display trees. Two to three weeks prior to and during nest building a male would display by flying high above a display tree. He would then fold in his wings and fall straight towards the ground while emitting a high-pitched call.

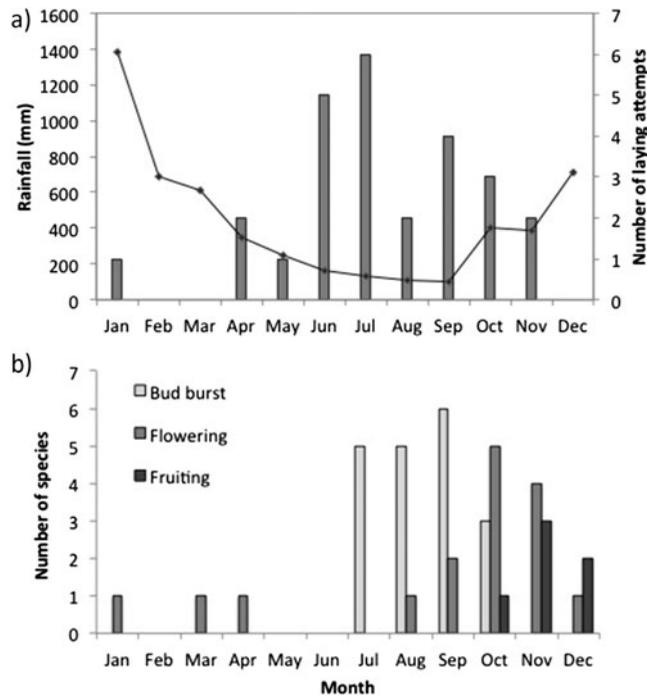


Figure 1. a) The months in which Ma'oma'o nesting occurred depicted by the bars, based on the nesting dates of active nests found during the study ($n = 10$) and the estimated nesting dates based on the age of the observed juveniles ($n = 16$). The average monthly rainfall for 2011–2012 is depicted with a dark line. b) The phenology of key Ma'oma'o resource trees and plants at the study sites.

During nest building and incubation, males showed increased territorial defence by vigorously chasing away any conspecifics and other passerine species that got within c.30 m of the nest. They also defended nectar resources at this time. The intensity of territorial defence declined and was significantly less in both males and females in breeding pairs following the successful fledging of a chick compared to the amount of territorial defence observed from pairs following a failed nesting attempt (paired *t*-test, female, $t = 2.39$, $df = 5$, $P = 0.04$, male, $t = 3.17$, $df = 5$, $P = 0.02$).

Nests

We found 10 Ma'oma'o nests. Only females were seen building the nest, although the male inspected the nest during construction. Males fed females during nest building and during incubation, but these events were infrequent, i.e. less than once per day. All nests were similar in structure and composition. They contained little lining and were constructed at the junction of branches from interlaced young branches stripped of leaves. All nests were oval cup-shaped, measured 14.0 ± 1.9 cm by 8.0 ± 1.4 cm, and were supported at the junction of branches ($n = 10$). Nests were constructed in a wide range of native and exotic trees (Table 1). The mean height of a nest above ground was 14.2 ± 3.7 m (range 8–20 m, $n = 10$) in forest with canopy heights of approximately 28–32 m.

Eggs

The eggs had an off-white background colour with irregular shaped brown spots on the blunt end. Each clutch comprised just a single egg. We only found two nests prior to eggs being laid which successfully hatched. One egg took 19–20 days to hatch and the other took 20–21 days.

Table 1. Nest site variables (species of nest tree, nest height and percentage nest cover) for the ten Ma'oma'o nests observed.

| Nest tree species | Nest height (m) | Nest cover (%) |
|--|-----------------|----------------|
| Ala'a <i>Planchonella garberi</i> | 15 | 0 |
| Native mistletoe <i>Loranthus samoensis</i> in tamalingi <i>Falcataria moluccana</i> | 12 | 60 |
| Species unknown (Dead branch) | 10 | 0 |
| Maota <i>Dysoxylum huntii</i> | 18 | 15 |
| Masame <i>Glochidion ramiflorum</i> | 14 | 20 |
| Pua lulu <i>Fagraea berteriana</i> | 8 | 20 |
| Rubber tree <i>Hevea brasiliensis</i> | 18 | 0 |
| Rubber tree <i>Hevea brasiliensis</i> | 20 | 80 |
| Salato <i>Dendrocnide harveyi</i> | 14 | 40 |
| Salato <i>Dendrocnide harveyi</i> | 13 | 50 |

