ECOLOGY AND DRIVERS OF DECLINE IN A TROPICAL ISLAND HONEYEATER: THE MA'OMA'O

A thesis presented in partial fulfilment of the requirements
for the degree of

**Doctor of Philosophy
in
Zoology**

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Declaration

This thesis is my own work, except where otherwise acknowledged
(see Preface and Acknowledgements).

Rebecca Stirnemann

September 2015

"If you never did, you should. These things are fun, and fun is good"

Dr Seuss

To my family
who have always encouraged me
and to my friends for all of their support
Thank you

Preface

This thesis is structured as a series of connected manuscripts. With the exception of the Introduction, these papers have all been published, accepted or submitted for publication at the time of thesis submission. These manuscripts are listed below and are referred to as chapters in the text.

1. Rebecca L. Stirnemann, Murray A. Potter, David Butler, and Edward O. Minot (2015) Acoustic differences enable sex discrimination in Ma'oma'o (*Gymnomyza samoensis*), a species with high sexual morphological overlap. The Wilson Journal of Ornithology: 127(3) 376-386.

2. Stirnemann, Rebecca, M.A. Potter, David Butler, and Edward Minot. 2015. Slow life history traits in an endangered tropical island bird, the Ma'oma'o. Bird Conservation International, available on CJO2015. doi:10.1017/S0959270915000234.

3. Stirnemann, R., M.A. Potter, D. Stojanovic and E. Minot. Nest success does not predict reproductive success in a tropical island honeyeater. Ibis. In review.

4. Stirnemann, Rebecca, M.A. Potter, David Butler, and Edward Minot. 2015. Compounding effects of habitat fragmentation and predation on bird nests. Austral Ecology. doi: 10.1111/aec.12282.

All papers were intended as stand-alone pieces of work. For this reason, there is some unavoidable repetition between chapters, for example in the description of study areas and experimental design. An introductory context statement has been provided at the beginning of this thesis. This introduction is not intended to be a complete literature review, but rather an explanation of the relationships between different aspects of the research which makes up the thesis.

I performed the majority of the work for the papers that form this thesis. This included developing the research questions, experimental designs, data collection, statistical analysis, and writing. My supervisors Murray Potter, Edward Minot and David Butler made substantial contributions to the conceptualisation of research and revision of the manuscripts. The co-authors of each paper provided comments during the revision of the manuscripts. Dr D. Stojanovic provided guidance on the mark analysis and towards the conceptual development of Paper 4.

Acknowledgements

Abstract

There is a worldwide decline in biodiversity. Few studies have explored the processes that underlie biodiversity decline in some tropical regions, especially on tropical oceanic islands, where there are many threatened species and a high level of endemism. Indeed, even basic biological information is lacking for many Oceanic species. The Ma'oma'o (*Gymnomyza samoensis*), an endangered honeyeater endemic to Samoa, is an example of this. Here, I report results from an investigation on: 1) the breeding biology of this island honeyeater, 2) how survival varies with life history stage, 3) how to sex this monomorphic species in the field, and 4) how landscape and local-scale vegetation features influence nest predation of these cup nesting birds. I used observational data on breeding biology and survival at different life history stages to determine why this species is declining, and a combination of vegetation mapping and artificial nest surveys to determine how landscape processes and predation by invasive species contribute to declines in Oceanic forest birds. I also collected morphometric measurements and calls of known-sex individuals to develop a method of sexing Ma'oma'o in the field and to assess whether the declining populations showed sex bias. I found that the decline of this species is driven by interactions between the life history traits, predation by the black/ship rat (*Rattus rattus*), and fine and large-scale vegetation and landscape attributes. The Ma'oma'o produces at most one chick per year and therefore has a small maximum annual reproductive success rate compared to other honeyeaters. Furthermore, compared to other honeyeaters, the Ma'oma'o remains in the nest for longer and has an extended fledgling dependency period. My study highlights how predation by black rats at the nest reduces reproductive success. I found that the probability of nest success was significantly reduced near plantations. However, interior forest did not have lower nest predation rates then edge forest. My findings indicate that the maintenance of large sections interior forest alone is unlikely to increase reproductive success for the Ma'oma'o or indeed for other forest bird species sensitive to black rat predation. The key

management strategy is to have intensive rat control at breeding sites during the reproductive

season.

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Chapter 1: Context Statement

Introduction

There is a worldwide decline in biodiversity (Blaustein and Wake 1990, Butchart et al. 2004, 2006). An understanding of the major threats to endangered and threatened species is needed urgently in order to develop useful management strategies (Pressey et al. 2007). However, the majority of such studies have been done in temperate regions and on continental land masses (Kingsford et al. 2009). Few studies have explored the threatening processes affecting biodiversity in tropical regions, particularly on oceanic islands (Kingsford et al. 2009), despite the disproportionately high number of threatened species and the endemic richness of this region (Johnson and Stattersfield 2008). For example, while only 17% of the world's bird species are restricted to islands, the number of threatened island bird species is almost equal to the number of threatened species on the continental landmasses (Johnson and Stattersfield 2008, Johnson 2011).

The key factors reducing the breeding success and overall fitness of bird populations are thought to be habitat loss and degradation, invasive species, and exploitation (Blaustein and Wake 1990, Butchart et al. 2004, 2006). The influence of habitat loss, degradation and invasive species has been well studied in temperate islands such as New Zealand (e.g. King 1983, Wilson et al. 1998, Moorhouse et al. 2003, Innes et al. 2010). However, few studies have investigated the effect of these factors across the Polynesian and Micronesian Islands (but see Olson et al. 2006). This is despite evidence suggesting that species can differ in ecology between tropical and temperate regions (e.g. Heneghan et al. 1999, Dyer et al. 2007). We must therefore be cautious in our extrapolation of models developed in temperate regions. We discuss the effect of habitat loss, degradation and invasive species below in this context.

Introduced species

The introduction of alien taxa has played a key role in avifauna extinction and declines, especially on isolated islands such as New Zealand, Hawaii, Mauritius and many of the other Pacific islands (Innes et al. 2010). The high susceptibility of island species to invasive species has been related both to the small landmass of islands and to the evolution of island species in the absence of strong competition, herbivory, parasitism, or predation (Pimm et al. 1994).

The relationship between introduced mammals on islands and the extinction of island species has been well-documented (Key et al. 1998, Delgado García et al. 2005, Towns et al. 2006). Other taxa including plants, insects and invasive birds can also have a high impact on local species (Clavero et al., 2009). According to Ebenhard (1988), alien species can affect natives in a number of different ways. They can: (1) affect plant populations and thereby species living in the habitat structured by these plants; (2) be predators of native species; (3) induce resource interference or exploitation competition; (4) spread micro- and macro-parasites into native populations; (5) induce genetic changes to native species through hybridisation; and (6) provide additional prey to native predators. On islands, the presence of introduced species can lead to dramatic changes through all these mechanisms, though the last two are likely to have a lesser influence.

The most important introduced mammals, both in terms of numbers of introductions and resultant damages, in no particular order: rabbits (*Oryctolagus cuniculus*), cats (*Felis catus*), the three rat species (*Rattus exulans, R. rattus, R. norvegicus*), the house mouse (*Mus musculus*), feral goats (*Capra hircus*) and pigs (*Sus scrofa*) (Ebenhard 1988, Harris 2009, Innes et al. 2009). The three species of rats are implicated in the greatest number of extinctions of island bird species (Towns et al. 2006).

The impact of an invasive species is not likely to be equal across the landscape (Ringler et al. 2014). Research from Fijian forests suggests that rats are likely to have a stronger influence near

forest edges then in interior forest (Olson et al. 2006). The presence or abundance of invasive species may therefore be compounded by habitat loss and fragmentation (Olson et al. 2006). Thus, proximate causes of mortality may ultimately be caused by land use changes such as a decrease in good-quality vegetation that causes birds to spend more time foraging in risky areas (Innes et al. 2010). The impact of predation rates on populations also depend on the demography and behaviour of the species (e.g. Wilby et al. 2005, Vucetich et al. 2002). For example, the extent that predation influences population dynamics may be highly dependent on the age or sex class of the species preyed on (Engen et al. 2005, Low and Pärt 2009). For instance, population modelling indicated that the loss of adult yellowhead (*Mohoua ochrocephala*) females in New Zealand has a much greater effect on population trends than the loss of eggs and young (Elliott 1996). Estimates of age and sex specific survival over different life history stages are important for understanding demographic parameters of animal populations, and forms the basis of evaluating population viability (Streby and Andersen 2011, Wilson and Martin 2012). Therefore, reliable estimates of survival and fecundity are critical in scenarios where management depends on the outcome of population viability models. To our knowledge, however, no published studies from the South Pacific discriminate between both the different life history stages and sex in regards to their vulnerability to predation.

Habitat Loss

Habitat alteration is likely to be a driver of species loss in the Pacific. It has two distinct components: habitat loss and habitat fragmentation (Fahrig 1997). Habitat loss occurs when the amount of a particular habitat declines in the landscape (Innes et al. 2010). The simplest way in which habitat loss influences a population is through the loss of individuals in proportion to the extent of habitat loss (Bender et al. 1998). If too much habitat is lost, this may result in the local extinction of a species (Cale, 2003). Species traits such as trophic level, dispersal ability and degree of habitat specialisation influence species responses to habitat loss (Bender et al. 1998). For generalist species that use both the edge and the interior of a habitat patch and are not

limited by the surrounding matrix, population declines are unlikely to be as a result of pure habitat loss alone (Bender et al. 1998).

Fragmentation occurs when habitat is divided into smaller areas (Bender et al. 1998). Habitat fragmentation results in reduced patch size and decreased connectivity in the landscape. This leads to a reduced rate of dispersal which can strongly influence a species' population dynamics (eg. Cale, 2003). Fragmentation can also lead to an increase in the amount of habitat near an edge. Edge habitat can be quite different from interior habitat. Hence, for example, the population dynamics of interior forest requiring species may depend on the degree of fragmentation even where the habitats remain otherwise unaltered. Indeed, a number of studies have suggested that predation rates are higher near habitat edges (Donovan et al. 1995, but see Lahti, 2009).

Fragmentation can also occur without habitat loss (Fahrig 2003). In reality, however, both forms of habitat alteration typically occur together and it can be difficult to separate the effects of habitat loss from the effects of fragmentation (Harrison and Bruna 1999). For interior species, the decline in population size associated with habitat fragmentation will be greater than that predicted from pure habitat loss alone (Bender et al. 1998). However, resident species with low population densities and a low proportion of habitat cover are the most at risk from habitat destruction in general (Bender et al. 1998).

Extinction risk from both habitat loss and the impacts of invasive species will vary between species and across space because of the combined and interactive effects of a species' ecology, life history and geography (Lee and Jetz 2011). Factors that affect the balance between fecundity and longevity, such as introduced predators, are likely to have a disproportionately larger effect on taxa with slow rates of population growth (Owens & Bennett 2000). Habitat loss is likely to be a particular threat to taxa that are ecologically specialized with small ranges (Owens & Bennett 2000, Kingsford et al. 2009).

The threats to many species in Oceania are often broadly categorised as being due to habitat alterations and the presence of novel introduced predators (MNRE, 2006; BirdLife International, 2012). These broad generalisations do not enable management to be targeted. For instance, it also does not indicate when pest control should be implemented. Yet, a pest control program can be more effective at reducing adult mortality and increasing nest success if targeted to coincide with the breeding period (Innes et al., 1999). This requires a detailed understanding of why population declines are occurring. For many South Pacific bird species this will require improved knowledge of species basic biology (Kingsford et al. 2009, BirdLife International, 2012).

The Ma'oma'o, a giant forest honeyeater, is one such data deficient species (MNRE 2006). The Ma'oma'o, like many bird species in Oceania, is range restricted and threatened. Because effective conservation action for threatened species requires sound ecological knowledge (Fahrig & Merriam 1994, Ford et al. 2001), the first step for the Ma'oma'o and other threatened species is to understand its basic life history and ecology. The Ma'oma'o has many features that make it an excellent model species on which to develop techniques and protocols for the conservation of tropical island forest birds. This study used the Ma'oma'o as a case study species to provide the ecological foundation needed to inform decision-making for the conservation management of sensitive forest species in the South Pacific in general and the Ma'oma'o in specific.

Study species

The Ma'oma'o

The Ma'oma'o or Mao (*Gymnomyza samoensis*) is an endangered honeyeater endemic to the Samoan archipelago (Fig. 1). Of the honeyeater family Meliphagidae, the Ma'oma'o is one of three honeyeater species in the genus *Gymnomyza*. The other two species are also restricted to islands in the southwest Pacific Ocean. The Crow honeyeater (*Gymnomyza aubryana*) is endemic to New Caledonia while the Giant honeyeater (*Gymnomyza viridis*) is only found in Fiji. Very little is known about the biology of any of the species within this genus. This is a

cause for concern since the Crow honeyeater is listed at critically endangered and the Ma'oma'o as endangered by the IUCN. Furthermore, though the Giant forest honeyeater of Fiji is not uncommon in Fiji it is absent from some of the large Fijian islands such as Kadavu, Gau and Ovalau. Like the other two species in its genus, the Ma'oma'o has decreased in range. The Ma'oma'o was once found throughout the forests of Savai'i and Upolu (Samoa) from the coast to the highest elevation mountaintops. It was also observed and captured on Tutuila Island in American Samoa (Amerson *et al.* 1982). Indeed, the Whitney South sea expedition collected three specimens, two males and one female, in February 1924 as museum specimens (Mayr, 1932). Ma'oma'o were also reported in Tutuila in 1977 (Engbring and Ramsey 1989). However, surveys on Tutuila in American Samoa in 1982, 1986, and 1992-1996 did not detect the Ma'oma'o (Amerson *et al.* 1982, Enbring and Ramsey 1989, Freifeld 2015 *in litt*.) given the high detectability of this species early in the mornings and evenings it is extremely likely that this species in locally extirpated in this area of its range.

Currently Ma'oma'o are still found on Upolu and Savai'i, the two largest islands in Samoa (MNRE 2006). In 1984, the Ma'oma'o was reported as common in the undisturbed upland forests of Upolu and Savai'i (Bellingham & Davis 1988). Surveys conducted in 2005-2006 found Ma'oma'o at seven sites on Upolu and Savai'i. This survey was used to roughly estimate population numbers at 500 individuals suggesting that numbers have been declining in Samoa. However, there was no detailed survey of the Ma'oma'o before the 2005 survey and little information exists in regards to the species abundance and distribution (MNRE 2006). In response to these declines the status of Ma'oma'o was changed from 'vulnerable' in 1994 to 'endangered' in 2000 (IUCN 2012). The population is in ongoing decline and in need of urgent attention (MNRE 2006).

In 2006 the Government of Samoa developed a recovery plan for the Ma'oma'o (MNRE 2006). The recovery plan identifies a goal of securing the Ma'oma'o, maintaining its existing populations on Upolu and Savai'i, and re-establishing populations at former sites (MNRE

2006). The cause of their decline and endangered status is unclear, but habitat loss and invasive

species are presumed to pose a serious threat to the remaining populations (MNRE 2006).
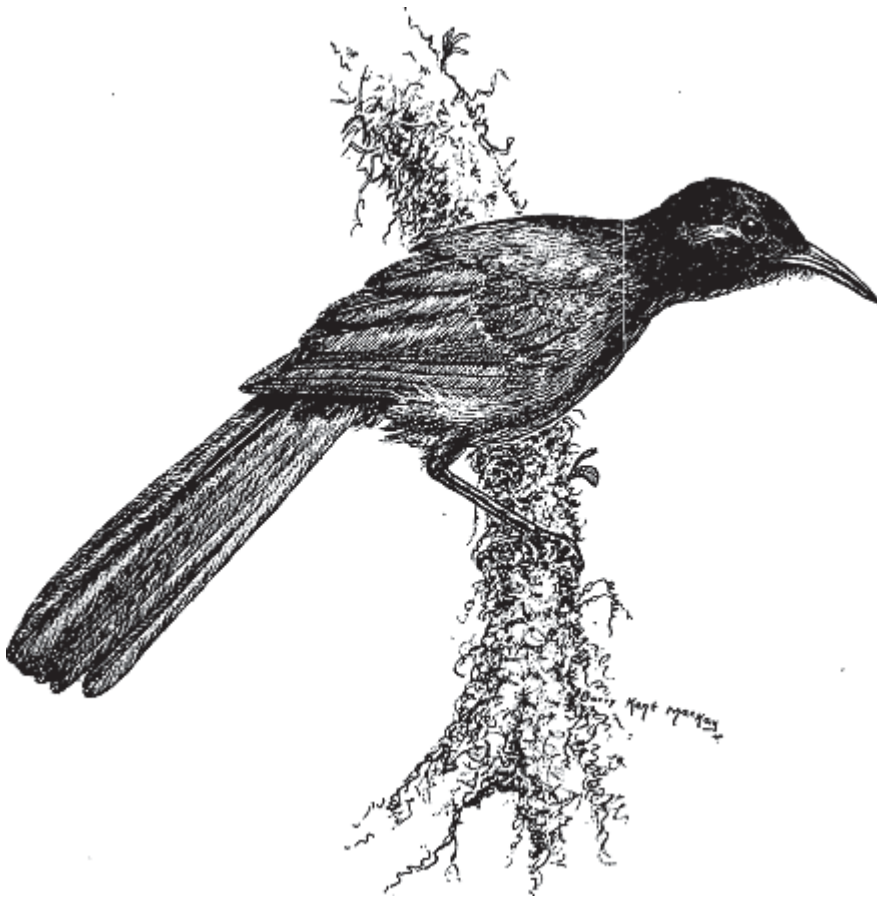
Figure 1. Drawing of a Ma'oma'o (copied from Orenstein, 1979)

Study Area

Samoa (13°-15°S, 168°-173°W) is in the South Pacific. It forms part of the Samoan archipelago,

northeast of the Fiji archipelago. It is politically divided into Samoa and American Samoa. In

Samoa, the two main islands are Upolu (1110 km^2 area, 1100 m elevation) and Savai'i

(1820km^2, 1860 m). The main wet season is from December to March, but there is high rainfall

at high elevation (+600 m) all year (approx. 600–800 cm of rainfall annually) (Ward and

Ashcroft 1998). Across Samoa, large scale clearance of native forests has taken place to develop

land for agriculture (Taule'alo 1993). Most cleared land in Samoa is farmed by villagers on a

customary land using a combination of subsistence and cash-crop agriculture (Ward and

Ashcroft 1998).

Habitat loss in Samoa has been extensive in recent years and the amount of forested land area had declined by 18% from 1987 to 1999. Forest loss since 1999 has not been quantified. In addition to loss of forest, the quality of the forest that remains has become increasingly degraded. An analysis in 1999 identified 32% of the total forest cover as 'open' forest (less than 40% tree cover) and less than 0.05% as 'closed' forest, largely as a result of Cyclones Ofa and Val (MNRE 2006). As a result the montane forest in Samoa is now extremely open and patchy and is increasingly vulnerable to invasive weeds (MNRE 2006).

