



## A major myna problem; invasive predator removal benefits female survival and population growth of a translocated island endemic

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### ABSTRACT

Invasive predators are a major driver of extinctions and continue to threaten native populations worldwide. Island eradications of (mostly mammalian) invasive predators have facilitated the reestablishment of numerous island-endemic populations. Other invasive taxa, such as some predatory birds, could pose a more persistent threat due to their ability to fly and actively reinvade even remote and isolated islands. However, the impact of invasive predatory birds has been largely overlooked. We report on a novel sex-specific impact of an invasive-nest predator, the common myna (*Acridotheres tristis*), on a reintroduced population of Seychelles warblers (*Acrocephalus sechellensis*); translocated from Cousin Island to Denis Island in 2004. Regular post-translocation monitoring revealed that female mortality was 20 % higher than males, leading to a 60–70 % male-biased population sex-ratio between 2005 and 2015. This was attributed to common mynas inflicting severe injuries to incubating female Seychelles warblers while attempting to prey upon eggs in their nests. These effects likely contributed to the slower-than-expected population growth observed (relative to previous translocations of Seychelles warblers to other islands) over the same period. An eradication programme beginning in 2011 removed all common mynas from Denis by 2015. Subsequently, we observed a balancing of sex-specific survival and the population sex-ratio of Seychelles warblers and, consequently, accelerated population growth. This study demonstrates the importance of assessing the threat posed by all invasive taxa (not just mammals) to island conservation. Furthermore, we show how extended monitoring is needed to identify problems, and develop solutions, post-translocation.

### 1. Introduction

The introduction of invasive predators is responsible for almost 60 % of contemporary vertebrate extinctions, arguably making them the most damaging animal group for global biodiversity (Doherty et al., 2016). Island endemics are particularly susceptible to invasive predators as ecological and evolutionary isolation leaves them ill-equipped to recognize and respond to novel predation, often leading to population declines and local extinctions (Sih et al., 2010; Simberloff et al., 2013; Carthey and Banks, 2014). For their small

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surface area, oceanic islands harbour a disproportionate amount of the Earth's biodiversity, yet have also experienced the fastest rates of species loss (Simberloff, 2000; Fernández-Palacios et al., 2021). Understanding and mitigating the impacts of invasive predators on island species is, therefore, crucial for global biodiversity conservation.

Invasive predators are established on the majority of oceanic islands and continue to be one of the most intensive threats to endangered island species (Dueñas et al., 2021). Controlling invasive predators can facilitate the re-establishment and growth of native island populations (Jones et al., 2016; Prior et al., 2018), with perhaps the best examples being the recovery of island bird species following the removal and/or suppression of invasive mammalian predators (e.g. Donlan et al., 2007; Lavers et al., 2010; Blanvillain et al., 2020). However, since invasive species research tends to focus on species considered to have the most severe impact (i.e. predatory mammals), the impact of other invasive groups can be overlooked (Pyšek et al., 2008). For example, predation of island endemic birds by invasive birds is widespread and, in some extreme cases, has caused extirpations/extinctions (see Evans, 2021). Furthermore, the ability of many invasive birds to actively disperse long-distances means they can (re)colonise islands without anthropogenic assistance (in contrast to most invasive mammals) and thus pose a unique challenge for island species conservation and eradication programs (Avery and Feare, 2020; Trakhtenbrot et al., 2005). Nonetheless, the impact of invasive birds on native species (or: native island species) remains poorly understood (Evans, 2021), and studies investigating the benefits of their removal are scarce.

Eradication of invasive predators may not always be sufficient to enable the reestablishment of native species. Extirpated island species with limited dispersal capabilities may be unable to naturally recolonize areas of invasive predator exclusion, requiring translocation (the intentional release of a species) to reestablish populations (Griffith et al., 1989; Towns et al., 2016). A key determinant of translocation success is ecological suitability at the release site, including the absence of invasive predators (Magdalena Wolf et al., 1998; Morris et al., 2021). For example, translocated population growth can be limited by re-invasions of the release site by invasive predators (e.g. Norbury et al., 2014), dispersal of the translocated population beyond areas of invasive predator control (Richardson et al., 2015; Irwin et al., 2021), and contact with new and/or unexpected invasive predator species (e.g. Emery et al., 2021). Hence, invasive predators can be responsible for both the need for, and failure of, translocations (Short et al., 1992; Bubac et al., 2019).