The chick

Chicks fledged at least 22–24 days following hatching ($n = 6$). The newly hatched nestlings were blind and naked with a yellow culmen and pale-yellow flange. At 9–10 days old, the first feather tracts erupted and the culmen darkened. Footage from the nest camera showed the chicks' faecal sacs were removed by the female and discarded directly below the nest or else consumed. The female was never observed flying away with the faecal sacs.

Nest camera footage revealed that after the chick was approximately 12 days old, the female perched on a branch above the nest to sleep at night. Prior to this she slept in the nest. Just before fledging, the chick filled the entire nest. It was active, standing on the side of the nest and stretching its wings. The plumage of the nestling was olive, similar to that of the adult female, but with a darker head than the adult and with a yellow gape. At this stage the eyes of all of the observed chicks were a milky brown as opposed to the adult birds' bright blue or brown eyes. Fledging proceeded over several days, with the young gradually moving out along supporting branches during the day and returning to the nest at night.

Post-fledging

Three Ma'oma'o chicks were captured on the day they fledged. All three were later DNA sexed as male and they all weighed as much as an adult male (Table 2). The length of the tarsus at fledging was also similar to that of the adult, while the wing, tail, and beak lengths were 72%, 31% and 62% of the adult, respectively.

Pin feathers on the face and down on the head were obvious and were present for a few days after fledging. The beak was bright yellow with a dark grey culmen, which gradually became darker with age. Upon fledging the chicks flew poorly and remained close to the nest for the first 3–10 days. During this period some fledglings spent time on the ground or on low bushes. Fledglings were highly vocal in soliciting food and used a begging call continuously. After 3–4 weeks, fledglings were observed trying to forage independently, but were still reliant on the parents for most of their food. At two months, juvenile Ma'oma'o still had enlarged flanges on the sides of the beak which was almost completely black. Also, the juveniles' eyes had begun to change colour from milky brown to the blue or clearer brown of the adult birds. The female adult Ma'oma'o cared for the young for 2–2.5 months post-fledging. The male stayed within the territory during this period. He defended the juvenile if it was threatened, but territory defence was reduced compared to before and during the early breeding stages.

Comparison with the breeding biology of other honeyeaters

There is considerable variation in the maximum clutch size of honeyeater species (Fig. 2a). The maximum reported average clutch size is 3.5 eggs (Fig. 2a). In addition to having a large

Table 2. Morphometrics (SD) of male chicks ($n = 3$) measured on the day they fledged the nest compared to morphometric measurements from the same sex adult birds (% difference). The sample size of adult male birds is indicated in the table (n).

| | Beak length (mm) | Wing (mm) | Tail (mm) | Tarsus (mm) | Weight (g) |
|--------------------------------|------------------|--------------|--------------|-----------------|--------------|
| Chicks | 26.1 ± 1.5 | 105 ± 36 | 42 ± 3 | 43.0 ± 3.1 | 103 ± 17 |
| Adults (n) | 42.1 ± 3.3 (14) | 145 ± 55(14) | 136 ± 8 (14) | 43.1 ± 1.5 (14) | 106 ± 14 (5) |
| % difference | 38% | 28% | 69% | 0% | 0% |

clutch size, many honeyeaters are also multi-brooded, enabling most species to achieve a maximum annual reproductive capacity of approximately 6–10 chicks per year (Fig. 2b). The Ma'oma'o had the lowest maximum reproductive capacity of all recorded honeyeaters (Figure 2a&b). There is also considerable variation in the length of the incubation, nestling, and independence periods of honeyeater species. We investigated whether the duration of these stages in Ma'oma'o are typical for a honeyeater of its size. When we use female body mass for allometry to explain the length of the incubation period ($R^2 = 0.24$, $n = 44$, $P < 0.001$) we predict that Ma'oma'o would hatch after 15 days (Fig. 3a). This is 4–6 days shorter than the observed incubation period (Figure 3a). Adult female mass is a good predictor of the length of the nestling period for honeyeaters. We found that an allometric relationship across honeyeaters for the maximum length of the nestling period versus adult female mass ($r = 0.5$, $n = 41$, $P < 0.001$). Based on this we would predict that Ma'oma'o chicks remain in the nest for 14.5 days (Fig. 3b). This is 7.5 days less than the 22 days we observed. There was no observed relationship between time to independence ($R^2 = 0.0001$, $n = 10$, *ns*). Nevertheless, irrespective of size, Ma'oma'o had a period of post-fledging care that is 30–47% longer than that for any other honeyeater species (Table 3).