Samoa has three introduced rat species, the ship rat (*Rattus rattus*), Norway rat (*Rattus norvegicus*) and Pacific rat (*Rattus exulans*) (MNRE 2006). These invasive predators as well as cats are presumed to have the largest effect on the survival of birds, yet there is currently limited data available to quantify this impact on South Pacific forest birds (Towns et al. 2006, Medina et al. 2011, Russell et al. 2011).

Thesis layout

The overarching aim of my PhD research was to understand the factors that were resulting in severe population declines in the Ma'oma'o and other forest nesting Oceanic species. Specifically I asked: 1) how predation and habitat loss/fragmentation influenced the population decline of the Ma'oma'o; and 2) how the life history and behaviour traits of Ma'oma'o influence reproductive success and survival. This study works toward developing an understanding of why bird population declines are occurring in Oceania and the conservation management required.

This thesis is based around four research chapters, each written as a stand-alone contribution for an international peer-reviewed journal. Therefore, some repetition was necessary to make each

an independent piece. I have, however, standardised the formats to make the entire thesis more cohesive.

The first paper outlines the development of a reliable non-invasive method for accurately determining the sex of the Ma'oma'o a species with extensive sexual morphometric overlap in the field (Chapter 2). In the following two chapters, I seek to clarify the demographic characteristics, breeding behaviour, and measure the reproductive success of Ma'oma'o whilst establishing threats at different life history stages. The first of these chapters aims to determine the life history and breeding behaviour of the Ma'oma'o (Chapter 3). The second evaluates the survival and threats to Ma'oma'o over the nesting, post-fledgling (pre-dispersal) phase, and as a breeding adult (Chapter 4). I then quantify how the habitat at landscape and local scales are influencing nest success of cup nesting birds in Samoa (Chapter 5). The final chapter identifies the major results of this study and the implications for management of Ma'oma'o. Priorities for further research and management are identified (Chapter 6).

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STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Rebecca Stirnemann

Name/Title of Principal Supervisor: Professor Murray Potter

Name of Published Research Output and full reference:

1. Rebecca L. Stirnemann, Murray A. Potter, David Butler, and Edward O. Minot (2015) Acoustic differences enable sex discrimination in Ma'oma'o (Gymnomyza samoensis), a species with high sexual morphological overlap. The Wilson Journal of Ornithology. 127(3) 376-386.
2. Stirnemann, Rebecca, M.A. Potter, and David Butler, and Edward Minot. 2015. Slow life history traits in an endangered tropical island bird, the Ma'oma'o. Bird Conservation International, available on CJO2015. doi:10.1017/S0959270915000234.
3. Stirnemann, R., M.A. Potter, D. Stojanovic and E. Minot. Nest success does not predict reproductive success in a tropical island honeyeater. Bird Conservation International. In review
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In which Chapter is the Published Work: 2,3,4,5

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- The percentage of the Published Work that was contributed by the candidate:

   and / or

- Describe the contribution that the candidate has made to the Published Work:

   Rebecca Stirnemann performed the majority of the work for the papers that form this thesis. This included developing the research questions, experimental designs, data collection, statistical analysis, and writing. My supervisors Murray Potter, Edward Minot and David Butler made substantial contributions to the conceptualisation of research and revision of the manuscripts. The co-authors of each paper provided comments during the revision of the manuscripts. Dr D. Stojanovic provided guidance on the mark analysis and towards the conceptual development of Paper 4.

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Chapter 2: Acoustic differences enable sex discrimination in a species with high sexual morphological overlap

Measuring the wing length of the Ma'oma'o (*Gymnomyza samoensis*)

Abstract

A field technique to identify sex is critical for facilitating conservation of species where declines are potentially unequal between the sexes. Although morphometrics are often used to sex individuals in the field, for many tropical and seabird species there is extensive morphometric overlap between the sexes. Accurate sexing of individual birds for research and conservation is thus reliant on genetic analysis, which is not instantly available. In this study we use an endangered tropical bird, the Ma'oma'o (Mao) (*Gymnomyza samoensis*), as a case study to investigate reliable methods for accurately determining sex in the field for a species with extensive sexual morphometric overlap. We provide the first comprehensive description of its vocalisations and morphology and examine whether individuals of this sexually monomorphic species can be accurately sexed using three features: morphometrics, eye colour, and vocalisations. Acoustic analysis, which measured the central frequency of Ma'oma'o alarm calls, allowed sex of all sampled individuals to be correctly identified and was the most accurate mechanism for sexing Ma'oma'o in the field. Our results also indicated that despite high morphometric overlap binomial generalised linear models enabled 54% of the Ma'oma'o to be sexed with 95% confidence in the hand. Individuals that had a high probability of being incorrectly sexed could also be identified. Eye colour did not allow strict delineation of the sexes, although the only birds with blue eyes were adult males. We propose that using vocalisations to differentiate sex should be investigated further in other bird species. Not only can it provide an accurate method that does not require capture, but it may also be useful when combined with automatic sound recorders for monitoring sex ratios in bird populations where the greater decline of one sex is suspected.

Keywords: *sexing, morphology, sex determination, calls, Mao, sex ratio, population monitoring*

Introduction

Establishing the sex of adult birds is critical for both scientific research and for conservation (Ewen et al. 2001; Clout et al. 2002; Steifetten and Dale 2006; Ewen et al. 2011; Tuni and Berger-Tal 2012). However, distinguishing between the sexes remains a challenge particularly with species where males and females share similar plumage and are of a similar size (Baker 1974; King and Muddeman 1995; Palestis et al. 2012). One relatively recent technique for sexing birds is the use of molecular markers (Griffiths et al. 1998; Monceau et al. 2013). Still, this technique is costly, time consuming and requires a laboratory. However, as it can be used on DNA from a molted feather, it is not always necessary to capture the bird. Techniques that overcome these restrictions are needed for robust management and conservation, particularly for declining species [e.g. Kaka (*Nestor meridionalis*) (Wilson et al. 1998); and Swift Parrot (*Lathamus discolor*) (Stojanovic et al. 2014)]. A quick, simple, field-based test of sex is particularly vital where a greater decline in one sex is suspected or knowledge of the sex ratio present in a population is needed for wildlife management (Martin 1996; Winkler and Preleuthner 2001; Wolfe et al. 2010). For example, in Swift Parrots and Kaka, only the female incubates and as a result experiences higher mortality on the nest from predators. Unequal predation across the sexes results in unequal sex ratios, which may contribute to the decline of the species (Wilson et al. 1998; Moore et al. 2010; Stojanovic et al. 2014).

The Ma'oma'o or Mao (*Gymnomyza samoensis*), is endemic to the islands of Samoa, and currently listed as endangered by the IUCN (MNRE 2006; BirdLife International 2012). As part of conservation efforts, the Ma'oma'o is the subject of ongoing management studies and field research. However, the ability of managers to reverse these declines and manage threats effectively is currently limited by a lack of basic biological information about this species. Indeed no published information on the morphology or acoustics of the Ma'oma'o to our knowledge exists. Furthermore, mortality may not be equal between the sexes. Recent research shows that only the female sits on the nest (Stirnemann et al. in review) and that the mortality of female Ma'oma'o may be higher than that of males during the nesting period (Stirnemann,

unpubl. data). It is thus possible that unequal sex ratios contribute to the population decline of this already endangered species. However, it is difficult to determine sex-ratio inequality in a Ma'oma'o population because sex cannot be distinguished easily by using plumage or size.

Sexing individual Ma'oma'o in the field and avoiding a lengthy wait for DNA analysis would be useful. One potential method for determining sex is to use the eye colour of individual birds (e.g. Rosenfield et al. 2003). In Ma'oma'o, adult birds have been observed with blue-grey or brown eyes (Stirnemann unpubl. data). It has also been noted that juveniles have milky brown eyes, which then change to blue-grey or brown (Stirnemann et al. in review). In other species male and female birds are differentiated using morphometric measurements. For example Great Bittern (*Botaurus stellaris*) can be sexed by bill length, tarsus, wing length and body weight while in the New Zealand, Stitchbird (or Hihi; *Notiomystis cincta*) tarsus length and body weight are used (Low 2006; Dmitrenok et al. 2007). Vocal characteristics can also be used to sex individuals in some species (Bourgeois et al. 2007). For example, call temporal, frequency characteristics (Little Spotted Kiwi, *Apteryx owenii*), and syllable stereotype and the amplitude of the harmonics (Northern Cardinal, *Cardinalis cardinalis*) have been reported to vary between the sexes (Yamaguchi 1998; Digby et al. 2013).

In this study we investigate inter-sexual differences in vocalisations, morphology and eye colour in the Ma'oma'o, and provide the first acoustic and morphometric data for this species. We also introduce an accurate method for assessing the probability of morphometric measurements correctly determining the sex of an individual in the field. We show how these models are useful for species with high sexual morphological overlap. The utility of acoustic and morphometric methods for identifying sex in the Ma'oma'o is discussed.

Methods

Study site

The Samoan archipelago (13°-15°S, 168°-173°W) is in the South Pacific, northeast of the Fiji archipelago. It is politically divided into Samoa and American Samoa. In Samoa, the two main islands are Upolu (1110 km^2 area, 1100 m elevation) and Savai'i (1820 km^2, 1860 m elevation). We monitored Ma'oma'o at two study sites on the island of Upolu (Fig. 1). The first site was 3 km from Magiagi village in the Vaisigano water catchment (Upolu Island, 13°54.5' S, 171°44.3' W). The second study site was near Lake Lanoto'o at 13°54.3' S, 171°49.3' W at an elevation of 700 - 800 m (Fig. 1).
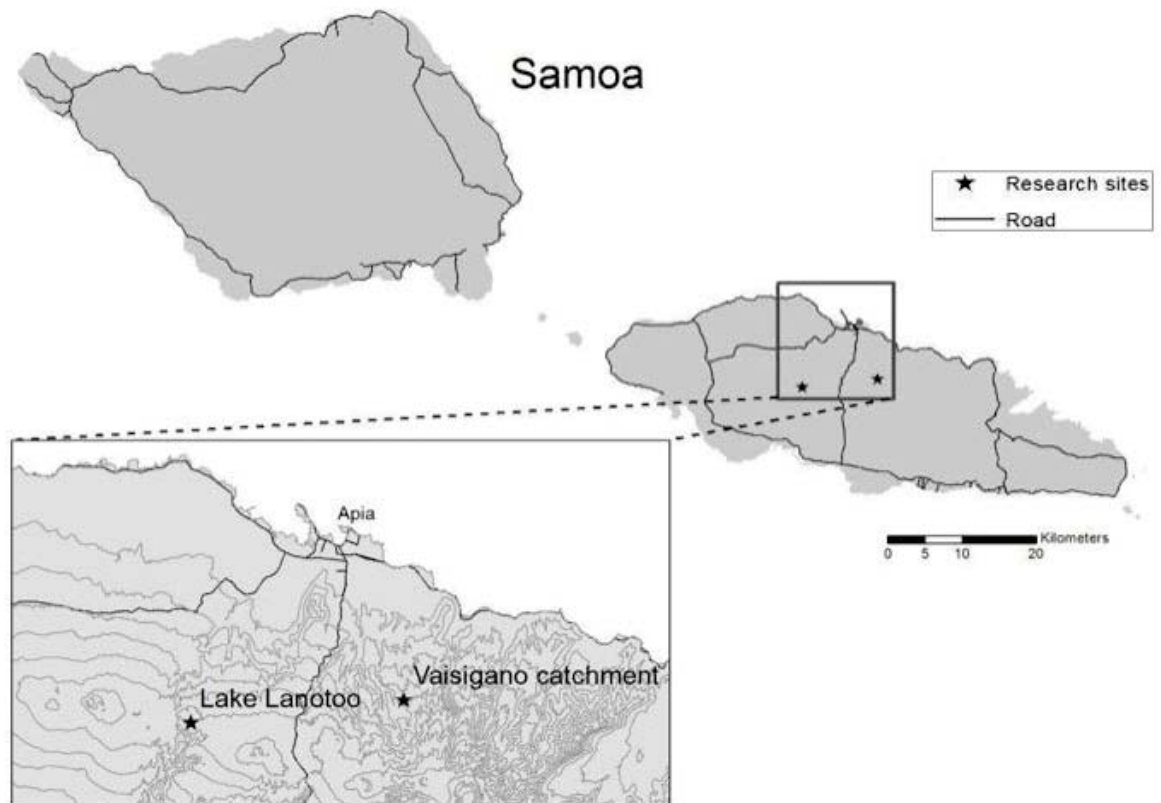
Figure 1. Map of Samoa, showing Ma'oma'o study areas on the island of Upolu.

Study species

The Ma'oma'o is a giant forest honeyeater endemic to the islands of Savai'i and Upolu, Samoa, and formerly occurred on Tutuila, American Samoa. It has not been recorded in American Samoa since the 1920s (MNRE 2006). Populations in Samoa have been declining (MNRE 2006; BirdLife International 2012). Causes of decline for this species in Samoa, and extinction in American Samoa, are unknown. However, the remaining Ma'oma'o populations are threatened by habitat loss and predation from invasive species, such as rats.

Acoustic Analyses

The Ma'oma'o has complex vocalisations (songs and calls). However, in this study we measure only the alarm call, a simple single note that was frequently made by both sexes (Fig. 2). Ma'oma'o pairs were sexed, either through DNA analysis or observations of sex-distinguishing behaviour, such as nesting behaviour (see Stirnemann et al. in review), during three breeding seasons (May-December 2011, 2012 and 2013) at two study sites on Upolu. The sound recordings were collected with a Telinga Twin Science microphone and a Telinga 53-cm foldable parabolic acoustic reflector connected to a Marantz PMD661 digital recorder (WAV format; 44.1 kHz; 16 bits). We recorded 240 alarm calls from 12 birds (120 calls from six males and 120 calls from six females) with at least 10 calls per bird. Forty calls (20 per sex) were randomly selected and removed for testing model adequacy following model selection. The majority of individuals were recorded several times during the same session, but some birds were recorded over two or three different dates. In order to predict sex by acoustic analysis, we measured six parameters that were relatively insensitive to recording conditions. We measured peak energy (peak frequency), centre frequency, highest frequency, the 5th percentiles of the energy distribution, delta frequency and note duration (Table 1).
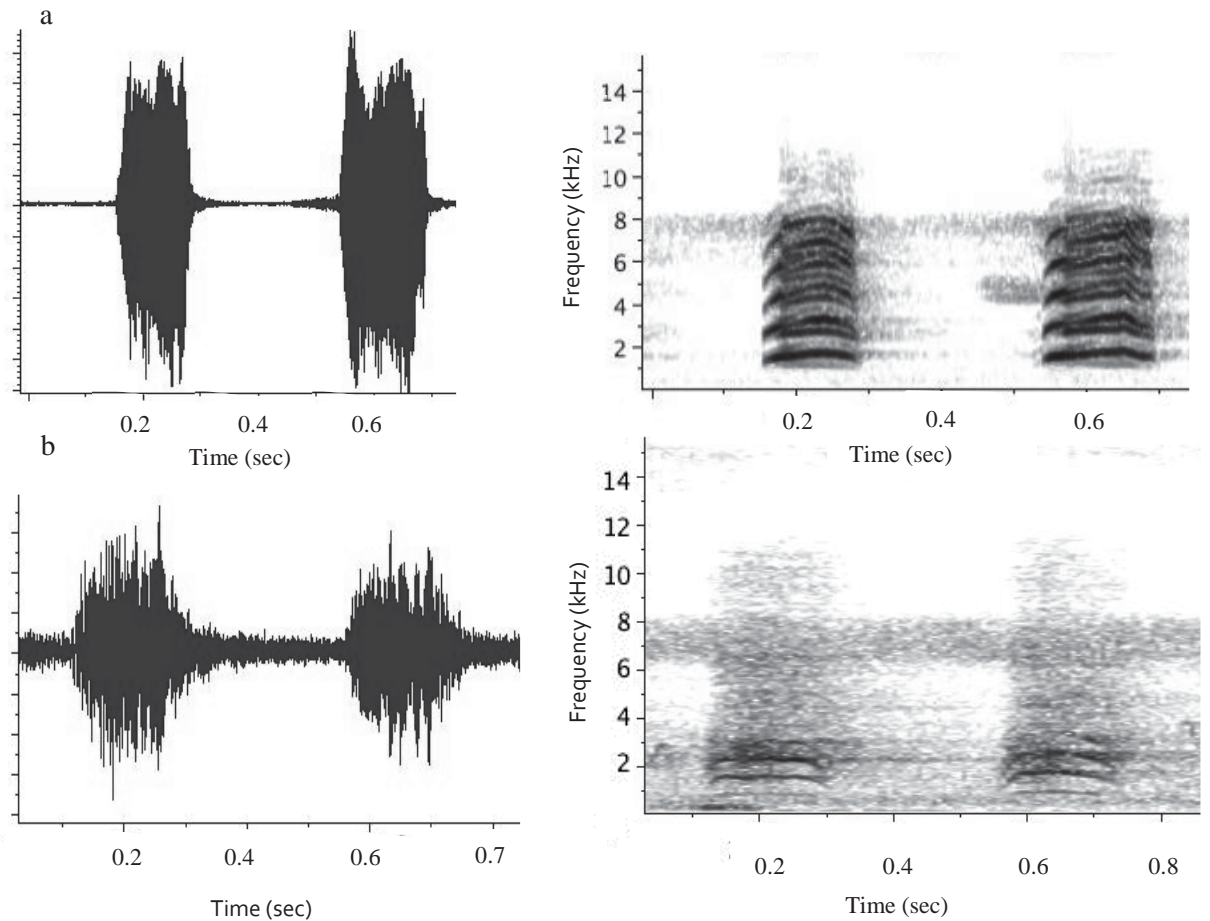
Figure 2. The waveform and sonagram of an alarm call of (a) male and (b) female Ma'oma'o.

Call parameters were measured from a spectrogram with a 598 sample Hann window, 50% overlap and 3 dB bandwidth of 212 Hz. To minimise measurement errors, we only analysed high-quality sonograms that were free from substantial distortions. Calls were analysed with Raven Pro 1.5 software (Bioacoustics Research Program 2014).

Morphological Measurements

In the field, we captured six adult Ma'oma'o with canopy mist nets. We measured morphometric characteristics and recorded eye colour of all birds. The following measurements were taken: bill length, wing length, tail length and tarsus length. Bill length (culmen) was measured with the lowest point of feathering as the starting point. Wing length was measured in mm with a metal ruler from the carpal joint to the tip of the longest primary on the right wing.