One rarely studied, but potentially important, impact of invasive predators on threatened island populations is an imbalance in the operational sex-ratio; the number of males to females available for mating at any one time. Deviations from a 1:1 operational sex-ratio limits the availability of mates for the more abundant sex – especially in monogamous breeding systems – leading to reduced reproductive output and increased competition among individuals (Nunney, 1993; Le Galliard et al., 2005; Heinsohn et al., 2019). In small populations, these effects can reduce population growth rate and genetic diversity and, ultimately, increase extinction risk (Stephens and Sutherland, 1999; Engen et al., 2003; Bessa-Gomes et al., 2004; Jamieson, 2011). Therefore, sex-ratios are an important consideration when conserving and reintroducing threatened species (Komers and Curman, 2000; Wedekind, 2002).

For socially monogamous species, a 1:1 operational sex-ratio maximizes the effective population size and growth rate. However, sex-ratios in some taxa, such as birds, tend to be male-skewed, particularly in threatened species and in small and/or declining populations (Donald, 2007; Székely et al., 2014; Morrison et al., 2016). This pattern has been attributed to females having higher rates of mortality and/or dispersal, with the resulting male-skew restricting population productivity (Steiffetten and Dale, 2006; Grüberler et al., 2008). In some species, for which females provide the majority of parental care to offspring, a major driver of female mortality is predation during nesting (e.g. Rymešová et al., 2012; Ramula et al., 2018), meaning that increases in predator species abundance, such as the introduction of invasive predators, can increase female (but not male) mortality and cause a male-skewed sex-ratio (e.g. Lehtikoinen et al., 2008; Stojanovic et al., 2014). Further, the authors of these studies suggest that reducing female-specific mortality (i.e. removing predators) would disproportionately benefit the recovery of those populations; however, there have been few (if any) empirical tests of this.

Here, we report on the impact of an invasive nest-predator, the common myna (*Acridotheres tristis*), on the establishment of a translocated island population of Seychelles warblers (*Acrocephalus sechellensis*). In 2004, 58 adult Seychelles warblers (of approximately equal sex-ratio) were translocated to Denis Island following the successful elimination of mammalian predators (Richardson et al., 2006). While individuals started breeding immediately after the transfer, the initial population growth rate was slower compared to previous translocations of the species to other islands (Brouwer et al., 2009). Additionally, post-translocation monitoring revealed that females were gaining injuries and had higher mortality rates (compared to males) which subsequently resulted in a male-biased adult sex-ratio (unpublished reports: Brouwer et al., 2007; van der Woude and Wolfs, 2009; van der Woude and Ploegaert, 2010; van de Woude and Ploegaert, 2011; van der Woude et al., 2013). These observations were attributed to the presence of common mynas, which were seen attacking incubating female Seychelles warblers while attempting to prey upon eggs or chicks in the nest. Incubating females do not evade common myna attacks despite the risk of injury, as sitting tight on the nest is an evolved response to deter smaller native nest-predators (Veen et al., 2000). We hypothesised that the impact of common myna predation on reproductive success and sex-ratio was contributing to the slower than expected population growth. An eradication effort from 2011 to 2015 successfully removed common mynas from the island (Feare et al., 2017); however, the effects of this on Seychelles warbler demography had not been assessed. The addition of further data collected in 2022 enabled us to compare rates of sex-specific survival, sex-ratio and population growth before and after the removal of common mynas, and to that of common myna-free (i.e. control) Islands. This quasi-experimental study provides a rare opportunity to explore the impact of sex-ratio bias, mediated by invasive predation, on island species conservation.

## 2. Methods

### 2.1. Study system

The Seychelles warbler is a small insectivorous passerine endemic to the Seychelles. Thought to be common and widespread across the Seychelles archipelago historically (Spurgin et al., 2014), by the mid-20th century the species nearly became extinct as a result of habitat loss and the introduction of invasive predators. By 1960, only ca 29 individuals remained, occupying a single hectare (ha) of mangrove forest on Cousin Island (4.3315° S, 55.6620° E, 29 ha; Loustau-Lalanne 1968). However, with the restoration of native habitat, the Cousin population rapidly increased and stabilized at around 320 individuals from 1980 onwards (Komdeur and Pels, 2005; Brown et al., 2021). Seychelles warbler populations are structured into clearly defined territories that are defended year round by a pair-bonded breeding pair, but may also include 1–5 sexually mature subordinates (Richardson et al., 2002) which sometimes engage in helping behaviour and cobreeding (Richardson, Komdeur and Burke, 2003; Hammers et al., 2019). Paired males exhibit mate-guarding behaviour and are generally more aggressive/responsive to territorial intruders than are females due to high rates of extra-pair paternity in this species (Komdeur, 2001; Richardson et al., 2001; Bebbington et al., 2017).