Discussion

Our findings provide the first information on the reproductive biology of the Ma'oma'o, an endangered tropical island honeyeater. Our results indicate that Ma'oma'o have an extremely low maximum annual fecundity. We discuss the reasons for the low maximum fecundity and its influence on future conservation approaches.

Ma'oma'o were found to lay only a single-egg clutch. This is rare in passerines and in birds as small as the Ma'oma'o (e.g. Jetz *et al.* 2008), though it has been noted to occur more frequently on islands (e.g. Komdeur *et al.* 2002) and recently recorded in a number of New Guinean passerines (Freeman and Mason 2014). A decrease in clutch size has also been observed as the equator is approached and climatic conditions become more tropical (Russell 2000). Small clutches do not

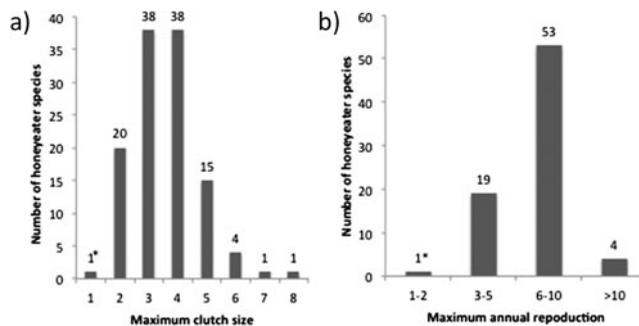


Figure 2. a) Maximum clutch size of 118 honeyeater species, and b) maximum annual reproductive output (max. clutch size x max. no. of broods) of 76 honeyeater species. The Ma'oma'o is indicated with an asterisk (*).

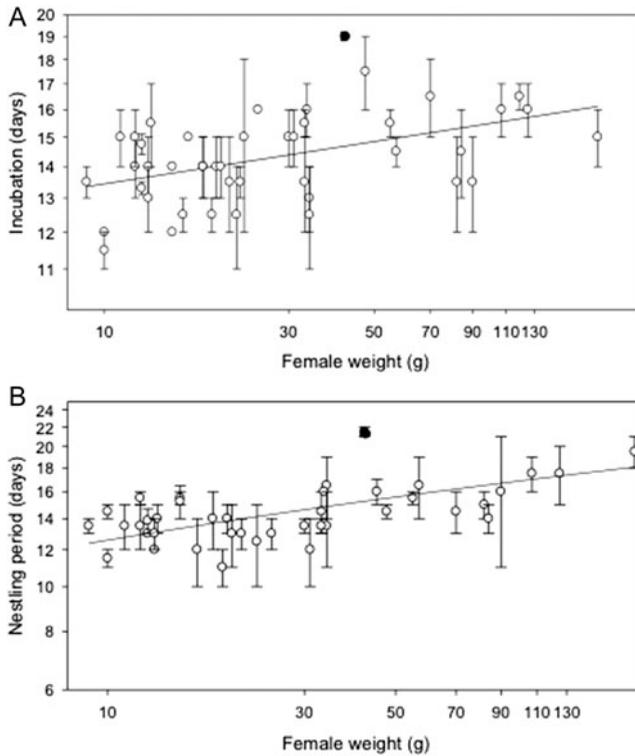


Figure 3. Body weight log-log plots of adult honeyeater species (Table 3) versus the range of days a) of incubation period and b) the nestling is in the nest. The circle symbol depicts the Ma'oma'o whilst triangles represent other species. The linear regression is fitted to the midpoint of the range data and excludes the Ma'oma'o, the error bar depicts the range.

necessarily mean the maximum annual reproductive success of a species is reduced since multiple clutches may be produced. However, we also found no evidence of a second breeding attempt by Ma'oma'o following successful fledging of a chick.