The wing was flattened during measuring. Tail length was measured to the nearest mm from the point of insertion of the central feathers (determined by pushing a metal ruler to the point of resistance) to the tip of the outermost tail feather on each side. Tarsus length was measured by bending the foot to 90° and measuring from the notch of the intertarsal joint to the base of the toes. Captured birds were banded with coloured split bands and butt ended Y-sized metal bands (New Zealand banding scheme). Three feathers were plucked from under the wing coverts of all captured Ma'oma'o for DNA analysis in the lab as per Norris-Caneda and Elliott (1998). Analyses were completed by the Equine Parentage and Animal Genetic Services Centre, Institute of Veterinary Animal and Biomedical Sciences lab, Massey University, New Zealand.

Further measurements were also collected from Ma'oma'o in museum collections. For each museum specimen ($N = 32$) origin, date of capture, sex and eye colour were collected from museum labels. The same morphometric measurements were taken of all museum specimens as described with the live captures. Any museum specimens that were in some way damaged were removed from the sample ($N = 7$). This resulted in a sample size of 31 specimens in which the sex had been identified (male $N = 14$; female $N = 17$). In total, 16 museum specimens had eye colour and sex recorded. When combined with the live specimens this resulted in a final sample size of 22 sexed individuals with identified eye colour.

Table 1. The six parameters that were measured to determine acoustic differences between male and female Ma'oma'o.

Parameters	Method of parameter calculation
Note length	Measured as the difference between begin time and end time for the call selection
Centre frequency	Calculated by dividing the call selection into two frequency intervals of equal energy. For the spectrogram view, the Centre Frequency fc is the smallest discrete frequency within the selection which satisfies the inequality formula below: $$\sum_{f=f_1}^{f_c}\sum_{t=t_1}^{t_2} S_{t,f} \geq \sum_{f=f_c+1}^{f_2}\sum_{t=t_1}^{t_2} S_{t,f}$$ where St, f is the value of the spectrogram power spectral density at discrete time t and discrete frequency f. The Centre Frequency is the smallest discrete frequency in which the left side of the formula exceeds 50% of the total energy in the call selected.
5th percentiles of the energy distribution (Q1)	The frequency that divides the selection into two frequency intervals containing 5% of the energy in the selection. The computation of this measurement is similar to that of Centre Frequency, except that the summed energy has to exceed 5% of the total energy instead of 50%.
Highest frequency	Measured as the upper frequency of the call selected
Peak frequency	The frequency at which peak frequency (darkest point in the spectrogram) occurs within the call selected. If the peak frequency occurs at more than one time and/or frequency, the lowest frequency at the maximum time at which the peak frequency occurs is selected.
Delta frequency	Calculated as the difference between the upper and lower frequency limits of the call selected

Statistical Analyses

We used two-sample t-tests to determine if measurements were significantly sexually dimorphic between male and female Ma'oma'o for each acoustic and morphological variable. To determine the optimal combination of call variables predicting sex, two stepwise regressions, with logit link functions, of binomial GLM were used. Our goal was to investigate whether a) Ma'oma'o calls could be used to determine sex and b) which of the morphometric measurements best predict Ma'oma'o sex (McCullagh and Nelder 1989; Zuur et al. 2009). We assessed collinearity in the explanatory variables using pairwise scatterplots, correlation coefficients, and Variance Inflation Factors (Zuur et al. 2009). Variance Inflation Factors for the acoustic and morphological variables were all below the preselected threshold of three suggesting our explanatory variables were not collinear (Zuur et al. 2009); therefore all

variables were retained for the analysis. We constructed binomial GLMs to investigate the probability of sex being correctly assigned. We used a binomial distribution in our model because this distribution is most appropriate for binary data (Zuur et al. 2009). A combination of call or measurement variables was considered to be optimal if comparisons between the full and final model showed that it improved (was the lowest Akaike Information Criteria (AICc)) (Burnham and Anderson 2002). Since multiple calls were analysed from some individuals to determine if there was high within-individual consistency in call structure, models were tested with and without bird identity as a random variable. We validated each of the optimal models after analysis by inspecting the residual plots to confirm that model assumptions were met.

The adequacy of an optimal call model was tested by applying the optimal model to a dataset of 40 sexed calls (20 per sex from all individuals). The proportion of Ma'oma'o that were correctly sexed was calculated from this separate data subset.

To test adequacy of the final best ranked morphological model we calculated the proportion of adults of known sex that would be classified correctly using the optimal model. Because we did not have an additional dataset and our original dataset was too small to subdivide for future model adequacy testing, we used all individuals included in the earlier analysis. This may overestimate the number of individuals that would be correctly sexed using the optimal model.

We used the R package nlme: Linear and nonlinear mixed effects models version 3.1-1.17 in the R 2.1.15 program to conduct all statistical analyses (R Core Team 2013). For all analyses, we used a probability level of $P<0.05$ for significance and point-wise 95% confidence intervals.

Results

Our results indicated that the non-invasive technique of collecting and analysing the alarm calls of the Ma'oma'o was as accurate as DNA analysis in sex discrimination. The optimal vocalisation model predicting Ma'oma'o sex included only the central frequency call parameter.

Including a random intercept term for identity did not improve the model (increasing Δ in AICc = 2.2) and it was not included in the final model. Calls with a centre frequency of < 2283 Hz were classified as female and >2324 Hz as male. Adequacy testing of the optimal call model, comprising only a measurement of central frequency, classified all the Ma'oma'o we measured correctly by sex.

All recorded Ma'oma'o alarm calls had a similar acoustic pattern in both the waveform and spectrogram (Fig. 2). However double voicing was observed in the spectrogram of most males, while only simple harmonics were observed in females (e.g. Fig. 2). A comparison of acoustic parameters in the Ma'oma'o alarm call showed that all measured parameters differed significantly between the sexes (Fig. 3, Table 3). Differences were consistent in the shape of the waveform with a more elliptical form in all females due to a sharp change in power and more continuous power strength throughout the call in all males (Fig. 2). Note length was significantly longer for the male than the female, and the high central and peak frequencies were all higher in the male than the female Ma'oma'o. The average frequency, however, was higher in the female than the male Ma'oma'o (Fig. 3). The ranges of measurements of central frequency did not overlap between the sexes (males: 2324 – 4134 Hz, females: 1809 – 2283 Hz).
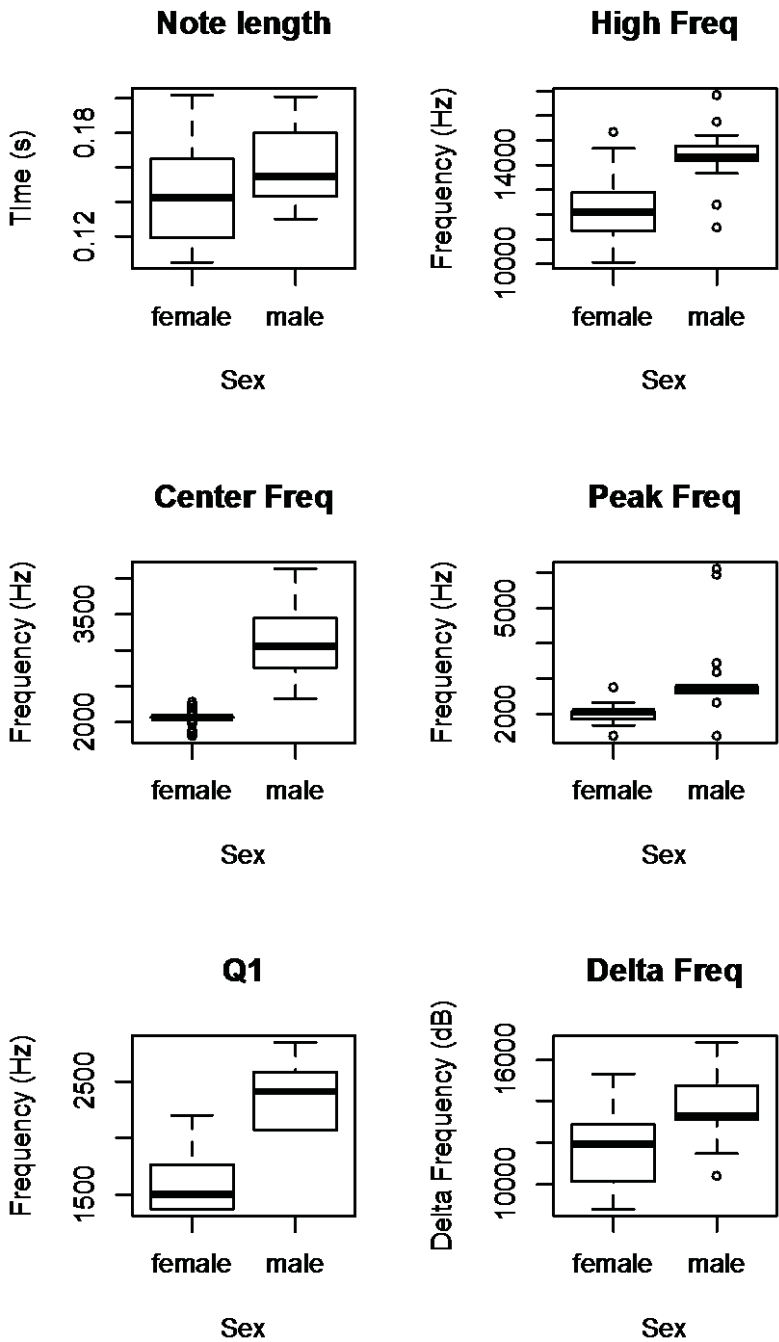
Figure 3. Boxplots showing the extent of variation between different acoustic parameters in male and female Ma'oma'o. The horizontal line in each box is the median, the boxes define the hinges (25-75% quartiles and the line is 1.5 times the hinge). Points outside this interval are represented as dots. Q1 (the 5th percentiles of the energy distribution) and freq (frequency).
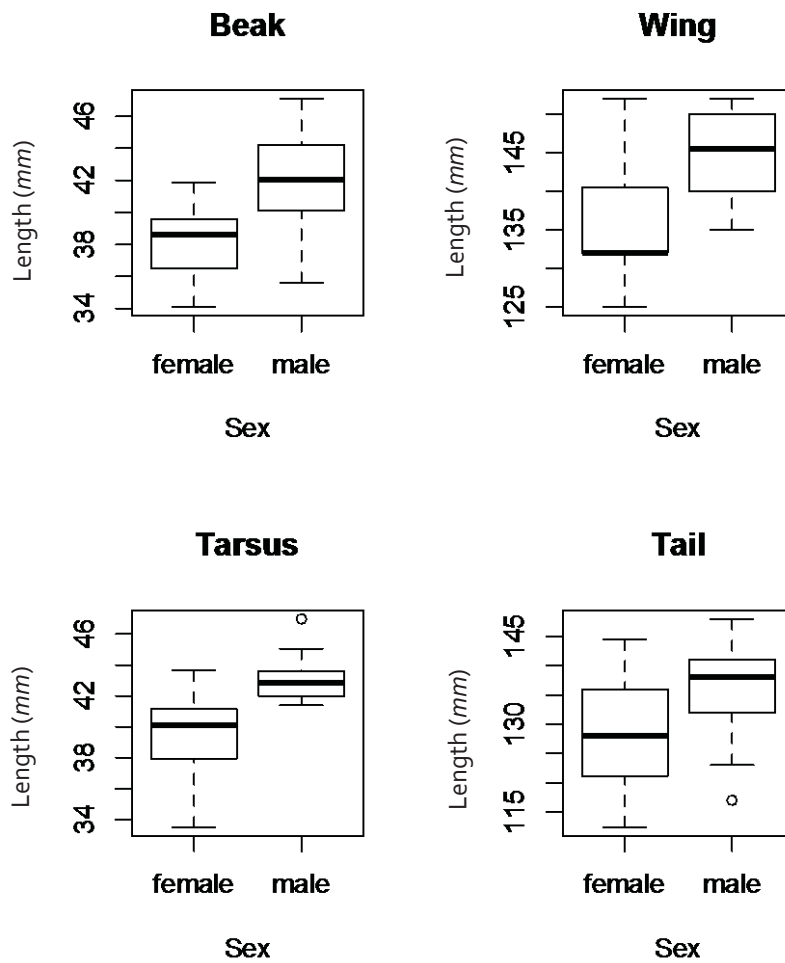
Figure. 4. Boxplots showing the extent of variation between different morphological parameters in male (*n*=14) and female (*n*=17) Ma'oma'o. The horizontal line in each box is the median, the boxes define the hinges (25-75% quartiles and the line is 1.5 times the hinge). Points outside this interval are represented as dots.

Our results also showed male Ma'oma'o were significantly larger than females with respect to wing, beak, tarsus and tail length (Fig. 4, Table 2). Yet despite all morphometric measurements of male Ma'oma'o being significantly larger than females, there was considerable overlap within all the measured morphometric variables between the sexes (Fig. 4, Table 2). The optimal morphological measurements predicting Ma'oma'o sex were tarsus length and beak length. Including a random intercept term for identity did not improve the model and was not included in the final model (increasing Δ in AICc = 2.7). The optimal morphometric model

predicting the probability of a captured Ma'oma'o being classified as female is determined by the following formula:

$$\pi_i = \frac{e^{71.13 - 1.42 \times \text{Tarsus length} - 0.29 \times \text{Bill length}}}{1 + e^{71.13 - 1.42 \times \text{Tarsus length} - 0.29 \times \text{Bill length}}}$$

This equation allows determination of the probability (π_i) of sex being identified as female based on an individual's measurements. To calculate the adequacy of our optimal model we fitted the final model, including tarsus length and beak length against the original morphometric data. The final model predicted that 59% ($N = 17$) of the females and 50% ($N = 14$) of the males in our original data sample would be correctly sexed with only a 5% probability of misidentification. An individual was therefore determined to be female if the probability was > 0.95 and male if the probability was < 0.05. This corresponds to an average (posteriori) classification success rate of 54% with a probability of misidentification of 0.05 using the optimal morphometrical model.

To determine if eye colour was sexually determined, eye colour was recorded and related to sex for 22 adult Ma'oma'o. Five adult birds had blue-grey eyes and 17 adult birds had brown eyes. Nine adult female birds and eight male birds had brown eyes and five male birds and zero female birds had blue-grey eyes. The Fisher exact test for the 2 x 2 contingency table gives a two-tailed probability of this result occurring of $P = 0.054$. Observations showed eye colour was also dependent on age. We found that when chicks hatched and were young the eye colour was milky brown independent of sex ($N = 6$). Captured juveniles which had hatched 2.5 months previously had eyes which were changing from the juvenile milky brown to the blue ($N = 2$ males) or bright brown ($N = 1$ male) seen in the adult birds.

Table 2. Results from morphometric measurements of male and female Ma'oma'o. The sample size for each sex is denoted by *n.* Parameters with statistically significant dimorphism are in bold.

Group measurement	Mean ± SD		t-test
	Male	**Female**	
n	14	17	
Beak (mm)	42.14±3.27	38.20± 2.51	**>0.001**
Wing (mm)	144.93±5.50	136.42± 8.05	**0.002**
Tail (mm)	136.21±8.40	128.12± 9.90	**0.021**
Tarsus (mm)	43.15± 1.52	39.35±2.50	**>0.001**

Table 3. Acoustic parameters of recorded male and female Ma'oma'o calls (N=12, 120 calls from six males and 120 calls from six females). The parameters that are significantly different between the sexes are in bold.

	Mean ± SD		t-test
	Male	**Female**	
Note Length (s)	0.16±0.02	0.14±0.03	**0.03**
High Freq (Hz)	14350.46±1145.35	12287.88±1177.94	**>0.001**
Centre Freq (Hz)	3086.41±456.98	2060.35±112.97	**>0.001**
Peak Freq (Hz)	3048.12±1156.78	2020.22±232.53	**>0.001**
Q1 (Hz)	2387.81±303.88	1606.18±256	**0.01**
Delta Freq (Hz)	13778.66±1533.5	11662.71±1699.84	**>0.001**

Discussion

Our results show that of the three techniques reviewed in this study, measurements obtained from acoustic patterns enabled the most accurate sexing of Ma'oma'o classifying sex correctly 100% of the time with 100% confidence. We found pronounced sexual differences in the alarm calls of Ma'oma'o allowed all sampled individuals to be correctly sexed. Of the morphometric measurements, we found that tarsus length and beak length were the best predictors for sex. However, sex discrimination using morphometrics only classified sex correctly 54% of the time

with 95% confidence. Furthermore, it is important to note that this proportion may also be overestimated because an independent dataset was unavailable to calculate the success rate of the model. Our results also suggest that eye colour may also be used to identify some adult male Ma'oma'o. We discuss each of these techniques and their potential use.

Vocalisations are an efficient means for surveying many bird species, particularly in the tropics where vegetation tends to be dense and a good understanding of bird calls and variation between the sexes is critical for effective population monitoring (Parker 1991; Acevedo and Villanueva-Rivera 2006). Acoustic surveys have previously relied on highly trained personnel to identify species. Recently, however, there has been an increased interest in using automatic sound recorders to monitor populations and automated techniques to recognise species (Haselmayer and Quinn 2000; Bardeli et al. 2010; Marques et al. 2013). In species where vocalisations are sexually dimorphic, such as the Ma'oma'o, using recordings and automatic techniques to recognise vocalisations may be useful for the future assessment of sex ratios. Employing such a method may be particularly useful for monitoring species where higher population declines are occurring in a single sex, such as Kaka (Greene and Fraser 1998; Wilson et al. 1998), Seychelles Magpie Robin (*Copsychus sechellarum*) (Gerlach and Le Maitre 2001) and Swift Parrot (Stojanovic et al. 2014). Understanding sex ratio differences may also be important in aiding conservation of the Ma'oma'o. Because only the female Ma'oma'o sits on the nest, she is more vulnerable to nest predation than the male and it is therefore probable that mortality rates are not equal between the sexes (Stirnemann et al. in review). Because automated software is still being developed, it is useful to note that we found Ma'oma'o sex could also be reliably determined from visual inspection of the alarm call in the waveform, since all female waveform patterns were oval-shaped whilst those of the males were more triangular, without undertaking measurements of the sonogram. It also seems likely that after a short training period in the field it is possible to learn to determine Ma'oma'o sex by hearing alone. Indeed one of the authors learnt to sex Ma'oma'o using their calls in the field and it is therefore considered a feasible monitoring technique.

Our study found male and female Ma'oma'o calls share a similar structure, but male calls contain higher frequency harmonics and are of longer duration than most female calls. These contrast with most other avian species, where females tend to produce higher frequency vocalisations than males (Mennill et al. 2005; Koloff and Mennill 2013). Reversed sexual dimorphic call frequency is usually explained by the female bird being larger than the male (Rosenfield and Bielefeldt 1991; Farquhar 1993). However, in contrast we found the body morphology of the female tended to be significantly smaller than the male.