Seychelles warblers are reluctant to fly over open water and thus fail to disperse to establish populations on other suitable islands (Komdeur et al., 2004). Consequently, a series of translocations were undertaken as part of the species action plan (Richardson, 2001) to establish insurance populations and increase the global population size; which exceeds 3000 across five islands (Wright et al., 2014; Fig. 1). In brief, 29 birds were translocated from Cousin to Aride (4.2129° S, 55.6648° E, 68 ha) and Cousine (4.3507° S, 55.6475° E,



**Fig. 1.** Map showing the present distribution of Seychelles warbler populations in the Seychelles (highlighted black; Cousin, Aride, Cousine, Denis and Fregate). Common myna populations are established on all other (grey) large islands except for North, where they were eradicated in 2017 (Feare et al., 2021).

25 ha) in 1988 and 1990, respectively (Komdeur, 1994). A further 58 birds were translocated to Denis (3.8053° S, 55.6676° E, 142 ha) in 2004 and 59 birds to Fregate (4.5837° S, 55.9386° E, 219 ha) in 2011, from Cousin (Wright et al., 2014; Richardson et al., 2006). These islands were selected for translocations as they contained suitable native-forest habitat and lacked mammalian invasive predators. For all translocations, the founding populations had approximately equal sex-ratios, were demographically similar (e.g. age-structure, body size/condition) and were released at sites with good quality habitat (i.e. high insect abundance; Richardson et al., 2006; Wright et al., 2014; Komdeur et al., 1995a).

Common myna have been introduced beyond their native South Asian range to many parts of the world and are considered one of the most damaging invasive species in the world (Lowe et al., 2001; Magory Cohen et al., 2019; Evans et al., 2021). In the Seychelles, common mynas are found on all large islands (>250 ha) and many smaller islands that contain suitable (anthropogenic) habitats such as agricultural and recreational land use (Evans, 2021; Fig. 1). On these smaller islands (e.g. Denis, North, Bird and Fregate), common myna densities were (until recent eradication efforts) considerably higher than most continental introduced populations in South Africa and Australia; 3.4–6.4 versus 0.03–1.9 and 0.6–3.3 birds/hectare, respectively (Feare et al., 2017). Common myna have been observed preying on eggs and interfering with the breeding of native bird species, such as Seychelles magpie robins (*Copsychus sechellarum*; Komdeur, 1996) and seabird colonies on Bird Island (Feare et al., 2015).

Common mynas invaded Denis from nearby islands and, at the time of the Seychelles warbler translocation, a large population of ca. 1000 birds had established on Denis (Feare et al., 2017). In subsequent years, head injuries (bald patches, scars, and eye damage) were observed on ca. 8 % of caught Seychelles warblers and several individuals of other endemic passerine species (van der Woude and Wolfs, 2009), which had not been seen to the same severity or frequency in other Seychelles warbler populations on common myna-free islands (i.e. Cousin, Aride, Cousine and Fregate). Video observations of common mynas attacking a ‘dummy’ nesting Seychelles warbler (a taxidermy reed warbler (*Acrocephalus scirpaceus*) sitting on an artificial nest) then confirmed that common mynas can inflict such injuries (van der Woude and Neddermeijer, 2010). This motivated a three-phase eradication, which saw 1186 birds removed between 2011 and 2015 (see Feare et al., 2017 for details). By 2012, ca. 90 % of the common myna population was removed, with the remaining population removed in 2015. Similar successful eradications have taken place on two other Seychelles islands; North (201 ha; Feare et al., 2021) and Fregate (219 ha; Canning, 2011). In the years since all common myna were eradicated from Denis and Fregate, small groups of birds have been discovered (and quickly removed) which demonstrates the species ability to reinvade small islands > 50 km from their nearest breeding population (Dhami and Nagle, 2009; Fig. 1).