The ability of a female Ma'oma'o to produce multiple clutches is somewhat limited by its extended parental care period which takes c.100–120 days until a chick is independent from the female. Nevertheless, Ma'oma'o breed over a 9–10 month period, so it would be possible to fit in a second clutch into one season if an early nesting attempt is successful. However, we found that even pairs which fledged a chick early in the breeding season did not attempt to re-nest. We also found that their territorial behaviour was significantly reduced after a chick was successfully fledged. Therefore, our results suggest the maximum annual fecundity for the Ma'oma'o is just one chick. In contrast, Australian and New Zealand honeyeaters typically lay 2–3 egg clutches (range 1–3) and frequently have more than one brood within a season (Beruldsen 2003, Higgins *et al.* 2001, del Hoyo *et al.* 2008). A few honeyeaters, which may not be routinely multi-brooded, lay up to four eggs in a clutch (Beruldsen 2003, Higgins *et al.* 2001, del Hoyo *et al.* 2008). Thus, the potential maximum annual reproductive capacity of most Australian and New Zealand honeyeaters is 6–10 chicks per year, though a number of species produce a maximum of 3–5 chicks per year (Beruldsen 2003, Higgins *et al.* 2001, del Hoyo *et al.* 2008). A maximum annual fecundity of only one chick has not been to our knowledge recorded for any other honeyeater.

Extended parental care in the Ma'oma'o is a result of both long incubation and nestling periods, and long periods of post-fledging parental care. A Ma'oma'o chick spends approximately 10% more

Table 3. Incubation (Incub.), nestling periods and time until independence (Indep.) for studied honeyeaters. Adult female weight is the average for each honeyeater species. Country indicates where the species is found: Australia (Aust), Tasmania (Tasm), New Zealand (NZ) and Papua New Guinea (PNG). Species only found in tropical locations are referred to as tropical.

| Common name | Scientific name | Adult female weight (g) | Incub. period (days) | Nestling period (days) | Time until indep. (days) | Country | Reference |
|----------------------------|--|-------------------------|----------------------|------------------------|--------------------------|------------------------|--|
| Dusky Honeyeater | <i>Myzomela obscura</i> | 10 | 12 | 14–15 | | Aust | Noske and Carlson (2011) |
| Brown-backed Honeyeater | <i>Ramsayornis modestus</i> | 11 | 14–16 | 12–15 | | Aust+PNG (tropical) | Maher (1988) |
| Rufous-banded Honeyeater | <i>Conopophila albogularis</i> | 12 | 13–15 | 12–15 | 30 | Aust | Noske (1998) |
| Crescent Honeyeater | <i>Phylidonyris pyrrhoptera</i> | 12.5 | 13.1–13.5 | 13 | 14–20 | Aust | Clarke and Clarke (2000) |
| Yellow-faced Honeyeater | <i>Lichenostomus chrysops</i> | 12.5 | 14.4–15.1 | 13.0–14.7 | 11–28 | Aust | Clarke <i>et al.</i> (2003) |
| New Holland Honeyeater | <i>Phylidonyris novaehollandiae</i> | 18 | 13–15 | 12–16 | 28 | Aust | Armstrong and Pyke (1991) |
| White-cheeked Honeyeater | <i>Phylidonyris niger</i> | 19.5 | 13–15 | 13–15 | | Aust | Armstrong and Pyke (1991) |
| Bell Miner | <i>Manorina melanophrys</i> | 23 | 12–18 | 10–15 | | Aust | Clarke (1988), Smith and Robertson (1978) |
| Bellbird | <i>Anthornis melanura</i> | 34 | 12–14 | 14–19 | 13 | NZ | Anderson (2003) |
| Helmeted Honeyeater | <i>Lichenostomus melanops cassidix</i> | 30 | 14–16 | 13–14 | 42 | Aust | Franklin <i>et al.</i> (1995), Smales <i>et al.</i> (2009) |
| Regent Honeyeater | <i>Xanthomyza phrygia</i> | 33 | 12–15 | 13–16 | | Aust | Oliver (1998) |
| Noisy Miner | <i>Manorina melanocephala</i> | 70 | 15–18 | 13–16 | 26–30 | Aust | Dow (1978) |
| Tui | <i>Prothemadera novaeseelandiae</i> | 90 | 12–15 | 11–21 | 8–14 | NZ | Dilks (2004) |
| Ma'oma'o | <i>Gymnomyza samoensis</i> | 94 | >19 | 21–22 | 60–90 | Samoa | Current study |
| Noisy Friarbird | <i>Philemon corniculatus</i> | 107 | 15–17 | 16–19 | <12–25 | Aust | Ford and Trémont (2000) |
| Red Wattlebird | <i>Anthochaera carunculata</i> | 125 | 15–17 | 15–20 | 15–30 | Aust | Ford and Trémont (2000) |
| Brown Honeyeater | <i>Lichmera indistincta</i> | 9 | 13–14 | 13–14 | | Aust | Franklin and Noske (2000) |
| Yellow-throated Honeyeater | <i>Lichenostomus flavicollis</i> | 33.5 | 15–17 | 16 | | Tasm | del Hoyo <i>et al.</i> (2014) |
| Long-billed Honeyeater | <i>Melilestes megarhynchus</i> | 47.5 | 16–19 | 14–15 | | PNG | Bell (1982) |
| Graceful Honeyeater | <i>Meliphaga gracilis</i> | 16.5 | 15 | 10–14 | | Aust-PNG | del Hoyo <i>et al.</i> (2014) |
| Elegant Honeyeater | <i>Meliphaga cinereifrons</i> | 22 | 11–14 | | | PNG | del Hoyo <i>et al.</i> (2014) |
| Singing Honeyeater | <i>Lichenostomus virescens</i> | 34 | 11–14 | 11–16 | | Aust | del Hoyo <i>et al.</i> (2014) |
| White-gaped Honeyeater | <i>Lichenostomus unicolor</i> | 33 | 15–16 | 13–14 | | Aust (tropical) | del Hoyo <i>et al.</i> (2014) |