As well as being used to sex individual birds, vocalisations can be used in some species to identify individual birds (Fox et al. 2008). This would theoretically provide a mechanism for non-invasive mark-recapture. In this study however, we did not detect features in the call of the Ma'oma'o that would enable individuals to be discriminated. The development of a non-invasive mark recapture technique to identify individual Ma'oma'o based on vocal characteristics thus requires further investigation. Other advantages to sexing a species or identifying an individual using acoustic techniques is its simplicity and non-invasiveness, which are particularly important for an endangered species. Further research is needed to improve our understanding of vocal variation between species, sexes and individuals to improve effectiveness of avian monitoring.

This paper shows that differences in the calls of the Ma'oma'o can be used to sex individuals. However, we were also interested in determining whether morphology could be used to sex a species with high morphological overlap such as the Ma'oma'o. Though our results showed that male Ma'oma'o are on average larger than the females in all measured morphological characters, we also found morphometric measurements overlapped significantly. In species with a high sexual overlap in morphometric measurements, it is critical to determine the probability of correctly assigning sex in the field to an individual. Yet, many studies that attempt to sex species based on morphology calculate the degree of error in correctly assigning sex over an entire sample group (e.g. Dechaume-Moncharmont et al. 2011; Landers et al. 2011; Montalti et

al. 2012; De Marchi et al. 2012). We provide an example of how a binomial model (logistic regression) can be used to determine the probability that an individual bird is correctly or incorrectly sexed. This model can easily be used while in the field and measurements are being collected. This provides an opportunity to select an alternative sexing technique, such as DNA sequencing, if the probability of sexing an individual correctly is low. Using a model to predict the probability of correctly sexing an individual means that even where males and females have extensive overlap of their sex-distinguishing measurements, at least some individuals can be sexed with a high degree of confidence. We suggest similar models may be useful for increasing the accuracy of sex delineation in other species with a high degree of morphometric overlap across the sexes. Though the development of such a model does require a prior knowledge of a species' morphometric measurements, by consolidating data from specimens in museum collections, measurements may be made and a model developed even for endangered species, such as the Ma'oma'o.

We also investigated if eye colour could be used to determine sex in the Ma'oma'o. This technique is somewhat limited since birds must be within 8 metres of an observer with binoculars. However, this technique would be particularly useful for sexing adult birds whilst monitoring nests with nest cameras. The eye colour of an adult bird can often be clearly observed in the nest camera (Stirnemann unpubl. data). Therefore, though we found Ma'oma'o eye colour did not allow strict delineation of the sexes; our results were still potentially useful. Blue-grey eyes were recorded only in adult male birds, while adults of both sexes were found with brown eyes. Other studies have found eye colour can vary with age, both while in the nest (Scharf and Balfour 1971) and for the first year or more of life (Baker 1974; Counsilman and King 1977). Ma'oma'o eye colour has previously been observed to change as chicks grew from nestlings to juveniles (Stirnemann et al. in review). In this study we observed that the eye colour of juvenile males changed to the blue-grey and brown seen in adult birds two months after they fledged. Therefore, the differences we observed between adult male Ma'oma'o cannot be explained solely by age variation in eye colour. It is possible that blue eyes in the Ma'oma'o are

a sexually dependent trait, though non-strict sex dependent variation in adult bird eye colour has been recorded in few bird species (but see Pyle et al. 2004). Iris colour is an important secondary sex character in female mate preference in Red Jungle Fowl (*Gallus gallus*) (Zuk et al. 1992). The role of eye colour as a sexually selected trait may explain the presence of blue eyes in only the adult male Ma'oma'o. Further research into its role as a sexually selected trait may thus be of interest.

We recommend further study into sex-specific vocal differences in the Ma'oma'o and other species where unequal declines are suspected since they are likely to play a key role in detecting and monitoring declines in sex ratios and thus are likely to become a useful conservation tool. This method is likely to be particularly important for species where sexes are difficult to distinguish visually and difficult to catch.

Acknowledgements

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STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Rebecca Stirnemann

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Please indicate either:

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  Rebecca Stirnemann performed the majority of the work for the papers that form this thesis. This included developing the research questions, experimental designs, data collection, statistical analysis, and writing. My supervisors Murray Potter, Edward Minot and David Butler made substantial contributions to the conceptualisation of research and revision of the manuscripts. The co-authors of each paper provided comments during the revision of the manuscripts. Dr D. Stojanovic provided guidance on the mark analysis and towards the conceptual development of Paper 4.

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Date

Chapter 3: Slow life history traits in an endangered tropical island bird, the Ma'oma'o

The Ma'oma'o has the lowest maximum reproductive capacity of all honeyeaters so far recorded.

Abstract

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. Despite being endangered, the life history and breeding behaviour of the Ma'oma'o has not been previously documented. 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 verses 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.

Keywords: Ma'oma'o, Mao, Gymnomyza samoensis, life history traits, reproduction, breeding biology, conservation strategy, low maximum reproductive rate, population 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, Hau et al. 2010, Jetz et al. 2008, 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 little data is 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 (IUCN 2012). Ma'oma'o are found both in native forest habitat and at the forest edge where tall trees still remain. A large honeyeater approximately 28–31 cm long, the plumage of the Ma'oma'o is dark, 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 beak is long, curved and black in an adult. Little is known about the species' breeding ecology 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 et al. 2006). In Samoa, invasive mammals such as rats and forest loss are assumed to be impacting populations (MNRE et al. 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.

Method

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 km^2 and are mountainous with the highest elevation at 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 a.s.l. and dissected by many creeks. At high elevation, 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°54'36 S, 171°49'37 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 at this site 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 feed, 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 recordings of conspecific adult or chick calls. Conspecific calls were played through speakers placed within 5 meters of the mistnets. Mistnets were also placed near to a nest site when possible. 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 measured 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 adult male Ma'oma'o were taken from ten museum 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 unpublished 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 fledgling 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 ground, percentage nest cover and tree species.

Phenology of key resource plants

Key resource plant species, utilised for food by the Ma'oma'o in the study site (Stirnemann unpublished 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 ten most frequently used resource plant species within the birds' home ranges at the two study sites. Individual plants were selected which occurred in both study sites and were within the territories of the monitored breeding pairs. Of the ten 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 berteroana*). We also monitored two

non-tree species: mistletoe and ginger (*Etlingera cevuga*). For each species, ten 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 within species 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 ten year average (2004- 2014) of the Afiamalu weather station showed similar monthly rainfall patterns as two years of our 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 the 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 produce per year.

We were also interested in whether the length of incubation, nestling period and time until independence were purely due to the large size of the Ma'oma'o or if even with its size taken into account it was extended compared to other honeyeaters. We expected, *a priori*, that the relatively large Ma'oma'o would develop slowly but an allometric analysis of log transformation prior to analysis should correct for size. We fitted a linear regression of female body weight of honeyeater species where data was available (without Ma'oma'o) against the length of each development period (incubation period, nestling period 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. 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 which all resulted in a laying. Three of the ten nests resulted in fledglings. The timing of 16 further breeding efforts was 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 three occasions after failure.

The breeding season

Ma'oma'o have a protracted breeding season which can occur over 9-10 months of the year (Fig. 1a). Although a peak in egg-laying appears to occur from late May though to October (Fig. 1a). Nesting was uncommon during the period when rainfall was highest (Dec- Mar) and only a single (unsuccessful) nest was found during this period. Incubation, chick rearing and post-fledgling care of a single chick takes ca 100–120 days (see below).
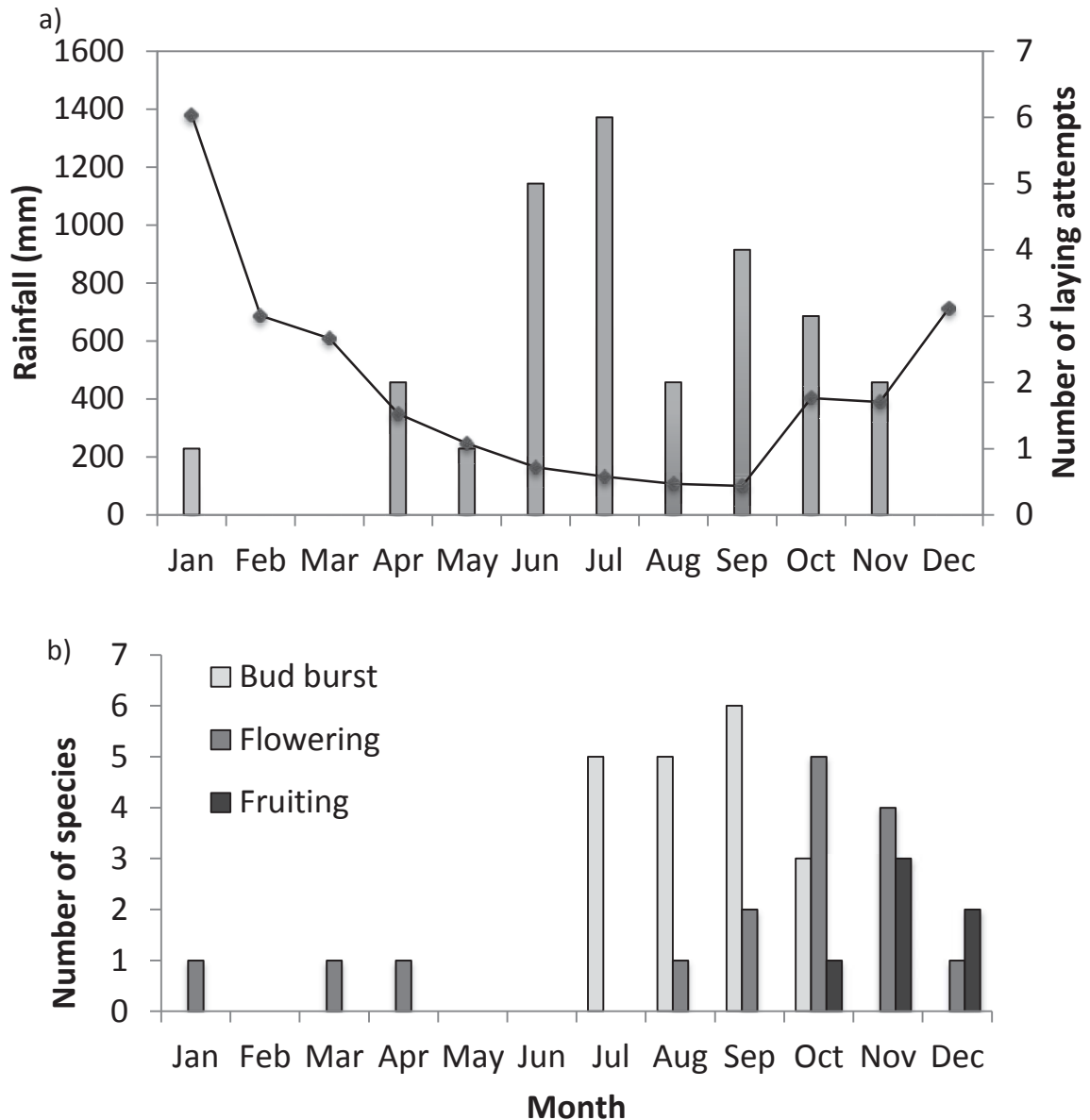
Figure 1. a) The months in which Ma'oma'o nesting occurred depicted by the bars, based on the nesting dates of active nests found during the study (*n*= 10) and the estimated nesting dates based on the age of the observed juveniles (*n*= 16). The average monthly rainfall for 2011-2012 is depicted with a dark line. b) The phenology of key Ma'oma'o resource trees and plants at the study sites.

Seasonality of plants

The phenology of budburst, flowering and fruiting of plants used for food by Ma'oma'o showed clear seasonal patterns (Fig. 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 – 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 (Fig, 1a&b). Budburst did not coincide with the period of highest rainfall in our study sites (Fig. 1a&b).

Breeding behaviour

Territorial defence was effected through song, chasing and occasional physical contact. Both sexes exhibited territorial defence prior to and during to 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. During nest building and incubation, males showed increased territorial defence by vigorously chasing away any conspecifics and other passerine species that got within ~30 m of the nest. They also defended nectar resources at this time. We tested if territorial defence by male and female birds in a breeding pair was significantly reduced following the successful fledging and rearing of a chick compared to the amount of territorial defence observed from pairs following a failed nesting attempt. We calculated the number of defensive acts per individual per unit of time summed over 30 minute periods (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 and

measured 14.0 ± 1.9 cm by 8.0 ± 1.4 cm and supported in 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, $n = 12$) in forest with canopy heights of

approximately 28-32 metres.

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 (*Planchonella garberi*)	15	0
Native Mistletoe (*Loranthus samoensis*) in		
Tamalingi (*Falcataria moluccana*)	12	60
Species unknown (Dead branch)	10	0
Maota (*Dysoxylum huntii*)	18	15
Masame (*Glochidion ramiflorum*)	14	20
Pua lulu (*Fagraea berteroana*)	8	20
Rubber tree (*Hevea brasiliensis*)	18	0
Rubber tree (*Hevea brasiliensis*)	20	80
Salato (*Dendrocnide harveyi*)	14	40
Salato (*Dendrocnide harveyi*)	13	50

Eggs

The eggs had an off-white background colour with brown irregular shaped spots on the blunt

end of the egg. Each clutch comprised just a single egg. We only found two nests prior to eggs

being laid which successfully hatched. One egg took between 19-20 days to hatch and the other

took 20-21 days.

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 it had a yellow gape. At this stage the eyes of all of the observed chicks were a milky brown as opposed to the adult bird's bright blue or brown eye. 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.

Table 2. Morphometrics (*sd*) of male chicks (n=3) measured on the day they fledged the nest compared to morphometrical 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%

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 average maximum clutch size reported is 3.5 eggs (Fig. 2a). In addition to having a large clutch size, many honeyeaters are also multi-brooded, enabling most species 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 (Fig. 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 (Fig. 3a). Adult female mass is a good predictor of the length of the nestling period for honeyeaters. We found an allometric relationship across honeyeaters for the maximum length of the nestling period verses adult female mass ($R^2 = 0.25$, $n= 41$, $P< 0.005$). 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 ($R^2 =0.0001$, $n= 10$, $P< 0.2$). 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).
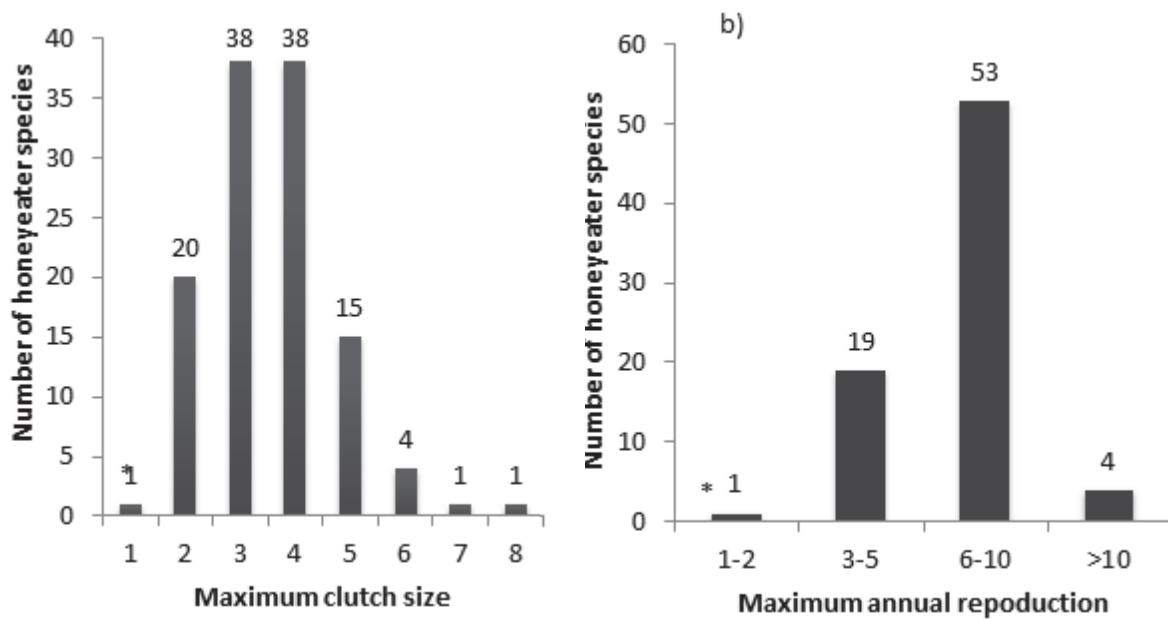
Figure 2. a) Maximum clutch size of 118 honeyeater species, and b) maximum annual reproductive output (max. clutch size x max. no. of broods) of 76 honeyeater species. The Ma'oma'o is indicated with an asterisk (*).
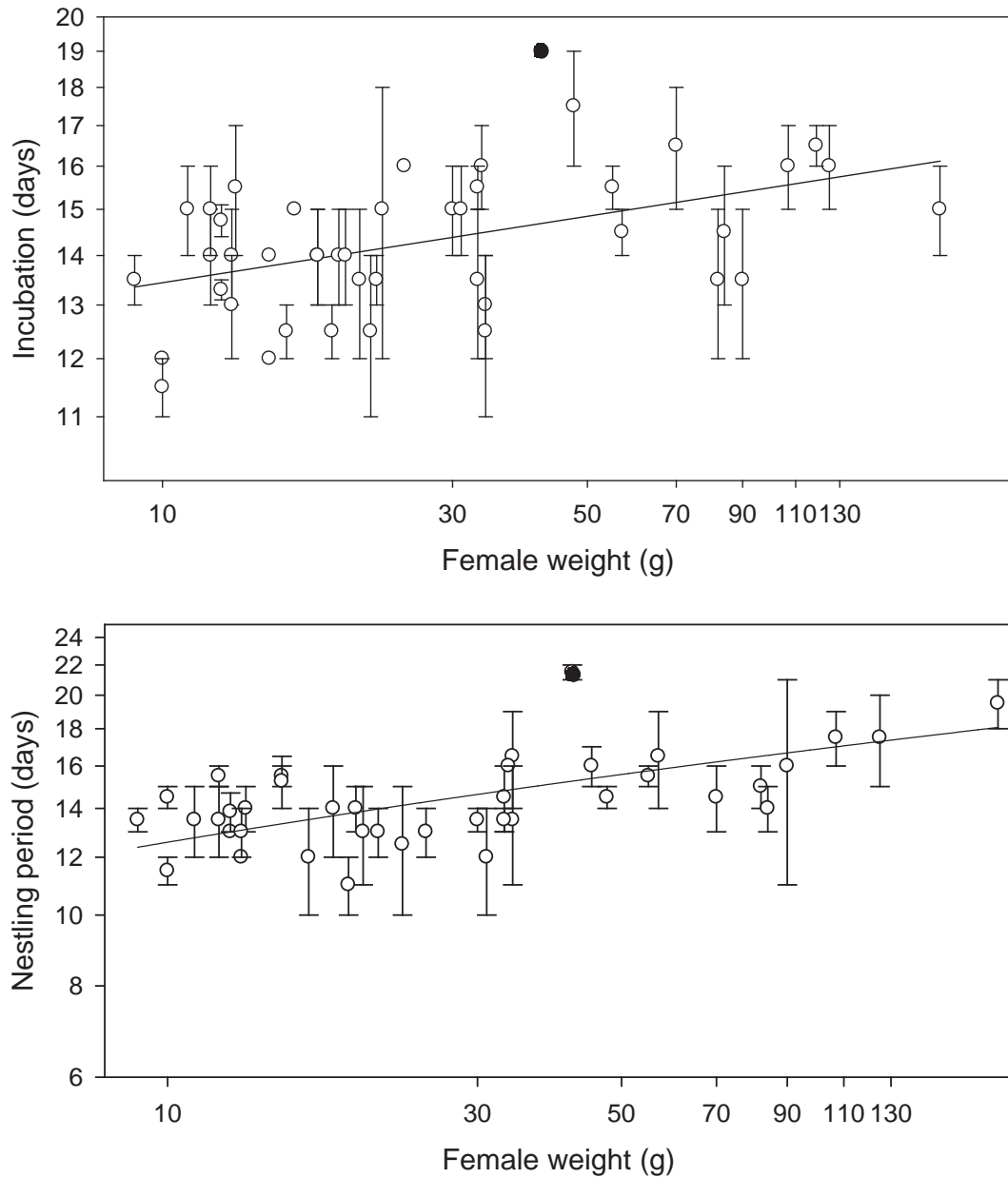
Figure 3. Body weight log-log plots of adult honeyeater species (Table 3) versus the range of days a) of incubation and b) the nestling is in the nest. The black closed circle symbol depicts the Ma'oma'o whilst open circle represent other species. The linear regression is fitted to the midpoint of the range data and excludes the Ma'oma'o, the error bar depicts the range.