## 2.2. Data collection

Post-translocation monitoring of Seychelles warblers on Denis were conducted each year from 2005 to 2015 (except for 2008, 2012 and 2014) and then most recently in April 2022. The duration of monitoring events (hereafter field seasons) ranges from three weeks to two months and involves two or three observers searching the entire island for Seychelles warblers. Individuals are located visually by listening for their songs, calls, or the snapping of their bills while foraging. Individuals are also attracted and located by whistling, ‘pishing’ and using playback of song along paths. Most sighted individuals were followed for ca. 15 min to determine territory boundaries and the presence of any associated individuals (e.g., social partner, additional birds and fledglings within the territory; Richardson et al., 2007). Since males are more likely to be attracted to whistling and playback, following sighted individuals to find associated individuals also reduces the likelihood of male-biased sightings. The movements of individuals and locations of interactions with neighbouring individuals (e.g. fights, alarm calling) were used to infer territory boundaries. Individuals ringed during or before a given field season were visually identified from their unique combination of three colour bands and a British Trust for Ornithology (BTO) metal ring. For the 2004–2015 field seasons, ca 60–90 % of the observed population were ringed. The probability of re-sighting ringed Seychelles warblers during this period was high (2005–2006 = 95 %, 2011–2013 = 91 % and 2013–2015 = 82 %) and, importantly, did not vary between sexes (Brouwer et al., 2007, 2009; van der Woude et al., 2013). Furthermore, migration between islands by Seychelles warblers is virtually non-existent (Komdeur et al., 2004). Therefore, ringed individuals that are not seen in a given field season can be confidently assumed dead.

During each field season, individuals are captured using mist nets in conjunction with conspecific playback to simulate an intruder in the focal birds’ territory (see Kingma et al., 2016 for details). Newly caught individuals are given a unique combination of colour bands and a metal ring with a unique number (to facilitate future identification), blood sampled and classed as juveniles (<8 months old) or adults based on eye colour, which transitions from grey to red-brown (Komdeur, 1992). The sex of individuals is confirmed molecularly using a PCR-based method (outlined by Griffiths et al., 1998) using 25ul of blood drawn with a microcapillary tube from the brachial vein. This procedure is a routine, nonlethal way to sample blood from passerine birds and has been shown to have no measurable impact on condition or survival (Sheldon et al., 2008). Furthermore, the monitoring and catching methods outlined are routinely and consistently performed by members of the Seychelles warbler project across all five island populations (Davies et al., 2021; Brown et al., 2022).

During the 2004–2015 field seasons, catch effort was preferentially targeted towards unringed individuals (for example, revisiting territories to catch known unringed occupants) as maintaining a high proportion of ringed individuals in the population was necessary for censusing (see below). In contrast, catch effort in 2022 was regularly distributed across the island in space and time, as the vast majority (>90 %) of the population was unringed at the start of the field season. This non-targeted catch approach was adopted to ring/sample as many individuals as possible within the limited time-frame of the field season (three weeks) to facilitate population estimates (see below). A drawback of this non-targeted approach is the potential for male-biased catches, since males typically display a stronger response to playback (i.e. fly closer to the speaker placed near mist nets) than do females.

### 2.3. Population estimates

At the end of each field season, all observations made during visual monitoring and catching are collated and plotted on a map to determine territory boundaries and occupants, i.e., all individuals sighted in territories. From 2004–2015, it was possible to perform full censuses due to the very limited population size and high proportion of ringed individuals on Denis. Hence, for this period the sum number of observed individuals represents the estimated population size for a given field season. In 2013 and 2015, these estimates were corrected following resighting probabilities, which assume 9 % and 18 %, respectively, of the true population was unobserved. In 2022, we were unable to observe and/or capture the majority of individuals present due to a substantial increase in population size and the long length of time since the last period of ringing (2015–2022). Therefore, we estimated population size by extrapolating observed Seychelles warbler densities in comprehensively surveyed areas. We calculated average territory size (hectares) and average group size (number of resident individuals in territories), from a subset (62.5 %) of mapped territories for which we had sufficient observational data to confidently ascertain territory/group size e.g. territorial disputes, group interactions, repeated sightings etc. Using these two values we estimated Seychelles warbler population density (birds/hectare).

Population size was estimated by multiplying the estimated density by the total land area of Denis Island (132 ha), excluding unusable areas; beaches, grassland, buildings, and intensified agricultural land (9.65 ha). This population estimate (hereafter ‘maximum estimate’) assumes that density is constant across the island. While our survey confirmed the presence of territories across the whole island (except unusable areas), the frequency of observed territories was lower (ca 50 %) in coconut palm forest and plantation areas compared to the native forest (Fig. S1), which is consistent with prior knowledge that these are less suitable habitats (Johnson et al., 2017). Therefore, we produced two more population estimates using the following scenarios: 1) zero occupation of the palm forest/plantation area (26 ha) by Seychelles warblers (hereafter “ultraconservative” estimate), and 2) the density of Seychelles warblers in the palm forest/plantation area is 50 % of the estimated density (hereafter “moderately-conservative” estimate).