Table 3. Continued.

| Common name | Scientific name | Adult female weight (g) | Incub. period (days) | Nestling period (days) | Time until indep. (days) | Country | Reference |
|----------------------------|-----------------------------------|-------------------------|----------------------|------------------------|--------------------------|-----------------|-------------------------------|
| Yellow Honeyeater | <i>Lichenostomus flavus</i> | 25 | 16 | 12–14 | | Aust (tropical) | del Hoyo <i>et al.</i> (2014) |
| Yellow-tufted Honeyeater | <i>Lichenostomus melanops</i> | 31 | 14–16 | 10–14 | 42 | Aust | del Hoyo <i>et al.</i> (2014) |
| Purple gapped Honeyeater | <i>Lichenostomus cratitius</i> | 22.5 | 13–14 | | | Aust | del Hoyo <i>et al.</i> (2014) |
| Yellow-plumed Honeyeater | <i>Lichenostomus ornatus</i> | 21.1 | 12–15 | 12–14 | | Aust | del Hoyo <i>et al.</i> (2014) |
| White-plumed Honeyeater | <i>Lichenostomus penicillatus</i> | 20 | 13–15 | 11–15 | 12 | Aust | del Hoyo <i>et al.</i> (2014) |
| White-fronted Honeyeater | <i>Purnella albifrons</i> | 19 | 12–13 | 10–12 | | Aust | del Hoyo <i>et al.</i> (2014) |
| Yellow-throated Miner | <i>Manorina flavigula</i> | 55 | 15–16 | 15–16 | | Aust | del Hoyo <i>et al.</i> (2014) |
| Spiny-cheeked Honeyeater | <i>Acanthagenys ruficularis</i> | 57 | 14–15 | 14–19 | 12 | Aust | del Hoyo <i>et al.</i> (2014) |
| Little Wattlebird | <i>Anthochaera chrysopetera</i> | 82 | 12–15 | 14–16 | 7–21 | Aust | del Hoyo <i>et al.</i> (2014) |
| Yellow Wattle bird | <i>Anthochaera paradoxa</i> | 190 | 14–16 | 18–21 | 17 | Aust (Tasm) | del Hoyo <i>et al.</i> (2014) |
| Rufous-banded Honeyeater | <i>Conopophila albogularis</i> | 13.2 | 14–17 | 13–15 | 30 | Aust+PNG | del Hoyo <i>et al.</i> (2014) |
| Rufous-throated Honeyeater | <i>Conopophila rufogularis</i> | 13 | 13–15 | 12 | | Aust (tropical) | del Hoyo <i>et al.</i> (2014) |
| Black Honeyeater | <i>Sugomel nigrum</i> | 12 | 14–16 | 15–16 | | Aust (all) | del Hoyo <i>et al.</i> (2014) |
| Scarlet Myzomela | <i>Myzomela sanguinolenta</i> | 10 | 11–12 | 11–12 | 10 | Aust | del Hoyo <i>et al.</i> (2014) |
| Micronesian Myzomela | <i>Myzomela rubratra</i> | 15 | 12 | 15–16 | | Micronesia | del Hoyo <i>et al.</i> (2014) |
| Cardinal Myzomela | <i>Myzomela cardinalis</i> | 13 | 12–14 | 12–14 | | Solomons-Samoa | del Hoyo <i>et al.</i> (2014) |
| Tawny-crowned Honeyeater | <i>Gliciphila melanops</i> | 16 | 12–13 | | | Aust | del Hoyo <i>et al.</i> (2014) |
| White-naped Honeyeater | <i>Melithreptus lunatus</i> | 15 | 14 | 14–16.5 | | Aust (Tasm) | del Hoyo <i>et al.</i> (2014) |
| Blue-faced Honeyeater | <i>Entomyzon cyanotis</i> | 119 | 16–17 | | | Aust+PNG | del Hoyo <i>et al.</i> (2014) |
| Little Friarbird | <i>Philemon citreogularis</i> | 84 | 13–16 | 13–15 | 10 | Aust+PNG | del Hoyo <i>et al.</i> (2014) |