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), 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	*Myzomela obscura*	10	12	14-15		Aust	(Noske and Carlson 2011)
Brown-backed Honeyeater	*Ramsayornis modestus*	11	14–16	12–15		Aust+PNG (tropical)	(Maher 1988)
Rufous-banded Honeyeater	*Conopophila albogularis*	12	13–15	12–15	30	Aust	(Noske 1998)
Crescent Honeyeater	*Phylidonyris pyrrhoptera*	12.5	13.1-13.5	13	14-20	Aust	(Clarke and Clarke 2000)
Yellow-faced Honeyeater	*Lichenostomus chrysops*	12.5	14.4-15.1	13.0-14.7	11–28	Aust	(Clarke et al. 2003)
New Holland Honeyeater	*Phylidonyris novaehollandiae*	18	13–15	12–16	28	Aust	(Armstrong and Pyke 1991)
White-cheeked Honeyeater	*Phylidonyris niger*	19.5	13-15	13–15		Aust	(Armstrong and Pyke 1991)
Bell Miner	*Manorina melanophrys*	23	12–18	10–15		Aust	(Clarke 1988, Smith and Robertson 1978)
Bellbird	*Anthornis melanura*	34	12–14	14-19	13	NZ	(Anderson 2003)
Helmeted Honeyeater	*Lichenostomus melanops cassidix*	30	14–16	13–14	42	Aust	(Franklin et al. 1995, Smales et al. 2009)
Regent Honeyeater	*Xanthomyza phrygia*	33	12–15	13-16		Aust	(Oliver 1998)
Noisy Miner	*Manorina melanocephala*	70	15–18	13-16	26-30	Aust	(Dow 1978)
Tui	*Prosthemadera novaeseelandiae*	90	12–15	11–21	8–14	NZ	(Dilks 2004)
Ma'oma'o	*Gymnomyza samoensis*	94	>19	21-22	60-90	Samoa	Current study
Noisy Friarbird	*Philemon corniculatus*	107	15–17	16–19	<12-25	Aust	(Ford and Trémont 2000)
Red Wattlebird	*Anthochaera carunculata*	125	15–17	15-20	15-30	Aust	(Ford and Trémont 2000)

Brown honeyeater	*Lichmera indistincta*	9	13-14	13-14		Aust	(Franklin and Noske 2000)
Yellow-throated honeyeater	*Lichenostomus flavicollis*	33.5	15–17	16		Tasm	(Del Hoyo et al. 2014)
long billed honeyeaters	*Melilestes megarhynchus*	47.5	16-19	14-15		PNG	(Bell 1982)
Graceful Honeyeater	*Meliphaga gracilis*	16.5	15	10–14		Aust-PNG	(Del Hoyo et al. 2014)
Elegant Honeyeater	*Meliphaga cinereifrons*	22	11–14			PNG	(Del Hoyo et al. 2014)
Singing honeyeater	*Lichenostomus virescens*	34	11–14	11–16		Aust	(Del Hoyo et al. 2014)
White-gaped honeyeater	*Lichenostomus unicolour*	33	15–16	13–14		Aust (tropical)	(Del Hoyo et al. 2014)
Yellow honeyeater	*Lichenostomus flavus*	25	16	12–14		Aust (tropical)	(Del Hoyo et al. 2014)
Yellow-tufted Honeyeater	*Lichenostomus melanops*	31	14–16	10–14	42	Aust	(Del Hoyo et al. 2014)
Purple gapped Honeyeater	*Lichenostomus crattitius*	22.5	13–14	12–14		Aust	(Del Hoyo et al. 2014)
Yellow-plumed Honeyeater	*Lichenostomus ornatus*	21.1	12–15	11–15		Aust	(Del Hoyo et al. 2014)
White-plumed Honeyeater	*Lichenostomus penicillatus*	20	13–15	10–12	12	Aust	(Del Hoyo et al. 2014)
White-fronted honeyeater	*Purnella albifrons*	19	12–13	15-16		Aust	(Del Hoyo et al. 2014)
Yellow-throated Miner	*Manorina flavigula*	55	15–16	14–19		Aust	(Del Hoyo et al. 2014)
Spiny-cheeked honeyeater	*Acanthagenys rufigularis*	57	14–15	14–16	12	Aust	(Del Hoyo et al. 2014)
Little wattlebird	*Anthochaera chrysopetera*	82	12–15	18–21	7–21	Aust	(Del Hoyo et al. 2014)
Yellow wattle bird	*Anthochaera paradoxa*	190	14–16	13–15	17	Aust (Tasm)	(Del Hoyo et al. 2014)
Rufous banded honeyeater	*Conopophila albogularis*	13.2	14–17	12	30	Aust+PNG	(Del Hoyo et al. 2014)
Rufous throated honeyeater	*Conopophila rufogularis*	13	13–15			Aust (tropical)	(Del Hoyo et al. 2014)
Black honeyeater	*Sugomel nigrum*	12	14–16	15-16		Aust (all)	(Del Hoyo et al. 2014)
Scarlet myzomela	*Myzomela sanguinolenta*	10	11–12	11–12	10	Aust	(Del Hoyo et al. 2014)
Micronesian Myzomela	*Myzomela rubratra*	15	12	15-16		Micronesia	(Del Hoyo et al. 2014)

Common name	Species					Region	Reference
Cardinal Myzomela	*Myzomela cardinalis*	13	12–14	12–14		Solomons-Samoa	(Del Hoyo et al. 2014)
Tawny-crowned Honeyeater	*Gliciphila melanops*	16	12–13			Aust	(Del Hoyo et al. 2014)
White-naped Honeyeater	*Melithreptus lunatus*	15	14	14-16.5		Aust (tasm)	(Del Hoyo et al. 2014)
Blue-faced honeyeater	*Entomyzon cyanotis*	119	16-17			Aust+PNG	(Del Hoyo et al. 2014)
Little friarbird	*philemon citreogularis*	84	13-16	13-15	10	Aust+PNG	(Del Hoyo et al. 2014)
Striped Honeyeater	*Plectorhyncha lanceolata*	45		15-17		Aust	(Del Hoyo et al. 2014)
Painted honeyeater	*Grantiella picta*	18	13-15			Aust	(Del Hoyo et al. 2014)

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 necessarily mean the maximum annual reproductive success of a species is reduced since multiple clutches maybe produced. However, we also found no evidence of a second breeding attempt by Ma'oma'o following successful fledgling 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 ca 100-120 days until a chick is independent from the female. However, because birds were found breeding over a 9-10 month period it is possible to fit in a second clutch in to the season if an early nesting attempt is successful. However, we show 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. Our results suggest the maximum annual fecundity for the Ma'oma'o is therefore most likely 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 in any other honeyeaters (Del Hoyo et al. 2008).

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. Indeed, a Ma'oma'o chick spends approximately 10% more time prior to fledging at the nest than a Red Wattlebird chick (*Anthochaera carunculata*) a tropical species with a similar body size. Indeed 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 gain a body weight equal to or greater than that of the same sex adult. However, despite any weight gain, the tail and wing feathers are not fully formed at fledging and the chick 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 fledging 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 seems to be timed to take advantage of increased insect availability during budburst in Samoa and plant flowering (Stirnemann unpublished data). Ma'oma'o breeding appears to also stop or 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 egg 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 of the slow breeding tropical species requires management over a longer period of years to increase the population to the same degree as that of a 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. It may therefore be necessary to focus management efforts on specific demographics, such as increasing survival of adult birds, to maintain viable populations.

Further studies monitoring Ma'oma'o reproductive success at the fledgling stage are critical to determine the sensitivity of populations to mortality at this life history stage. Furthermore, although no data exist on the longevity of Ma'oma'o, 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).

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 conspicuous call. We

recommend systematic visits to territories to search for fledglings during June- 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.

Acknowledgements

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STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Rebecca Stirnemann

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2. Stirnemann, Rebecca, M.A. Potter, David Butler, and Edward Minot. 2015. Slow life history traits in an endangered tropical island bird, the Ma'oma'o. Bird Conservation International, available on CJO2015. doi:10.1017/S0959270915000234.
3. Stirnemann, R., M.A. Potter, D. Stojanovic and E. Minot. Nest success does not predict reproductive success in a tropical island honeyeater. Bird Conservation International. In review
4. Stirnemann, Rebecca, M.A. Potter, David Butler, and Edward Minot. 2015. Compounding effects of habitat fragmentation and predation on bird nests. Austral Ecology. doi: 10.1111/aec.12282

In which Chapter is the Published Work: 2,3,4,5

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  Rebecca Stirnemann performed the majority of the work for the papers that form this thesis. This included developing the research questions, experimental designs, data collection, statistical analysis, and writing. My supervisors Murray Potter, Edward Minot and David Butler made substantial contributions to the conceptualisation of research and revision of the manuscripts. The co-authors of each paper provided comments during the revision of the manuscripts. Dr D. Stojanovic provided guidance on the mark analysis and towards the conceptual development of Paper 4.

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Chapter 4: Reproductive success and mortality in a tropical island honeyeater

Female Ma'oma'o and chick

Abstract

Compared to species in temperate regions, we know little about population processes and variation in survival rates in tropical bird species, especially outside the neotropical region. Annual productivity and adult survival were monitored in a population of endangered Ma'oma'o, *Gymnomyza samoansis,* in Samoa. We measured reproductive success directly by monitoring breeding pairs until their nesting attempt failed or their fledglings left their natal territory at 2.5-3 months post fledging. We also identify causes of breeding failure. Mean annual reproductive success over two years (2010/11: $n = 12$, 2011/12: $n = 19$) was 0.25 and 0.37, respectively per surviving Ma'oma'o female per breeding year. The main cause of Ma'oma'o reproductive failure in our study was depredation of eggs and chicks at the nest. Black rats, *Rattus rattus,* were responsible for two predations, but we were unable to identify the predator responsible for other nesting failures. Chicks that survived to fledge had 100% survival in the 2-2.5 months until independence ($n = 9$). Two breeding females, but no adult males, disappeared during the breeding season in 2012-2013 (Females $n = 19$, Males $n = 18$) and further investigation is needed to determine if an unequal sex ratio might be a factor contributing to the population decline. Management targeting rat and cat depredation rates may be required to increase reproductive success in this endangered tropical island species.

Keywords: Rattus rattus, survival, South Pacific, Ma'oma'o, introduced predator, sex-biased mortality

Introduction

Identification of factors that limit population growth is essential for understanding why populations increase or decrease, but this requires an understanding of when, how and why mortality occurs (Anders and Marshall 2005). Research into population limitation in birds has shown that passerine nest success can be affected by an array of factors including food availability (Donazar et al. 1993; Zanette et al. 2003), breeding site quality (Siikamäki 1998), nest site choice (Wilson et al. 1998), the availability of territories (Donazar et al. 1993), brood parasitism (Payne and Payne 1998), mate availability (Steifetten and Dale 2013) and nest predation (Zanette et al. 2003). A different suite of factors are likely to affect survival of fledglings once they leave the nest but prior to independence from their parents (Ringsby et al. 1998; Wiens et al. 2006). Despite different causes of mortality occurring in these life stages, studies of passerine reproductive success typically rely exclusively on nest success, i.e. the proportion of eggs that result in fledged offspring, and do not include the post-fledgling period as a proxy for reproductive success (Thompson et al. 2001; Streby et al. 2014). These data are notoriously difficult to collect, but the fledgling period may be the most risky period for many birds (Tarwater and Brawn 2010; Vormwald et al. 2011; Sim et al. 2013). Only evaluating nest success may therefore provide an incomplete or misleading measure of true reproductive success, because more easily collected nest survival data may not reflect subsequent survival of vulnerable offspring. Surprisingly, reproductive success, defined as the total number of young raised through to independence per adult female per year, independent of the number of breeding attempts, has rarely been measured directly and compared to nest success (Murray 2000; Streby et al. 2014).

Many South-Pacific bird species are declining (Pimm et al. 1994; Cowie and Robinson 2003), and island endemics are disproportionately threatened by extinction. Invasive predators such as rats (*Rattus* spp.) and cats (*Felis catus*) are presumed to have the largest effect on the survival of birds yet there is limited data available to quantify this impact in South Pacific forest birds

(Towns et al. 2006; Medina et al. 2011; Russell et al. 2011). In particular, few studies discriminate between different life history stages in vulnerability to predation and survival rates. Estimates of survival over different life history stages are important for understanding demographic parameters of animal populations, and forms the basis for evaluating population viability (Streby and Andersen 2011; Wilson and Martin 2012; Steifetten and Dale 2013). Some life history stages are more difficult than others to study because, for example, animals might become dispersive or cryptic. For this reason, most studies on survival and reproductive success of birds' present data derived from monitoring nests, which are relatively easy to monitor compared to counting fledglings and sub-adults. Nevertheless, population viability models can be sensitive to estimates of survival of these life history stages, so reliable estimates of survival and fecundity are critical in scenarios where management depends on the outcome of such modelling.

The Ma'oma'o (*Gymnomyza samoensis*) is an endangered honeyeater endemic to the Samoan archipelago. Ma'oma'o are only found on Upolu and Savai'i, the largest islands in Samoa, and are extinct on American Samoa (MNRE 2006). The cause of their decline and endangered status is unclear, but habitat loss and invasive species are presumed to pose a serious threat to the remaining populations (MNRE 2006). The species exhibits several characteristics that make it vulnerable to anthropogenic change, including a low reproductive potential, small clutch size and low reproductive success (Stirnemann et al. 2015a). Ma'oma'o are emblematic of the conservation challenges facing birds in the south Pacific in that they are data deficient, range restricted, threatened by interactive and cumulative anthropogenic changes (Stirnemann et al. 2015 a,b), and lack a coordinated management strategy. We use the Ma'oma'o as a case study to examine approaches to evaluating life history parameters across several stages. We evaluate the threats to Ma'oma'o over three life history stages, nesting, post-fledgling but pre-dispersal phase, and territory holding adult.

Methods

Study area

Our study was conducted on Upolu, Samoa, in the South Pacific. The island covers an area >1,000 km2 and has a maximum elevation of 1,900 m and a wet season from December to March (Whistler 2004). We monitored Ma'oma'o at two study sites (Fig. 1). The first site was 3 km in the Vaisigano water catchment (13˚54.5' S, 171˚44.3' W) comprised steep ridges and slopes up to 300 m elevation. The second study site was near Lake Lanoto'o (13° 54.6' S, 171° 49.6' W) and was characterised by gentle slopes at 700 - 800 m elevation.
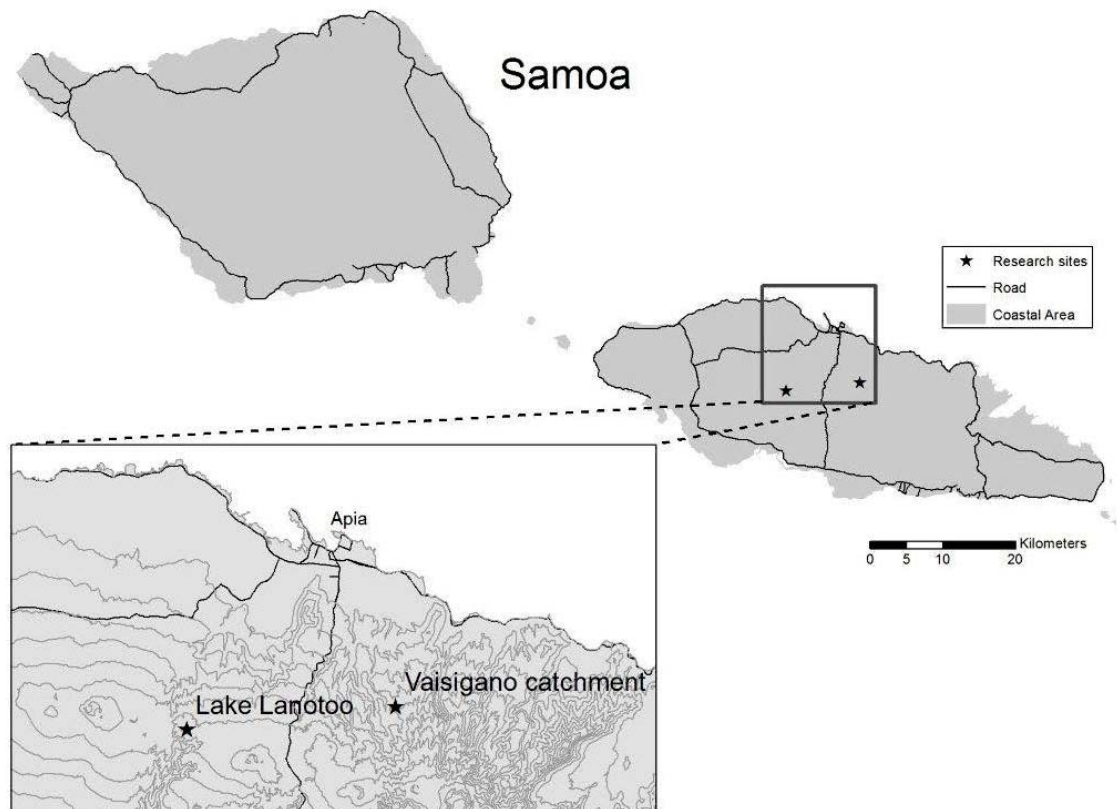

Figure 1. The location of the two study sites in Upolu, Samoa.