The population size of common mynas on Denis was estimated each field season from the beginning to the end of the eradication (2010 – 2015) using transect point counts. The Island was divided into six areas based on habitat type, with five fixed 200 m transects in each area. Counts were conducted at five points along 200 m transects at 50 m intervals. During counts, a single observer counted all common mynas sighted within a 25 m radius within a two-minute duration. Counts were performed in the morning, with each transect (within the same area) being counted twice in a random order. For each field season, all counts were completed within 4 – 8 days in similar weather conditions. Population size was estimated as the sum of birds counted per transect (averaged across replicated counts) multiplied by the proportion of the islands area which was surveyed (total island area (132 ha)/surveyed area (5.89 ha)).

### 2.4. Statistical analyses

All statistical analyses were performed in RStudio (version 1.2.5033 and R version 4.0.3, Rstudio Team, 2020). Survival, defined as whether or not an individual present in the previous field season was observed (i.e. alive) in the current field season, was fitted as binomial responses (yes vs. no) with a log link function in a Generalized Linear Mixed Model (GLMM) in lme4 (v1.1–25; Bates et al., 2015). To test where survival rates differed between males and females, sex was entered as a fixed effect. The time interval between field seasons (hereafter ‘interval’), was not consistent; while the majority were annual, some were biennial (2007–2009, 2011–2013, 2013–2015) and the two most recent field seasons were seven years apart (2015–2022). Because the proportion of surviving individuals decreases with time between field seasons, interval was entered as a controlling fixed effect. Individuals that were present across field seasons had multiple measures of survival; thus, individual identity was included as a random intercept. Similarly, field season ( $n = 9$ ) was also included as a random intercept to control for non-independence of survival measures (Brouwer et al., 2006). In addition to testing whether there is an overall sex-specific difference in survival rates, we were interested in whether sex-specific survival differed across field seasons, with the prediction that female survival will increase and be equal to male survival in the period after the common myna eradication compared to before. For this, we ran multiple univariate binomial General Linear Models (GLMs), with survival as a function of sex, for each field season. For field seasons with intervals greater than one year, we report annual survival (i.e., raw survival probabilities per sex-adjusted for time (years) between field seasons) for easier interpretation.

We were interested in whether the male-bias in the adult population had decreased since the common myna eradication. The population sex-ratio for each field season is estimated by the proportion of the caught adult population (for which sex is known) that are males. In 2022, only ca 30 % (269/875) of the estimated population were caught and sexed, in contrast to 60 – 90 % during the 2004–2015 period. We expect the 2022 catches to be male-biased as males, being more territorial, are more frequently caught using non-targeted catching methods that utilise conspecific playback. Therefore, rather than comparing the 2022 sex-ratio to that in previous years, we compared contemporary catch rates (male versus female) across populations; Denis 2022, Frégate 2022 and Cousine 2019. If the Denis population sex-ratio remains male-biased, we would expect the probability of catching males to be higher than on Frégate and Cousine; on which an equal sex-ratio is assumed. Frégate 2022 and Cousine 2019 were chosen for comparison as these field seasons similarly involved catching a sample of individuals from a largely unringed population. Crucially, neither population has been exposed to large populations of common mynas, nor has a known history of male-bias (Komdeur et al., 1995b), in contrast to Denis. Using a binomial GLM, the sex of catches (excluding juveniles) was regressed against field season (categorical; Denis 2022, Frégate 2022 and Cousine 2018).

To examine population growth (i.e., population size as a function of time) on Denis we used a segmented regression analysis from the segmented package (v1.6–0; Muggeo, 2022). In contrast to a simple linear regression, segmented regression identifies points in the x-y relationship where the slope changes, termed change points. Therefore, segmented regression analysis is suited for investigating the effects of interventions on time-series data (Wagner et al., 2002). We predicted that a change point would occur after the common



myna eradication, with faster population growth compared to before the eradication. The Davies test was used to determine whether regression slopes before and after the change point were significantly different. We compared the variance explained by the segmented model to that of competing regression models assuming linear and exponential growth, respectively, using adjusted  $R^2$ .

### 3. Results

#### 3.1. Sex-specific survival

Since being translocated to Denis and before the eradication of common mynas (2004–2015), females in the Seychelles warbler population have had lower survival rates than males (mean annual survival probability; females = 0.70 ( $n = 399$ ), males = 0.86 ( $n = 692$ ), GLMM-Sex;  $\beta = 0.985 \pm \text{SE} = 0.142$ ,  $z = 6.956$ ,  $P < 0.001$ ; Fig. 2). This is in contrast to the source population on Cousin Island, for which annual survival is 0.85 for both sexes (Hammers et al., 2015; Brown et al., 2022). When sex-specific survival was analysed separately by year, female survival was significantly lower in all years except 2005, 2006 and 2010. The magnitude of difference between male and female survival was broadly similar between 2005 and 2015 (Fig. 2). In contrast, survival of females and males from 2015 to 2022 (denoted as 2022 in Fig. 2) were nearly identical (mean annual survival probability; females: 0.87 ( $n = 69$ ), males: 0.88 ( $n = 149$ ), GLM-Sex;  $\beta = 0.224 \pm \text{SE} = 0.444$ ,  $z = 0.505$ ,  $P = 0.614$ ), based on 12 % of females and 14 % of males alive in 2015 being resighted in 2022, reflecting an increase in female survival.