| Striped Honeyeater | <i>Plectorhyncha lanceolata</i> | 45 | | 15–17 | | Aust | del Hoyo <i>et al.</i> (2014) |
| Painted Honeyeater | <i>Grantiella picta</i> | 18 | 13–15 | | | Aust | del Hoyo <i>et al.</i> (2014) |

time prior to fledging at the nest than a Red Wattlebird chick *Anthochaera carunculata*, a tropical species with a similar body size. Our results suggest that even accounting for body weight, Ma'oma'o chicks are in the nest a few days longer than expected for a honeyeater of their size. Because there is little information on the breeding biology of other tropical island honeyeaters, we could not determine if this is a typical tropical island trait. A prolonged nestling period may increase the risk of nest predation from invasive predators. It may also allow Ma'oma'o chicks to attain a body weight equal to or greater than that of the same-sex adult. Despite this weight gain, the tail and wing feathers are not fully formed at fledging. The fledgling is a poor flier and can only glide for the first few days after leaving the nest. Other studies report that fledging date is correlated with a critical wing loading or a period in feather growth that allows for flight (Martins 1997, Michaud and Leonard 2000). In Ma'oma'o, it is possible that the time of fledging is determined by different attributes such as a critical minimum weight, size or condition. This slow development rate may be a common feature of tropical island species which have evolved without mammalian predators.

The length of the post-fledgling period of the Ma'oma'o was also extended. Our results indicate this cannot be due to its large size. Post-fledgling care of Ma'oma'o is 30–47% longer than it is for Australian honeyeaters with the longest recorded dependency period, and 78–85% longer than honeyeaters from the temperate islands of New Zealand. Extended parental care in the post-fledgling period may promote the survival of juveniles, and thus counteract the effects of smaller clutches (Russell 2000).

Though breeding in the Ma'oma'o is extended, it also shows some seasonality and in Samoa seems to be timed to take advantage of increased insect availability during budburst and plant flowering (Stirnemann unpubl. data). Ma'oma'o breeding appears also to stop or to become reduced during the months when most rain falls. This is consistent with observations on the timing of breeding by tropical honeyeaters in Papua New Guinea, which also occurs prior to the wet-season rains (Bell 1982). Yet these results contrast with the timing of breeding in other tropical landbirds, such as those from Timor and the Northern Territory, which breed throughout the wet season (Frith and Davies 1961, Noske 2012). Further studies on the breeding biology of birds in the South Pacific are required to clarify the processes that limit breeding in the tropics overall.