Study design

We monitored 12 focal Ma'oma'o pairs from June 2010−January 2011 and 19 focal pairs from June 2011−January 2012. Where possible Ma'oma'o were captured using canopy mist nets and call playback, however birds were largely unresponsive unless defending a nest containing a

chick close to fledging. Captured birds were banded with coloured split rings and metal bands (New Zealand banding scheme). We determined the number of fledglings each Ma'oma'o pair produced over the two-year study period. Territories within the study sites were mapped by recording space use and the locations of interactions between adjacent pairs. Territory boundaries varied little over the two years of monitoring for any of the identified pairs

Pairs were observed for signs of breeding, which included one or both adults carrying nesting material or food items. Nests were monitored every 1-4 days using visual checks, and by observing parental behaviour from a distance. When possible, a nest camera (Brightstar day/night cameras DR-IR100 www.starweb.com.au) was deployed to video active nests continuously, enabling the identification of predators. We also assessed fledgling survival by monitoring six chicks from fledging to independence.

Reproductive success

We measured reproductive success, defined as the total number of young raised through to independence per adult female per year independent of the number of breeding attempts. We monitored 12 paired females in 2010/11 and 19 paired females in 2011/12. Active searches were made in all territories for nests and fledglings. Ma'oma'o fledglings make loud distinctive begging calls whilst following an adult bird for a 2-2.5 month period (Stirnemann et al 2015 a,b) during the post-fledging dependency period. Detectability of all fledged chicks was measured by recording the length of time until detection at each visit. To take into account chick age when calculating detectability, we calculated detectability for the chicks 0-4 weeks post-fledging, and independently assessed the detectability of chicks 4-10 weeks post-fledging. All additional newly fledged chicks (determined by their calls and behaviour) found at either of the study sites were monitored until the fledgling was no longer present at the natal territory. The age of a newly discovered fledgling was estimated based on its flight ability and morphological characteristics, specifically the presence of fluffy head feathers and tail length (Stirnemann et

al., 2015a). A mortality event was assumed to have occurred if the fledgling was not detected within the natal territory in the first two months after fledging because until independent, fledglings rarely stray far (Stirnemann et al 2015a). Fledglings were assumed to have survived if they persisted in the natal territory and towards the end of the 2-3 month dependency period firstly became increasingly independent from the mother bird until they were rarely seen together and then it disappeared from the parental territory.

Monitoring survival of adult birds

To determine detectability of adult Ma'oma'o, we recorded the length of time from when we entered a territory until a bird was detected. Searches for marked adult birds were conducted until 1000 h to maximise detectability, and each territory was searched for 30-40 min. Territories of marked birds were visited on average six times over a period of three weeks throughout the breeding season. Mortality was assumed to have occurred if a known individual was not sighted in its territory after five visits which were of longer duration than 40 minutes. Behaviour of the paired bird was also noted and whether it was responding. We noted that if a paired bird went missing the calls of the mate increased in both volume and frequency (Stirnemann et al 2015 a,b).

Estimating the population growth rate

We developed models of Ma'oma'o annual fecundity (F) to explore how variations in three demographic parameters, annual survival of adults (PA) and juvenile (PJ) females influence predictions about population growth rates. Despite double brooding being an important variable for modelling population growth rates in other species (Podolsky et al., 2007) it was not included in this model because prior research suggests that Mao only produce at most a single chick per annum (Stirnemann et al 2015a). Pulliam (1988) defined the finite rate of population growth (lambda) as $\lambda = PA + PJ * F = 1$ for a population at equilibrium, and $\lambda > 1$ for a source population, whilst a $\lambda < 1$ is defined as a sink population. Model assumptions are a closed

population (no dispersal and no recruitment); equal sex ratios and independence of PA of PJ and F survival. Since Ma'oma'o have only been recorded with a maximum clutch size of a single egg we are confident of the homogeneity of brood sizes so this is not an assumption which needs to be assessed for this species. We compared estimates of lambda for all model scenarios to examine the sensitivity of lambda to changes in annual female survival, juvenile survival and reproductive success. Because knowledge of juvenile behaviour post dispersal is poor we used a number of parameter to assess the sensitivity of this parameter.

Results

Twelve Ma'oma'o territories were monitored in 2010-2011. In 2011-2012 we monitored seven female birds in addition to the 12 monitored females from the previous year. During the 2011–2012 breeding season two adult female birds disappeared from their territories reducing the number of monitored females to 17. The male birds in these territories did not form new pairs during the 2011–2012 breeding season.

Mean annual reproductive success, defined as the number of fledglings which survive per breeding female per year, for 2010–2011 and 2011–2012 was calculated to be 0.25 (3 juveniles per 12 adult females) and 0.37 (7 juveniles per 19 adult females) respectively per female per season, equating to an overall productivity of 0.34 chicks per surviving female per season over the two-year period. Based on these missing females, our estimate of annual adult female survival during the breeding season (PA) over the two years was 0.95 ± 0.07 while all males survived.

To calculate nest survival we modelled survival of 12 Ma'oma'o nests. Some of these nests were found outside the sites where reproductive success was monitored. We assumed *a priori* that survival was constant because our sample size was too small to determine variation in survival over time. Using the parameter estimates from this model, we estimate the daily

survival rate of Ma'oma'o nests at 0.91. This equated to a survival probability over the 42-day nest period of 0.028 ($\pm$ 0.041 se).

Causes of nest mortality

Two nest predation events were identified on camera, both perpetrated by introduced black rats (*Rattus rattus*). No other species were identified as nest predators. Both nest predation events occurred while the adult female Ma'oma'o was incubating eggs during the night, one at 0041 h and the other at 0600 h. Cameras revealed that the predation events involved the rat driving the female off her eggs, and in one case, a rat leaped onto the incubating female Ma'oma'o's from the branch above. Footage showed that in this case the bird lost a number of feathers during the attack, but in both cases the female Ma'oma'o survived apparently uninjured. In both cases the rat removed the single Ma'oma'o egg whole from the nest and carried it away, leaving no traces of egg fragments or destruction of the nest. In the days following both events the adult birds remained in the territory and attempted to re-nest within 8-15 days.

Juvenile survival during the dependency period

Ten chicks were monitored from up to three days after fledging until independence. All chicks in the first 1-2.5 weeks following fledging sheltered in low bushes or on the ground. There was a high probability of detection for all monitored chicks in the post-fledging dependency period ($n = 10$) (Fig 2). In the first 3 weeks after leaving the nest, all fledglings were located after searching for less than 15 minutes resulting in a detection probability of 100% (Fig. 2). As the chick grew older, as much as 20 minutes was required to locate the chick with detection probability 100% (Fig. 2) and the spatial area the fledgling used increased (Stirnemann unpublished data). All chicks survived after fledging, and were detected after they were independent. Two female banded chicks were also sighted in the following year in territories close to their natal territory.
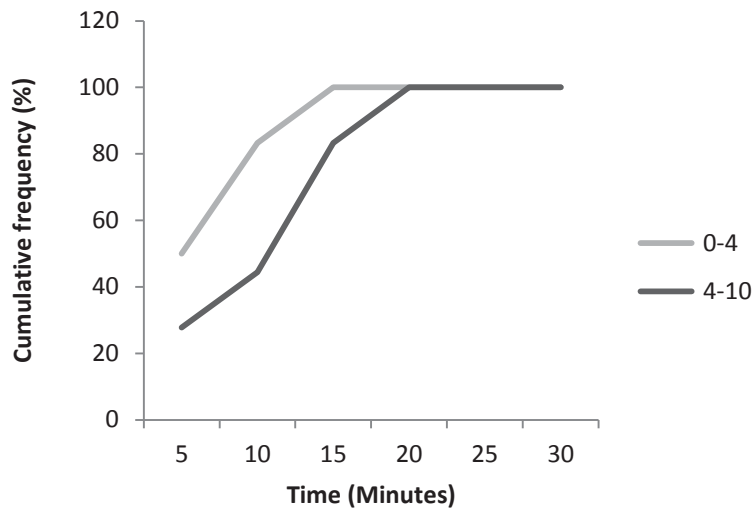
Figure 2. The average time required to detect the presence of ten fledglings, upon entrance to the territory, between the ages of the 0-4 (n= 60 visits) and over 4 weeks of age (n=80 visits) (legend) following fledging.

Sensitivity analyses

The sensitivity matrix suggested that adult mortality had the highest influence on growth rate. If a hypothetical Ma'oma'o population had a reproductive success rate of 0.31, the average reproductive success of the female birds, a juvenile survival rate of 45% and an adult survival rate of 90%, as is approximately estimated for our studied population, we estimate a lambda of 1.03. Yet our model also indicated that even with a reproductive success at its maximum of 1, adult female survival must be above 0.65 for the population to be increasing (Fig. 2). If adult female survival is at least 90% per annum reproductive success must be successful for at least 23% of the population otherwise lambda is <1 and the population is estimated to decline. Sensitivity analysis of each model parameter indicated that the population rate of change was four times more sensitive to adult female survival then juvenile survival.

Discussion

This paper quantifies the vital rates of the endangered Ma'oma'o at different life history stages and presents the first measures of reproductive success, juvenile survival rates during the dependency period, and adult survival of the endangered Ma'oma'o. Reproductive success in

the study sites was predominantly determined by high nest failure rates combined with high fledgling survival in the pre-dispersal period and low reproductive potential. Indeed, each Ma'oma'o breeding pair produced at most a single chick each year (Stirnemann et al 2015a). Our study identified the potentially large influence invasive rats have on Ma'oma'o nest survival. Footage from two nest cameras showed nest depredation by black rats (*Rattus rattus*).

Our results suggest that rats may also affect the survival rates of breeding female Ma'oma'o. Since only the female Ma'oma'o incubates the egg, it is at this period that she may experience a higher vulnerability to predation events then the male (Stirnemann et al 2015a). Further, Ma'oma'o may compensate for high nest mortality by repeatedly attempting to nest. Though this may increase the chances of reproductive success, repeated re-nesting attempts will increase time spent by female Ma'oma'o brooding. This may increase the probability of the adult female bird being depredated on the nest (Haas 1998). We calculated the sensitivity of adult female mortality and the loss of one adult female had four times the impact on populations then the loss of a single chick. Female-biased mortality has been observed previously in other island species in which only the female incubates. For example this has been observed in both the kaka (*Nestor meridionalis*) (Greene and Fraser 1998) and swift parrot (*Lathamus discolor*) (Stojanovic et al. 2014). The video footage gained in this study indicated a breeding female's presence on the nest did not dissuade rats from attacking, and birds showed no aggressive behaviour towards rats. Though we did not record mortality of adult female Ma'oma'o while nesting on camera, two-monitored female Ma'oma'o disappeared during the breeding season. In contrast none of the monitored male population disappeared. We believe that further investigation is needed to determine if a loss of breeding females has led to a sexually skewed population dominated by male birds. The impact of a sex ratio bias on population viability increases as a population becomes smaller (Tuni and Berger-Tal 2012; Grayson et al. 2014). The management of critically endangered populations such as the Ma'oma'o, and analyses of their viability, should therefore routinely include an assessment of the sex ratio. Methods

enabling sex to be established from calls may provide one mechanism for monitoring the sex ratio of the Ma'oma'o (Stirnemann et al. 2015b).

Post-fledging mortality during the dependence period

Our study showed Ma'oma'o fledgling survival up to the point of independence from the parents was high and we recorded no mortality events. To our knowledge, no other estimates of post-fledging survival of South Pacific passerines up to the point of independence exist. However, other studies of tropical birds also reported high survival rates between fledging and independence (range 0.42–0.69: (Anders et al. 1997; Schaefer et al. 2004; Brouwer et al. 2006; Sankamethawee et al. 2009). Our study shows how having data from only a single life stage can produce a misleading measure of individual fitness and population productivity (Streby et al. 2014).

Sensitivity analysis showed that given the reproductive success of our study populations and as long as the juvenile survival is greater than 45% and adult female survival is greater than 90% our study populations were slightly increasing with a lambda of 1.03. However, it is important to note that nest success and adult and chick survival may vary considerably between years (e.g. Morton and Stutchbury 2000). In this study we covered merely two study sites and only a small number of birds were monitored due to the logistical difficulties of working on this rare endangered species in difficult terrain. The results of our study should therefore be considered in context of well-established research on the effects of invasive predators on island endemics and with an understanding that the species is declining across its range. Ma'oma'o occur only on islands where anthropogenic change to habitat has been extensive and varied, and it is likely that other factors not observed in this study impact their survival. For instance, although we observed no cat depredation of fledged Ma'oma'o chicks during our study, previous studies have found cats to be a predator of island birds and the chicks displayed behaviour which made them extremely vulnerable to cat predation (Fitzgerald & Veitch 1985, Nogales et al. 1992). Cats therefore may still have a strong effect on the survival rate of fledged Ma'oma'o chicks in

Samoa despite our results. Ma'oma'o chicks are most likely to be at risk from cats in the two-week period after they fledge from the nest because they are poor fliers, vocal and spend a considerable amount of time on the ground in the early post-fledging period (Stirnemann et al. 2015a).

In conclusion, the results of this study provide critical information on the threats and vital rates during different life history stages to the endangered Ma'oma'o. Future management focusing on reducing the impact of rats and cats on nest and adult survival may be required to improve the conservation status of this tropical island species. However, the low reproductive potential traits of the Ma'oma'o will affect the time needed for the population to recover since the annual maximum productivity is low (Stirnemann et al. 2015a). This increased recovery period will escalate the costs of species recovery further increasing the difficulty of funding conservation efforts such as pest control.

Acknowledgements

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STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Rebecca Stirnemann

Name/Title of Principal Supervisor: Professor Murray Potter

Name of Published Research Output and full reference:

1. Rebecca L. Stirnemann, Murray A. Potter, David Butler, and Edward O. Minot (2015) Acoustic differences enable sex discrimination in Ma'oma'o (Gymnomyza samoensis), a species with high sexual morphological overlap. The Wilson Journal of Ornithology: 127(3) 376-386.
2. Stirnemann, Rebecca, M.A. Potter, David Butler, and Edward Minot. 2015. Slow life history traits in an endangered tropical island bird, the Ma'oma'o. Bird Conservation International, available on CJO2015. doi:10.1017/S0959270915000234.
3. Stirnemann, R., M.A. Potter, D. Stojanovic and E. Minot. Nest success does not predict reproductive success in a tropical island honeyeater. Bird Conservation International. In review
4. Stirnemann, Rebecca, M.A. Potter, David Butler, and Edward Minot. 2015. Compounding effects of habitat fragmentation and predation on bird nests. Austral Ecology. doi: 10.1111/aec.12282

In which Chapter is the Published Work: 2,3,4,5

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

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  Rebecca Stirnemann performed the majority of the work for the papers that form this thesis. This included developing the research questions, experimental designs, data collection, statistical analysis, and writing. My supervisors Murray Potter, Edward Minot and David Butler made substantial contributions to the conceptualisation of research and revision of the manuscripts. The co-authors of each paper provided comments during the revision of the manuscripts. Dr D. Stojanovic provided guidance on the mark analysis and towards the conceptual development of Paper 4.

Rebecca Stirnemann

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14/10/15

Date

Murray Potter

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16/10/15

Date

Chapter 5: Compounding effects of habitat fragmentation and predation on cup nesting birds

Rural development in Samoa has increased the proportion of forest edge near plantations. Our results suggest that this will increase the proportion of forest birds that experience nest predation from black rats.

Abstract

Habitat fragmentation and invasive species are two of the greatest threats to species diversity worldwide. This is particularly relevant for oceanic islands with vulnerable endemics. Here, we examine how habitat fragmentation influences nest predation by *Rattus rattus* on cup-nesting birds in Samoan forests. We determined models for predicting predation rates by *Rattus* on artificial nests at two scales: (i) the position of the bird's nest within the landscape (e.g. proximity to mixed crop plantations, distance to forest edge); and (ii) the microhabitat in the immediate vicinity of the nest (e.g. nest height, ground cover, slope). Nest cameras showed only one mammal predator, the black rat (*Rattus rattus*), predating artificial nests. The optimal model predicting nest predation rates by black rats included a landscape variable, proximity to plantations and a local nest site variable, the percentage of low (<15 cm) ground cover surrounding the nest tree. Predation rates were $22 \pm 13\%$ higher for nests in forest edges near mixed crop plantations than in edges without plantations. In contrast, predation rates did not vary significantly between edge habitat where the matrix did not contain plantations, and interior forest sites (>1 km from the edge). As ground cover reduced, nest predation rates increased. Waxtags containing either coconut or peanut butter were used as a second method for assessing nest predation. The rates at which these were chewed followed patterns similar to the predation of the artificial nests. Rural development in Samoa will increase the proportion of forest edge near plantations. Our results suggest that this will increase the proportion of forest birds that experience nest predation from black rats. Further research is required to determine if rat control is needed to maintain even interior forest sites populations of predator-sensitive bird species on South Pacific islands.

Keywords: habitat modification; invasive species; island forest; matrix composition; nest predation; *Rattus rattus*

Introduction

In areas where bird species co-evolved with mammalian predators they developed life-history and behavioural traits to counter predation (Fontaine and Martin 2006; Clarke and Martin 2007; Johnson 2011). In contrast, many native species living on islands that historically were free of mammalian predators have low diversity, simplified food webs and few adaptations to avoid predation by introduced mammals (Bergstrom and Chown 1999; Manne, Brooks, and Pimm 1999). These introduced mammalian predators can reduce reproductive success of native birds through increased nest predation (Thibault et al. 2002; Delgado García et al. 2005; Kingsford et al. 2009; Foster et al. 2011). Because tropical island bird species also have low maximum annual reproductive rates compared to mainland species, some populations are extremely sensitive to increases in mortality (Thibault et al. 2002; Martin 2007). These slow life history reproductive traits combined with ecological naivety have resulted in population declines and extinctions in numerous island bird species following the introduction of non-native predators (Marsden and Pilgrim 2002; Thibault et al. 2002; Towns et al. 2006).