#### 3.2. Sex-ratio and catch rates

The Denis adult population sex-ratio has been previously recorded as ca. 60–70 % male from 2005 to 2015, based on ca. 60–90 % of the population having been molecularly sexed in any given field season. Of the 266 individuals newly caught and sexed in 2022, 62 % of adults ( $n = 200$ ) and 48 % of juveniles ( $n = 66$ ) were male, respectively. Of adults caught on Fregate (2022,  $n = 111$ ) and Cousine (2019,  $n = 35$ ), 58 % and 54 % were male, respectively. The probability of an adult catch event being male (versus female) was not significantly different across the three populations (GLM, Predictor = Island (reference = Denis), Fregate;  $\beta = 0.399 \pm \text{SE} = 0.239$ ,  $z = -1.668$ ,  $P = 0.095$ , Cousine;  $\beta = -0.318 \pm \text{SE} = 0.369$ ,  $z = -0.860$ ,  $P = 0.390$ ), indicating that contemporary adult sex-ratios are similar despite the earlier impact of common mynas on Denis.

#### 3.3. Population growth

In 2022, we estimated population density at eight individuals per hectare and a total population size between 771 and 979 individuals (ultra-conservative and maximum estimates, respectively). The moderately-conservative population estimate (assuming 50 % density (4 birds/hectare) in the palm forest and plantation areas of the island) of 875 individuals still represents a two-fold (106 %) increase from 2015 and an annual growth rate of 15.1 %. However, the overall population growth rate (from 2004 to 2022) is considerably slower than what was initially observed on Aride and Cousine, which appeared to grow very rapidly post-translocation to reach asymptotic densities (i.e., carrying capacity) at ca. 8 and 6 years, respectively (Fig. 3). The initial population growth rate on Denis is more comparable to that observed on Fregate (Fig. 3).

The segmented regression model estimated a change point at 2013, with a significantly faster increase in population size occurring after 2013 compared to before (Davies test;  $P < 0.001$ ; Fig. 4). This is 1.5 years after the first phase of the common myna eradication, in which ca. 90 % of the common myna population was removed (Fig. 4). The pre-change point regression slope, describing population growth from 2004 to 2013, predicts a population size of 467 by 2022; 400 individuals less than our moderately-conservative estimate (Fig. 4). The segmented model had the highest adjusted  $R^2$  (0.99) followed by the exponential and linear regression models (0.98 and

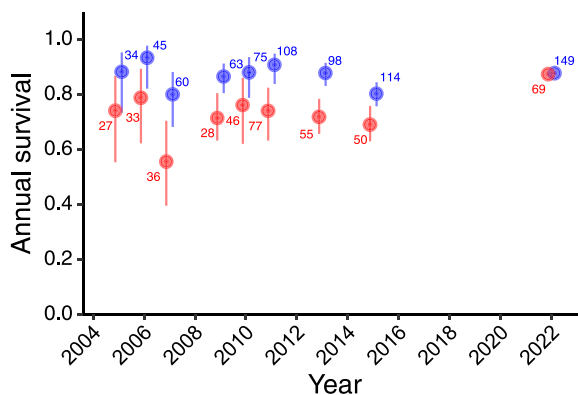
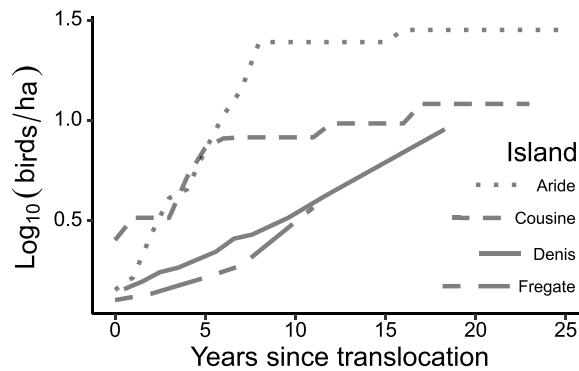
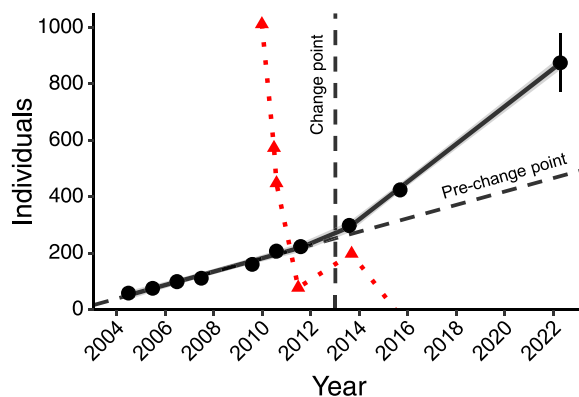