Conservation and life history traits

Species with slow breeding traits, such as the Ma'oma'o, recover slowly following a decline. This is because the recovery potential for species with high potential maximum reproductive success (multiple eggs and clutches) is much greater than that for species with low maximum reproductive success (single eggs and clutches) (Sæther and Bakke 2000). Furthermore, population growth in species with low maximum reproductive success following a year of low reproductive success is unlikely to compensate for the poor reproductive success in the prior year (Ainley *et al.* 1995). Therefore, species with small clutch sizes may need to have multiple good years to recover from a single bad year. Consequently, effective management to increase the population of a slow breeding tropical species will require management over a longer period of years than for an otherwise comparable species with a larger clutch size.

Invasive species have resulted in the decline of many bird species and island species are particularly affected because of their isolated evolutionary history (Clavero *et al.* 2009, Drake and Hunt 2009). The extended breeding season of the Ma'oma'o may enable it to withstand a small level of nest predation because it can re-nest following an earlier nest predation event. This behaviour contrasts with many seabird species that are physiologically or environmentally unable to produce a second clutch within the year (Jouventin and Dobson 2002). We do not know, however, if they can re-nest following the loss of a fledged chick. Thus, the Ma'oma'o population may be very sensitive to changes in fledgling survival and even low rates of fledgling predation may result in a population decline. Even if post-fledgling survival can be improved, it may also be necessary to focus management efforts on other demographics, such as increasing survival of adult birds, to maintain viable populations.

Species with life history traits that include low maximum annual reproduction often have long lifespans compared to other birds (Ashmole 1963, Gadgil and Bossert 1970). Long-lived populations

may persist for many decades beyond the development of factors that cause high chick or fledgling mortality. In such species it may be difficult to detect population declines or growth because high adult survival can mask changes in the population. Methods that monitor reproductive success or juvenile survival directly in these long lived species can be more effective at detecting population recovery than methods that assess the entire population such as point counts (Anders *et al.* 1997). No data exist on the longevity of Ma'oma'o or post-fledging survival rates, hence population assessments should be augmented with monitoring of reproductive success and a long-term study of individual survival.

Accurate measurement of reproductive success is an important component in monitoring and management of threatened species. In dense rainforests where nests are difficult to find, monitoring fledgling survival may be an easier and better measure of reproductive success than nest success (Anders *et al.* 1997). The remaining Samoan forests are dense and many are on steep terrain that makes monitoring of Ma'oma'o nests difficult. Finding Ma'oma'o nests is not easy and requires many hours of intensive territory monitoring over an extended breeding season. Experience from this study suggests that even with intensive fieldwork, insufficient nests will be found to provide a meaningful long-term measure of Ma'oma'o breeding success. The alternative approach is to monitor territories of known pairs. Fledglings remain in the territory for extended periods and can be detected readily by their distinct call. We recommend systematic visits to territories to search for fledglings during June and July, when nesting is at its peak, as an effective method of detecting successful breeding. A disadvantage of this method is the inability to distinguish between unsuccessful nesting attempts and failure to initiate breeding. The Ma'oma'o, however, has characteristics that facilitate monitoring of chick survival rates. The chicks are highly vocal and call continuously, have a long parental care period, and both the chick and the adults are highly territorial, all of which increase detectability.

The Ma'oma'o has many life history characteristics that make it vulnerable to introduced predators, habitat loss and other anthropogenic changes. These traits include low maximum reproductive capacity and extended development times. This study emphasises the importance of taking into account the life history attributes of a species when determining management strategies. Yet it also builds on our understanding of how reproductive traits vary across tropical bird species. Small clutch size is not unique to the Ma'oma'o in the Pacific (Freeman and Mason 2014). Further detailed studies on the breeding biology and life history traits of other tropical Pacific birds are required to determine how typical or unusual the Ma'oma'o is with regard to its reproductive strategy. Detailed reproductive knowledge of more species in the Pacific may also clarify the evolutionary mechanisms behind the development of slow reproductive traits in avifauna as well as clarifying conservation strategies.

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