The effects of some non-native species can be further exacerbated by landscape fragmentation by humans (Butler et al. 2014). With forests across South Pacific regions in decline, it is increasingly important to determine how habitat modification is altering predation rates in tropical forest birds (Woinarski 2010). For instance, in Fiji, predation pressure from introduced rats and the small Indian mongoose (*Urva auropunctatus*) are significantly less in the interior of forests (>1 km from the edge) than in edge habitats (Olson et al. 2006). Interior forest sites may therefore harbour vital source populations for species sensitive to the high predation rates near forest edges. Predation rates may also be affected by the composition of the matrix surrounding the forest patch (e.g. Malt and Lank 2009; Keyser 2002). To our knowledge no studies have investigated how variation in the matrix surrounding the edge influences nest predation rates in the South Pacific. Furthermore it is not clear whether interior sites outside of Fiji show similar patterns of reduced predation rates by non-native rat species. It is therefore not clear whether

maintaining large tracts of forest is sufficient in itself to reduce nest predation rates and maintain sensitive populations of endangered South Pacific forest species.

Four rodent species, the black rat or ship rat (*Rattus rattus*), Norway rat (*R. norvegicus*), the Pacific rat (*R. exulans*) and the house mouse (*Mus musculus*) are the most widespread and problematic invasive mammals affecting oceanic islands (Thibault et al. 2002; Towns et al. 2006; Drake and Hunt 2009; Traveset et al. 2009). The importance of reducing black rat populations has been shown to be critical for maintaining populations of the Rarotonga monarch (*Pomarea dimidiata*), kākerōri (*Pomarea dimidiate*) in the Cook Islands (Robertson et al. 1994). Following successful rat control, nest success and consequently numbers of this endangered bird have increased (Robertson et al. 1994). Yet it is not clear whether simular control is needed to maintain source populations of other sensitive bird populations in the Pacific.

In this study we were interested in gaining an understanding of the rat species affecting nest predation rates across the forest landscape. We identifying the rat species in the landscape and investigated whether nest predation rates varied at both the nest-vicinity scale (e.g. nest height, ground cover, slope) as well as across the landscape (e.g. proximity to plantations, distance to forest edge). We also compared rat chew rates on waxtags impregnated with two different lures to predation rates on artificial nests to determine if they show similar patterns. Information was also collected on nest predation by bird species. We compare our results to the available literature and make recommendations for conservation management of forest bird species in the South Pacific.

Methods

Study site

Samoa comprises two large South Pacific islands, Savai'i and Upolu. Both are over 1,000 km^2 and are mountainous with a maximum elevation of 1,900 m (Ward and Ashcroft 1998). The

main wet season is from December to March, but there is high rainfall at high elevation (+600 m) all year (approx. 600–800 cm of rainfall annually) (Ward and Ashcroft 1998). Across Samoa, large scale clearance of native forests has taken place to expand family plantations (Taule'alo 1993). The majority of cleared land in Samoa is farmed by villagers on customary land using a combination of subsistence and cash-crop agriculture (Ward and Ashcroft 1998). Land-use patterns in Samoa differ with distance inland. Near the coast, villages typically consist of a residential area with a village common ground. Further inland there is a mixed crop zone of fruit trees such as coca (*Erythroxylum coca*) and coconuts (*Cocos nucifera*), and towards the interior of the island there is a zone of primary food crops of bananas (*Musa spp.*), taro (*Colocasia esculenta*), and ta'amu (*Alocasia macrorrhizos*) (O'Meara 1990). A combination of the primary food crops is normally grown in plantations in newly-cleared forest sites where the soils are organically rich. With the expansion of the primary food crop zone of taro and bananas, the forest edge is cleared back forming an extensive plantation and native forest interface (O'Meara 1990).

Study design

Predation of artificial nests

To determine how nest position influences predation rates, artificial nests were placed in three habitat or treatment types (9 sites each): (1) within native forest 100-200 m from a mixed banana taro plantation (plantation interface); (2) within native forest within 100 m of cleared land (cleared interface); and (3) more than 1000 m from an edge interface (interior forest) (Fig. 1). Only cleared sites that had been deforested at least 1 year previously were included in the study to ensure mature plantations had time to form and to guarantee there was no bias between the cleared and the plantation interface. All sites had a hard edge maintained by the plantation owners, grazing cattle, logging or natural processes interfacing montane forest with full canopy. Artificial nests ($N = 324$) were placed in trees between October and December of 2012, during the peak in the breeding season of native forest insectivores (Stirnemann pers obs). Twelve nests were placed at each of 27 transects (9 transects per treatment). High nest density has been

shown to increase predation risk. To minimize this potential bias within each transect, the 12

artificial nests were placed >50 m apart. Though no data are available from Samoa on black rat

movement patterns, previous studies in Hawai'i indicate that the mean range length is less than

50 m (Tamarin and Malecha 1971). For logistical reasons, not all nests were placed out on the

same day. To reduce temporal bias, we always placed at least 12 nests in each forest type

(plantation interface, cleared interface and interior native forest site) within a single day. Nests

were placed at a variety of heights ranging between 5-26 m above ground at each site.
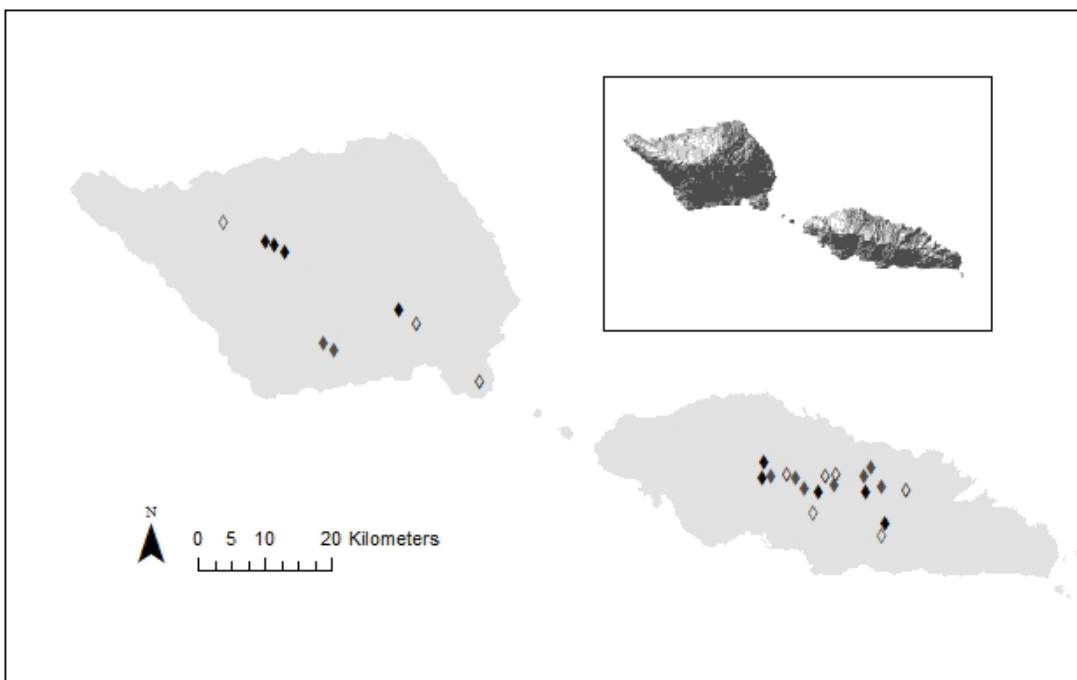
Figure 1. Map of Samoa showing the location of the 27 transects with their relation to the matrix depicted with diamonds. (a) Edge plantation- the forest edge with plantations present, hallow diamonds, (b) Edge no plantation- edge without plantations, grey diamonds, (c) Interior forest- within interior forest, black diamonds.

The oval-shaped artificial nests were constructed of wire (18 × 12 cm in diameter × 5 cm deep)

and lined with natural nesting material to mimic a Ma'oma'o (*Gymnomyza samoensis*) nest a

native Samoan cup nesting species. To reduce human odour they were exposed to the weather

for several days (≥ 2 days) before being placed in the field (Berry and Lill 2003). After

installation, one model plasticine egg was placed in each artificial nest. All the eggs were

shaped and coloured to match ma'oma'o eggs approximately 18×10 mm in size. The model eggs were attached to the bottom of the nest using a thin nylon line to minimise their removal. This line was also used to attach each nest to a branch. A pilot study indicated that predation rates were high and therefore all artificial eggs were left in each nest for just 24 h to provide a predation rate index that contained enough inter-site variation to be interpretable.

Predation was scored as having occurred if a nest was torn apart, or if the egg had marks on its surface, or was removed from the nest. Marks left on artificial eggs such as scratches, tooth and triangular beak impressions were used to indirectly identify the nest predators. We placed motion-triggered cameras (Scoutguard No SG550V) next to a subset of 60 artificial nests to identify which predator species were predating artificial nests. We equally distributed cameras to artificial nests in each of the three forest types and equally distributed on nests placed high and low in the trees. There was at least one camera on each transect.

For those nests with cameras, a separate identification of predators was made using both marks on the eggs and evidence from the photographs. This allowed direct comparison of these two identification methods, providing an assessment of identification error for those nests where cameras were not present. This technique enabled predators to be identified as specific species. Avian predators documented by nest cameras and the presence of peck marks were analysed separately from the rodents because we were primarily interested in the factors driving the predation rate of invasive predatory mammals.

Waxtag monitoring

We compared bite-mark rates of waxtags with artificial nest predation rates to determine if they showed similar patterns and thus whether waxtags could be used for monitoring large-scale variation in rat densities in Samoa. Commercial waxtags (N.Z. patent 516900), consisting of a triangle of plastic 5mm on the base and 16 mm high, with a 12 mm by 20 mm block of wax moulded to the sharpest point of the triangle, were placed in transects. We compared two

flavours, coconut or peanut butter waxtags, to determine which might be the more effective lure. Peanut butter ($n = 12$) and coconut ($n = 12$) flavoured waxtags were placed alternatively 50 m apart in a paired transact covering the area where the artificial nests had been the previous week. Each waxtag was attached to tree trunks 10 cm above ground. After a single night the waxtags were collected and the number of waxtags bitten by rats was recorded, along with their location. We checked the results from the waxtags with the artificial nest predation rate data to see if they showed simular large-scale patterns and therefore could be used to monitor population changes in local rat populations.

Statistical analysis

The data from artificial nests and waxtags were analysed separately. Waxtag data were separated by lure type for analysis. For all datasets we used hierarchical random effects with artificial nest / waxtag nested within transect to control for repeated spatial measures by decomposing the model variance into autocorrelative and residual components (see Pinheiro and Bates 2000).

We then examined the probability of nest predation or waxtag chew using data on whether each given nest or waxtag was preyed upon or not [1, 0] over a standardised 24-h period. Because nest predation and waxtag chews were binary variables, a binomial distributional family with a logit link function was used in a mixed-effects Generalised Linear Model (GLM) for both datasets. For artificial nests, fixed effects included both course and fine scale features. The presence or absence of a nest camera at each nest site was also included in the initial model for the artificial nest data to determine whether predation at the nests was influenced by the presence of a camera. For waxtag data, only the course scale landscape features (edge with plantation, edge with no plantation and interior forest) were included in the initial models.

Before analysis, we assessed our explanatory variables for collinearity ($r \geq 0.8$) using pairwise scatterplots, and correlation coefficients (Zuur et al. 2009). The presence of outliers and

leverage effects were tested in the explanatory variables using pairwise scatterplots, correlation coefficients and boxplots (Zuur et al. 2009). None of the explanatory variables showed strong collinearity between the coefficients or contained extreme outliers so we included all of the variables in the regression models.

To determine which of the variables in the initial model best explained the observed variation in the predation rates, we simplified our models based on backward or forward model selection using Akaike information criteria (AIC_c) values, with ANOVA comparisons (Zuur et al. 2009). To confirm that models fitted the data and determine whether there were any departures from the model assumptions, we plotted partial residual and logistic regression quantile plots. All statistical analyses were performed using the R software package (R Core Team 2013).

Results

Identification of nest predators

Twenty nine of the 60 artificial nests monitored with cameras were preyed upon by black rats, with no images recorded of either the Pacific rat or the Norway rat. In all cases where a rat was observed, the artificial eggs showed rat tooth marks. Four species of bird were also identified pecking artificial eggs on the nest cameras, one introduced species the Indian myna (*Acridotheres tristis*), and three native species the wattled honeyeater (*Foulehaio carunculat*), Polynesian starling (*Aplonis tabuensis*) and Samoan starling (*Aplonis atrifusca*).
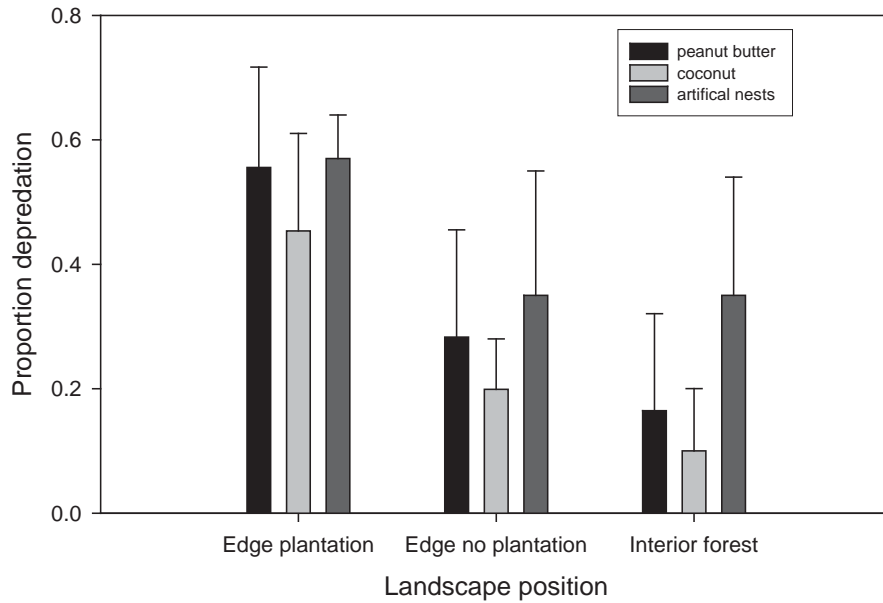
Figure 2. Predation rates by rats on artificial nests and waxtags according to position across the fragment matrix interface. Two different lures (a) peanut butter and (b) coconut were used in the waxtags. Error bars represent standard error.

Factors influencing black rat predation rates on artificial nests

Both course scale nest site habitat and fine scale measurements were included in the top model predicting nest predation by black rats. The probability of a black rat predating a nest was negatively correlated with the fine scale features of the nest such as the proportion of ground cover surrounding the nest tree (Table 1). The top model, which included low ground cover, indicates that as ground cover increased the probability of a predation event occurring at the nest decreased (Table 1, Fig. 3). There was no evidence that nest predation risk varied with the other fine scale variables we measured such as nest height or with the abundance of high understorey vegetation, and neither of these variables was retained in the final model.

Table 1. Final model showing the probability, estimated by a binomial logistic regression, of predation by black rats on artificial nests in relation to nest site variables

	ß	Std Error	Z value	P value
Intercept- (Edge no plantation)	-0.40	0.340	-1.165	0.244
Edge - with plantation	1.139	0.424	2.689	**0.007**
Interior forest	0.015	0.329	0.046	0.963
Ground cover	-1.513	0.547	-2.766	**0.006**

Rat predation risk varied at the landscape scale, with the position of the nest (interior forest, edge plantation and edge no plantation) at this scale appearing in the top-ranked model (Table 1, Fig. 3). There was a significant difference in nest predation risk for nests in edge habitat located near plantations and non-plantation areas, with artificial nests experiencing higher predation rates in sites near to mixed taro and banana plantations than in either interior forest sites or edge sites away from plantations where land has been cleared or transformed into cattle farms (Table 1, Fig. 2 & 3). Artificial nests suggested nest disturbance risk by black rats was 22% ± 13 higher, on average, at forest edges near plantations than at edges near clearings away from plantations (Fig. 3), but there was little difference in predation rates of nests at edge sites without plantations and interior forest sites (> 1 km from the edge) (Table 1, Fig. 3). Indeed black rats were detected even 5 km away from the forest edge in the interior forest. There was also no suggestion that the model would be improved by including interacting terms between ground cover and habitat type (change in AIC >2). There was no evidence that the placement of the cameras had any effect on nest predation levels and this variable was also not retained in the final model.
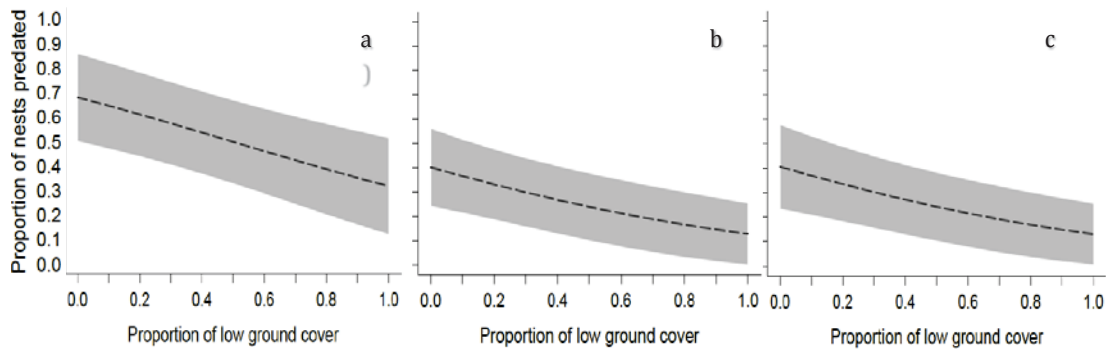
Figure 3. The probability black rat predation on artificial nests (black lines) according to the of ground cover and position of the nest in relation to the matrix (a) Edge plantation- the forest edge with plantations present, (b) Edge no plantation- edge without plantations (c) Interior forest- within interior forest. The grey shading represents 95% confidence intervals.

Can waxtags be used to show difference in large scale patterns of rat predation?

Both peanut butter and coconut flavoured waxtag lures showed simular landscape-related patterns in predation rates to the artificial nests (Table 2, Fig. 2). Significantly more waxtags were chewed on in areas with forest edge near to a plantation than in areas in the interior forest or in areas of edge forest away from a plantation (Table 2, Fig. 2). However, in edge habitat sites away from plantations chew mark rates were not significantly different from chew rates in the interior forest sites (Table 2).