Fig. 2. The annual survival probability of Seychelles warblers, based on the proportion of ringed individuals from the previous field season alive in the following field season (x-axis), relative to sex (red = female, blue = male). Points and error bars are mean survival and binomial 95 % confidence intervals of raw data, grouped by sex. Numbers refer to sample sizes i.e. ringed individuals present in the previous field season.



**Fig. 3.** Seychelles warbler population density estimates in the years shortly after translocation to Aride (1988), Cousine (1990), Denis (2004) and Fregate (2011), respectively.



**Fig. 4.** Population size estimates for Seychelles warblers (black) and common myna (red) on Denis Island relative to time (year). The solid fit line for Seychelles warblers is the segmented regression prediction. The dashed lines represent the change point of the segmented relationship (2013) and the continuation of the population growth rate before the change point. The error bar at 2022 depicts the minimum and maximum range of the estimated population size at this point.

0.91, respectively). Therefore, observed population growth is best described by models depicting an accelerated increase over time.

#### 4. Discussion

We found that the translocated population of Seychelles warblers on Denis Island had higher rates of female mortality compared to male mortality across much of its existence. A notable exception was the period after which common myna were removed from the island (2015–2022), when female mortality had decreased to become near identical to male mortality. Of adult individuals newly caught in 2022, 61 % were male. This appears to reflect a male-bias in our catching methods rather than a male-biased population, as similar male catch rates are achieved when sampling two other populations. This suggests that, in line with equal male-female mortality, the population sex-ratio is approximately equal after the removal of the common mynas. The rate of post-translocation population growth on Denis was initially slower than that observed on other (common myna-free) islands. However, since the removal of common mynas from Denis, population growth has accelerated.

Compared to source and/or resident populations, higher mortality in translocated populations may be expected for a variety of reasons, including new predation pressures (Bradley et al., 2012; Parker et al., 2013; Norbury et al., 2014). However, our study is, to our knowledge, unique in showing that post-translocation mortality and predation-pressure can be sex-dependent. Seychelles warblers (both males and females) on Cousin Island and males on Denis have very similar mortality rates; higher mortality was only observed in Denis females before the myna eradication. The most plausible explanation is common myna nest-predation, which can inflict life-threatening injuries to parent birds (van der Woude et al., 2013). As for many taxa, Seychelles warbler females spend more time at the nest – only females incubate and have higher nestling provisioning rates – than do males (van Boheemen et al., 2019), and thus are more vulnerable to common myna attacks. Dispersal by Seychelles warblers into anthropogenic habitats (i.e. agricultural and recreational; van der Woude and Wolfs, 2009) soon after translocation may have increased exposure to common myna-predation, as these habitats typically support higher densities of common mynas compared to native forest (Garrock et al., 2014; Feare et al., 2017). Thus, our study supports the idea that mortality in the more vulnerable sex will increase as small populations disperse into less suitable habitats (Dale, 2001; Richardson et al., 2015).

Despite common mynas being listed as being one of the world's worst invasive species, empirical evidence of their negative impacts on native species is lacking (Lowe et al., 2001). Previous studies have shown that the establishment of common mynas is associated with a decline in the abundance of native bird species (Grarock et al., 2012; Colléony and Shwartz, 2020), with competition (for food and nest cavities) and nest interference/predation being the assumed proximate causes (Blanvillain et al., 2003; Grarock et al., 2012). While numerous common myna-predation events (of native bird species) are documented, these normally concern egg and/or chick predation (Evans, 2021). Our study is the first to demonstrate that nest-predation attempts by common mynas can impact adult mortality at a population-level and thus limit population productivity more than expected from nest-predation alone. In the context of vulnerable island species conservation, our study warns that the impact of common mynas as an invasive species can be greater than previously thought (Evans et al., 2018). Evans (2021) identified 88 island bird species (native to small islands and of conservation concern) that are vulnerable to common myna nest-predation globally. Of these species, 22 (25 %) are smaller than common myna and have nesting habits broadly similar to Seychelles warblers (i.e. cupped nests in low vegetation and/or trees) and thus could be similarly impacted by common mynas injuring incubating adults (Table S3).