Table 2. Final model showing the probability, estimated by a binomial logistic regression, of predation by black rats on (a) peanut butter and (b) coconut waxtags in relation to nest site variables relation to nest site variables

(a) peanut butter	ß	Std Error	Z value	P value
Intercept - (Edge no plantation)	-0.8799	0.230	-3.821	**<0.005**
Edge - with plantation	1.1072	0.287	3.825	**<0.005**
Interior forest	0.4198	0.289	1.448	0.148

(b) coconut	ß	Std Error	Z value	P value
Intercept - (Edge no plantation)	-1.3633	0.239	-5.981	<0.005
Edge - with plantation	1.1776	0.307	0.344	<0.005
Interior forest	-0.1184	0.344	4.124	0.731

Discussion

Our results indicate an interaction between habitat modification and nest predation by black rats. Both artificial nests and waxtags experienced significantly higher rat predation rates in sites near to mixed taro and banana plantations than either edge sites away from plantations or interior forest sites. Thus it is the alteration of the matrix surrounding the forest rather than just the presence of land without forest which influences nest predation rates by these predators. These results suggest that as the proportion of forest edge near plantations increases, which is expected with continual plantation development, a larger proportion of forest bird populations will experience nest predation from black rats. It is plausible that these habitat modifications could drive declines in forest songbird populations even if otherwise suitable habitat exists (Donovan et al. 1995; Schmiegelow and Mönkkönen 2002). Further research is needed to determine to what extent survival of sensitive endemic forest bird species depend on effective pest control as plantations extend into former forest.

Our results also suggest that interior forest sites in Samoa (>1 km from the forest edge) experienced similar predation rates by black rats to sites within 100 m from a forest edge where no plantation was present. Comparable studies on nest predation rates by invasive rats across the landscape are sparse in the South Pacific. However, a study in Fiji by Olson et al. (2006) used visitation rates at bait stations as an index of rat and mongoose abundance along a transect from forest interior to forest edge. They found significantly less visitation rates at forest interior sites (>1 km from the edge) than at sites closer to the forest edge. Unlike Olson et al. (2006), we found no significant difference between edge habitats (away from plantations) and interior forest sites (>1 km from the edge).

Though the impact of black rats on interior forest nest survival rates were lower than in areas near plantations, they may still contribute to the population declines of avian fauna, especially of species sensitive even to low nest mortality. Our study suggests that the bird populations

breeding in these forest types may be experiencing nest predation simular to edge habitat away from plantations. Therefore purely preserving these forest tracts may not be a sufficient method to maintain high reproductive success of sensitive bird species in Samoa and some rat control may be required.

Our study also investigated whether factors at a local scale (around the nest tree) affected predation rates. Previous studies have found that the localised habitat around the nest can strongly affect rat spatial movements and consequently influence nest predation rates (Mezquida and Marone 2002). Our study suggests that the percentage of low vegetation (<15 cm) surrounding the nest tree can influence nest predation rates by black rats, with predation rates being higher in areas with less groundcover below the nest tree. Our results contrast with previous studies, which have reported black rats favouring dense understorey coverage (Whisson et al. 2007; Amarasekare 1994). Understorey vegetation increases in the years following cyclonic events because canopies are opened (Turton 1992; Pohlman et al. 2008), so this may be one mechanism by which cyclones are influencing bird populations. We found little evidence, however, to suggest that the other localised variables measured for this study, such as nest height or the percentage of high vegetation density, affected nest predation rates by rats. Nest height did not affect nest predation rates by rats and this is partially explained by data from the nest cameras that showed that agile black rats were the dominant, and possibly the only, *Rattus* species predating nests at both plantation and non-plantation sites. Based on nest height alone, our results suggest that birds nesting high or low in the canopy are at similar risk of predation by black rats.

One advantage of this study is the combined use of artificial eggs and nest cameras. These tools enabled us to isolate a single dominant invasive predator, the black rat, and thus the factors affecting its rate of predation on nests. No other rat species were detected despite trapping occuring with both cage traps and snap traps in a number of the sites. Nest predation is often oversimplified by generalising predator responses across multiple species (Lahti 2009; Lewis et

al. 2009; Vetter et al. 2013). However, clarification of the effects of habitat modification on nest predation rates across landscapes and communities needs predators to be isolated. Our study also isolated bird species that may be predators of native birds' eggs. All the native bird species that were identified as potential nest predators during this study were found throughout the studied landscape in areas with and without forest. However, the introduced myna bird species detected on the nest cameras was only located at the forest edge or within the matrix (Stirnemann unpublished data). Further studies are needed to determine the extent that spatial distribution and abundance of predator bird species within the landscape contribute to nest predation rates and population declines of native species.

Our study used artificial nests as a predation monitoring method. The use of artificial nests has been critiqued and it is now widely recognised that predation rates of artificial nests do not necessarily reflect the predation rates of real nests (Major and Kendal 1996; King et al. 1999; Zanette 2002; Noske et al. 2008). Artificial nests have been used successfully, however, as a surrogate to represent the relative rates or patterns of nest predation among different treatments, such as habitat type, patch size, or distance from edge (Martin 1995; Penloup et al. 1997; Noske et al. 2008). Furthermore, studies of this type are the only practicable means of standardising nest parameters, such as nest size and height above the ground, to enable comparisons among habitats. We compared artificial nest and waxtag predation rates and found support for the artificial nest results.

Indeed waxtags might provide an alternative method for monitoring rat predation rates over space. Our results suggest this method was effective for differentiating rat variation in predation rates at a large scale. However, waxtag effectiveness may be limited in areas with high rat abundance because of the potential of over saturation of the waxtags. Peanut butter was significantly more appealing than the coconut lure to the rats but since rat species in our study were likely to be predominantly *Rattus rattus*. Further research is needed to see if it is as effective a lure for other Pacific rat species, such as *Rattus exulans*.

Knowing the causes of nest failure of tropical forest birds is essential for aiding conservation management of threatened species. This needs to be combined with an understanding of the both the spatial and temporal behaviour of the predators (see Martin et al. 2011). Only then can management strategies be applied when and where it is required. In the South Pacific region our understanding of invasive predators is seriously hampered by a lack of data from systematic studies. Further research on the biology of predators and prey are recommended to prevent further island extinctions.

Acknowledgements

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Chapter 6: Synthesis

Introduction

Native species are declining across Oceania (e.g. Atkinson, 1977; Thibault et al., 2002; Powlesland et al., 2008) and endemic species are disproportionately threatened with extinction (e.g. Thibault et al., 2002; Moorhouse et al., 2003; Webb et al., 2012). Birds are one of the best studied taxa, and as such the decline of bird biodiversity has been well documented and the subject of numerous explanations. The main drivers of bird extinctions and declines on Oceanic islands are predation and competition from invasive species and habitat loss (Meyer, 2004; Hays & Conant, 2007; Howald et al., 2007; Clavero et al., 2009; Medina et al., 2011; Butler et al., 2014), with exploitation and disease also contributing (van Riper et al., 1986; Atkinson et al., 1995; Muller-Landau, 2007; Powlesland et al., 2008; Sreekar et al., 2015).

Despite evidence from around the world that complex interactions exist between the various drivers of native species decline (e.g. Didham et al., 2007), these are typically investigated or managed independently. Habitat modification might, for instance, drive increases in the local abundance or distribution of invasive species, with total invasive impact scaling in direct proportion to their abundance (Parker et al., 1999). Alternatively, habitat modification might change the functional response or action of the invasive species with the total impact scaling disproportionately to the abundance of the invasive species (Parker et al., 1999; Didham et al., 2007).

Detailed research is still required to determine where and how management should be targeted. Critical biological information that is needed to inform management decisions is missing for many South Pacific birds including even basic biological data such as clutch sizes and incubation length, and such data are particularly sparse for South Pacific forest birds (BirdLife International, 2012). Furthermore, few studies have quantified mortality rates across life history

stages, how predation events vary over space and at different scales, what this means for nest survival, and how this influences species declines.

In order to gain a full understanding of the impacts of invasive species on birds it is important to: (1) study invasive species impacts at multiple scales and (2) include data on different response variables (Parker et al., 1999). This allows models to be developed that can guide empirical work and explore general patterns, such as how different life history strategies are affected by predation rates. To my knowledge, previous studies of the impacts of invasive species in the South Pacific have not considered either scale or interactive effects. Instead, the majority of published studies have identified the native species present in particular areas and investigated the direct impact of a particular dominant driver of the species' decline (e.g. Robertson et al., 1994). However, even this type of investigation is lacking for most native South Pacific species (BirdLife International, 2012).

The Ma'oma'o (*Gymnomyza samoensis*), a giant forest honeyeater, is one such data-deficient species. It is endemic to the Samoan archipelago and is listed as endangered by the IUCN (MNRE, 2006). Threats to this species and reasons for its decline prior to this study were categorised broadly and presumed to be from habitat loss, reduction in habitat quality due to hurricanes, and the impact of introduced predators (MNRE, 2006; BirdLife International, 2012). These broad generalisations do not enable management to be targeted. For instance, they do not indicate whether targeted invasive predator control is required, what species should be targeted, or when pest control should be implemented. Such temporal information is important because, for example, pest control programs can be more effective at reducing adult mortality and increasing nest success if targeted to coincide with the breeding period (Innes et al., 1999), but the time of breeding is unknown for many South Pacific species. Furthermore, there may also be important interactions between space use, invasive species abundance, and habitat alteration (Parker et al., 1999).

To help redress this paucity of relevant data for forest birds in South Pacific, this study used the Ma'oma'o as a case study species to explore:

1. How predation and habitat loss/fragmentation influence the population decline of cup nesting species; and

2. How the life history and behaviour traits influence reproductive success and survival.

In the following paragraphs, I draw together key findings of my scientific papers and discuss their implications for theory and management. The findings from this research will provide the ecological foundation needed to inform decision-making for the conservation management of the Ma'oma'o and other large honeyeaters in the South Pacific. It will also allow us to build a more detailed understanding of why population declines are occurring, the management required in Oceania, and where further targeted research is required.

Empirical Findings

The main empirical findings are chapter-specific and were summarised within the respective chapters. This section is a synthesis of the empirical findings which answers the two core thesis questions.

1. How do predation and habitat loss/fragmentation influence the population decline of the Ma'oma'o?

     My results showed that:

- Nest predation by black rats is influencing total reproductive success of the Ma'oma'o.

- Nest predation by black rats of adult female Ma'oma'o (the sex which exclusively broods) while they are on the nest may be resulting in sex biased breeding female mortality. This would have demographic consequences for the population.

- Nests near plantations experience significantly higher predation rates than nests in interior forest or edge habitat away from plantations.

- Nest success in interior forests and in edge habitat away from plantations do not differ significantly.
- The percentage of low vegetation (<15cm) surrounding the nest tree also influenced nest predation rates by black rats. Predation rates were higher in areas in areas with less ground cover below the nest tree.

2. How do the life history and behaviour traits of the Ma'oma'o influence reproductive success and survival?

My results showed that:
- Ma'oma'o have extremely low reproductive success with a maximum reproductive success rate of only a single chick per annum.
- Breeding occurs over much of the year, but there is a peak breeding season that matches the phenology of budburst and flowering resources.
- The Ma'oma'o has other slow life history traits that increase its vulnerability to nest predation. These include an extended incubation period, a long period in the nest prior to fledging, and an extended post-fledging dependency period compared to other honeyeaters, even with their size taken into account.
- Ma'oma'o will re-nest following failure and this can increase their reproductive success rate and partially compensate for some nest predation. Re-nesting, however, can also have negative implications for the offspring of the later broods and for the re-nesting adults (Ydenberg, 1989; Muriel et al., 2015).
- The flight capabilities of the Ma'oma'o are poor during the first 2-3 weeks following fledging. It is during this period that the fledgling may be particularly vulnerable to mammal predators such as cats.

Theoretical implications

My results showed that strong synergistic interactions exist between habitat alteration and nest failure due to black rat predation. Nest predation rates by these predators are influenced by the alteration of the matrix surrounding the forest rather than just the presence of land without forest. My results also suggest that interior forest sites in Samoa (>1 km from the forest edge) experienced similar predation rates by black rats to sites within 100 m of a forest edge where no plantation was present. Comparable studies on nest predation rates by invasive rats across the landscape are sparse in the South Pacific. However, a study in Fiji by Olson et al. (2006) used visitation rates at bait stations as an index of rat and mongoose abundance along transects from the forest interior to forest edge. They found significantly lower visitation rates at forest interior sites (>1 km from the edge) than at sites closer to the forest edge. Unlike Olson et al. (2006), I found no significant difference between edge habitats (away from plantations) and interior forest sites (>1 km from the edge). The interaction between forest loss, habitat modification and nest predation needs to be further investigated on other South Pacific islands in order to fully understand the dynamics of invasive rats and to determine what management is required for sensitive island forest bird species.

Management implications

It is clear from this study that habitat alteration and rat predation are contributing to the decline of the Ma'oma'o through nest predation. Furthermore, it is possible that rats might be causing biased mortality of adult females while nesting, and cats may be causing mortality of fledglings for the first two weeks after leaving the nest.

This study has also used empirical findings to show that purely maintaining large tracks of forest is unlikely to be sufficient to maintain species such as the Ma'oma'o. The results from this study suggest that control of rats is required to maintain populations of Ma'oma'o. However, due to the slow maximum reproductive rate of this species, recovery is not expected to be fast. Relocating some individuals to American Samoa may be advantageous since there are

potential sites available there where rats could be completely removed. Thus little further management might be required to maintain the population, because although the Ma'oma'o has been extirpated from American Samoa, the local habitat remains intact. The following, in no particular order, are the key steps I feel are required to improve the status of this species.

1) Management of key forest areas where the species survives and reforestation (with native trees, especially flowering species such as mistletoe) in key sites. An integrated management plan for the species which includes ecosystem management will hold great advantages for the preservation of the ecosystem which the Ma'oma'o is reliant on however without pest control it is likely that the species will continue to decline. Therefore undertaking only this step alone is unlikely to lead to increases in the population over the long-term. Land-acquisition of priority sites either through tenders or direct purchase maybe required to ensure key habitat is maintained into the future.

2) Further research on Ma'oma'o distribution, habitat requirements and threats of introduced predators at different life history stages is still required. However, there should be an eclectic trade-off between the wish for more knowledge and the need to produce conservation results with the limited funds available. Recovery action should be orientated towards protecting and stabilising the existing population.

3) A long-term monitoring program needs to be developed for the species. A monitoring program would also give a much-needed estimate of population size, which would be useful for determining the urgency of action, and suggest targeting of sites. Monitoring should also follow-up the implementation of recovery activities and should allow for adaptive management of recovery action.

4) Cat and rat control should occur in target areas where Ma'oma'o are present and the effectiveness of the predator control methods assessed. This will allow the development of more effective management strategies that suppress invasive predators while still promoting species recovery.

5) Re-establish Ma'oma'o populations on rat/cat free islands. Discussions with American Samoa should also take place as to the potential reintroduction of this species since the habitat is intact and additional funding to maintain a stable population may be available here. Given that the Ma'oma'o is now on the American endangered species list this may be an increasingly viable option.

6) Research should be undertaken to determine if sex biased mortality of female Ma'oma'o is occurring. My first paper outlines a method to achieve this (Chapter 2).

Recommendation for future research

This is the first study of the Ma'oma'o. Many questions about this species and the impact of landscape features and invasive species remain unanswered. I discuss a few options below. Although there are many additional options for further research in the South Pacific on both invasive species and native forest bird species, I only touch on a few areas that relate directly to this study and the conservation of the species.

One of the key areas where further research is required is on invasive species in Samoa and other South Pacific islands. It is critical that there is a better understanding of seasonal and spatial drivers of abundance and dietary preference of the pest species causing the declines of species such as Ma'oma'o. In this thesis I began to investigate the spatial drivers of nest predation. Research is required to establish if these also predict rat abundance. Further research is also needed investigating how abiotic seasonal factors that affect food and water availability may drive changes in abundance and space use. I suggest that seasonal variation in both rat and cat space use is a key area to target for future research since these species are both likely to be driving declines of endangered birds in Samoa. However, for rare and declining species, such as the Ma'oma'o, action on the ground in the form of predator control might be required even while we build this knowledge base.

The effectiveness of various predator control methods need to be tested in order to develop effective management strategies that suppress invasive predators while still promoting native species recovery (Wilson et al., 1998; Smith et al., 2010, 2011). Compensatory predation may counter effects of predator control (Johnson et al., 2007). This should be investigated during any control operation. The relationship between distance from the forest edge and rat abundance also needs to be revisited on other Pacific islands in order to further understand the influence of invasive rats on native bird species and how they should be managed.

Missing, however, is a full survey of Samoa to determine where Ma'oma'o remain and what drives their distribution. This is a key area for further research and will allow estimation of the current population size and modelling of the population trends. If such a survey was to occur, I would recommend that an attempt be made to determine if sexual biased mortality is occurring. During my study I showed how calls could be used for such a survey (Chapter 2). However, this tool has not yet been used to survey populations or to compare total populations to adult female population size so trials maybe required. Appropriate management will depend on the underlying mechanisms driving native species decline and many questions remain to be answered.

Limitations of the study

Working on an endangered species with a small patchily-dispersed population presents problems and challenges. I was limited to working with only a few individual birds, which creates statistical challenges. Working on species with low population sizes also raises ethical issues, because the ecological impact of the study must be balanced against the value of the research. Faced with these problems, I had to consider alternative methods of obtaining information that would aid in the development of management strategies and accept that for some aspects of this study I would only be able to obtain observational data.

I assessed nest predation by using artificial nests and waxtags as a proxy for real nests. This method allowed me to undertake a study that would never be possible on the real nests of my study species. It raised new problems, however, because the use of artificial nests has been criticised (King et al., 1999; Zanette, 2002; Lewis et al., 2009). It is widely recognised that predation rates of artificial nests do not necessarily reflect the predation rates of real nests and that some species, such as snakes, are not attracted to artificial eggs (Zanette, 2002). Artificial nests however have been used successfully to represent the relative rates or patterns of nest predation among different treatments such as habitat type (King et al., 1999; Zanette, 2002). As a direct consequence of using artificial nests, I could not gain information on other potential predators. I did not detect any snakes, for instance. Further studies on real nests in Samoan forests are required to determine if snakes are important nest predators. Second, I could not gain a direct estimate of the predation rate. This will also require further research. Despite the problems of using artificial nests, they provided a good indicator for nest predation by rats, our primary species of interest. Using them allowed me to test a hypothesis about landscape use and nest predation at two different scales that would not have been possible otherwise.

Conclusion

This study is a first step toward building a better quantitative understanding of interactions between drivers of species loss in the South Pacific. I show that the benefits of maintaining large tracts of land are not a comprehensive solution to reducing the impact of invasive black rats on birds and is unlikely to be a sufficient method for maintaining species such as the Ma'oma'o. I also show how critical it is to understand the life history of species, such as the Ma'oma'o. Life history traits need to be taken into account when developing management plans. My research can be used to guide conservation actions for the Ma'oma'o and other native forest cup nesters.

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Fialelei Enoka with a Ma'oma'o