The tendency for small and isolated populations to have biased sex-ratios is well-documented, particularly a male-bias in bird taxa. While this is often interpreted as a consequence of higher reproductive costs in females, obtaining strong evidence – such as higher mortality in females – can be difficult (Dobson, 1987; Morrison et al., 2016). Male-skew in small isolated populations can also be caused by female-biased dispersal, and thus the tendency of females to leave populations, rather than female-biased mortality (Dale, 2001). However, this is not the case in the Seychelles warbler as dispersal is confined within our study area; thus, it is a reasonable assumption that the male-biased sex-ratio (from 2005 to 2015) was caused by female-biased mortality. Given that the majority of island reintroductions are of species with limited dispersal capabilities, sex-biased mortality is likely to be the primary driver of sex-ratio bias in translocated populations more generally.

Biased operational sex-ratios, in particular male-bias, have been implicated as a major limiting factor of population growth (Le Galliard et al., 2005; Steifetten and Dale, 2006; Eberhart-Phillips et al., 2017). Likewise, the male-biased Denis population exhibited slower population growth compared to previous translocations to Aride and Cousin (Johnson et al., 2017). However, population growth increased after the common myna eradication, which suggests that the proportion of unpaired adult males has since decreased (Steifetten and Dale, 2006; Brooke et al., 2012). Likewise, our comparison of contemporary sex-specific catch rates suggests that the Denis population has become less male-biased. We cannot exclude the possibility that other island-specific factors (e.g. area, habitat quality) contributed to differential population growth. These factors may explain why Fregate, being larger both in terms of absolute size and the proportion of unsuitable habitat, also exhibited relatively slow growth in population density (Johnson et al., 2017). Nevertheless, our results indicate that common myna-related impacts (i.e. nest-failure, female-mortality and male-biased sex-ratio) play an important role. Given that the success of translocations is typically quantified by population growth rate (Morris et al., 2021), our study reiterates the importance of managing factors that can distort population sex-ratio.

Managing and/or removing invasive predators is an expensive and time consuming enterprise, hence the importance of gathering strong evidence as to the benefits of such efforts (e.g. Jones et al., 2016). Eradication programs have successfully removed common mynas from three islands (including Denis) in the Seychelles, with the aim of facilitating the recovery and/or reestablishment of threatened native bird populations (Canning, 2011; Feare et al., 2017). However, empirical evidence on the success of this particular action is currently limited, circumstantial, or confounded by other conservation action; for example, when common myna removal coincides with the removal of other more damaging invasives (e.g. rats) from the same area (Blanvillain, 2020; Tindall, 2007). Population growth of Seychelles paradise flycatchers (*Terpsiphone corvina*) and Seychelles magpie robins on Denis (both introduced in 2008 and susceptible to common myna attacks) also increased after the myna removal, suggesting a positive effect on the establishment of those populations (Feare et al., 2022). Crucially, our study of Seychelles warblers goes further in showing that i) causes of low population productivity (i.e. female-mortality and male-biased sex-ratio) have lessened post-removal, and ii) a statistically-supported change-point in the population trajectory, coinciding with the removal, after which growth was significantly faster. Therefore, our study provides the strongest evidence yet that controlling common mynas can benefit the re-establishment of native island birds.

## 5. Conclusions

Invasive predators are a major driver of both island species decline and failures to increase the population size/range of island species. Care should be taken to determine the impact of novel invasive predation-pressures – not just those implicated in the initial decline of an island species – on efforts to re-establish island populations. Most post-translocation monitoring is short-term (1 – 4 years) and usually only concerned with translocation success; whether or not the population grows to an adequate size (Bubac et al., 2019). However, we show that predation (or attempted predation) can have subtle (but important) effects, such as causing suboptimal population structure and growth rate, which are only detectable with detailed and extended post-translocation monitoring. Therefore, our study demonstrates the importance of such monitoring for informing follow-up action (e.g. invasive predator control) and for promoting the success of future translocations of the same and similar species.

## Ethics statement

The work was conducted with the ethical approval and permission of the Seychelles Bureau of Standards and the Seychelles Ministry of Environment, Energy and Climate Change and complied with all local ethical guidelines and regulations.



## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

The data that support the findings of this study have been made openly available in Dryad Digital Repository at <https://doi.org/10.5061/dryad.cz8w9gj86>.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02584](https://doi.org/10.1016/j.gecco.2023.e02584).

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