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ORIGINAL ARTICLE

The importance of post-translocation monitoring of habitat use and population growth: insights from a Seychelles Warbler (*Acrocephalus sechellensis*) translocation

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Abstract
Translocations are a valuable tool within conservation, and when performed successfully can rescue species from extinction. However, to label a translocation a success, extensive post-translocation monitoring is required, ensuring the population is growing at the expected rate. In 2011, a habitat assessment identified Frégate Island as a suitable island to host a Seychelles Warbler (*Acrocephalus sechellensis*) population. Later that year, 59 birds were translocated from Cousin Island to Frégate Island. Here, we determine Seychelles Warbler habitat use and population growth on Frégate Island, assessing the status of the translocation and identifying any interventions that may be required. We found that territory quality, an important predictor of fledgling production on Cousin Island, was a poor predictor of bird presence on Frégate Island. Instead, tree diversity, middle-storey vegetation density, and broad-leafed vegetation density all predicted bird presence positively. A habitat suitability map based on these results suggests most of Frégate Island contains either a suitable or a moderately suitable habitat, with patches of unsuitable overgrown coconut plantation. To achieve the maximum potential Seychelles Warbler population size on Frégate Island, we recommend habitat regeneration, such that the highly diverse subset of broad-leafed trees and a dense middle storey should be protected and replace the unsuitable coconut. Frégate Island's Seychelles Warbler population has grown to 141 birds since the release, the slowest growth rate of all Seychelles Warbler translocations; the cause of this is unclear. This study highlights the value of post-translocation monitoring, identifying habitat use and areas requiring restoration, and ultimately ensuring that the population is growing.

Keywords Post-translocation monitoring · Habitat suitability · Occupancy modelling · Seychelles Warbler · Population growth

Zusammenfassung

Die Bedeutung von Habitatsnutzungs- und Populationswachstumsmonitoring nach Umsiedlung: Einblicke in eine Translokation des Seychellen-Rohrsängers

Umsiedlungen sind ein wertvolles Werkzeug im Artenschutz und können bei erfolgreicher Durchführung Arten vor dem Aussterben bewahren. Damit eine Umsiedlung als Erfolg bezeichnet werden kann, bedarf es allerdings eines intensiven Post-Translokationsmonitorings um sicherzustellen, dass die Population die erwartete Zuwachsrate zeigt. Eine Habitatanalyse hatte im Jahr 2011 Frégate als eine geeignete Insel für die Ansiedlung des Seychellen-Rohrsängers (*Acrocephalus sechellensis*) identifiziert. Später im selben Jahr wurden 59 Vögel von der Cousin Insel nach Frégate umgesiedelt. Hier untersuchen wir die Habitatnutzung und das Populationswachstum des Seychellen-Rohrsängers auf Frégate, bestimmen damit den Status der Umsiedlung und identifizieren möglicherweise notwendig werdende Eingriffe. Wir fanden heraus, dass die Revierqualität, die auf Cousin ein wichtiger Prädiktor der Produktion flügger Jungvögel ist, die Vogelpräsenz auf Frégate lediglich schwach voraussagt. Stattdessen war die Vogeldichte von der Baumdiversität, der Vegetationsdichte in der mittleren Waldschicht und der Dichte breitblättriger Vegetation positiv beeinflusst. Eine auf der Basis dieser Ergebnisse erstellte Karte der geeigneten Habitate ergab, dass Frégate überwiegend geeignetes bis moderat geeignetes Habitat mit Flecken ungeeigneter, überwachsener Kokosnussplantagen bereitstellt. Für eine möglichst

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hohe Populationsgröße des Seychellen-Rohrsängers auf Frégate empfehlen wir Maßnahmen zur Habitatregeneration, die den hochgradig diversen Anteil an breitblättrigen Bäumen und einer dichten mittleren Waldschicht schützen und die ungeeigneten Kokosnusspflanzungen ersetzen. Die Seychellen-Rohrsängerpopulation auf Frégate ist seit der Freilassung auf 141 Vögel angewachsen, was die geringste Wachstumsrate aller Umsiedlungen der Art bedeutet. Die Ursache dafür ist nicht geklärt. Die vorliegende Studie unterstreicht den Wert von einem Monitoring nach der Umsiedlung; die Bestimmung von Habitatnutzung und von Gebieten, die eine Instandsetzung benötigen, und letztlich die Gewährleistung, dass die Population wächst.

Introduction

Translocations can be a valuable tool within conservation, facilitating the return of a species into its extirpated range, or introducing a species into a suitable habitat outside this range (Fischer and Lindenmayer 2000). Translocations are responsible for numerous conservation successes by alleviating extinction pressures on some of the most threatened species (Griffith et al. 1989; Fischer and Lindenmayer 2000; Elliott et al. 2001). These species were largely forced into extirpation as a result of severe habitat alteration and through the introduction of invasive predators (Griffith et al. 1989). By restoration of altered habitats and removal of the invasive predators, areas can once again support threatened species (Armstrong and Seddon 2008). This allows a species' range to be extended and the eventual development of new metapopulations (Marsh and Trenham 2001). In addition, increasing a species' range can allow the worldwide population size to increase (Wolf et al. 1998). Both of these effects decrease the extinction risk caused by stochastic events such as disease or natural disasters, as well as increasing the chances of the prolonged survival of the species (Gog et al. 2002).

One species to be successfully translocated is the Seychelles Warbler (*Acrocephalus sechellensis*), an insectivorous passerine endemic to the Seychelles (Safford and Hawkins 2013). In 1968 the Seychelles Warbler global population consisted of just 26 birds, restricted to Cousin Island (4°20′S, 55°40′E, 0.29 km^2) (Komdeur 1992). To address the Seychelles Warbler's threatened status (BirdLife International 2016), the habitat on Cousin Island was restored and the population recovered, reaching a carrying capacity of 320 birds by 1982 (Brouwer et al. 2006). Subsequently, birds have been translocated to four additional islands, and populations have become well established on three of these, with the global population of the species now exceeding 3000 birds (Wright et al. 2014). However, the status of the most recent translocation, involving 59 birds moved from Cousin Island to Frégate Island (4°35′S, 55°56′E, 2.19 km^2) in December 2011, is less clear. The last population estimate, 18 months after the translocation, was 79 birds (Wright et al. 2014). This population increase is encouraging but limited, and short-term growth should be viewed with caution, as post-translocation assessments should extend up to a minimum of 5 years (Sutherland et al. 2010). To assess the long-term success of the Frégate Island translocation, it is important to perform a repeated census of the island and quantify the longer-term population growth.

One factor which may affect the population growth rate is the differences in habitat between Frégate Island and the source island. Cousin Island comprises primarily native broad-leafed woodland (Komdeur and Pels 2005), whereas Frégate Island is dominated by exotic forest and overgrown coconut plantation (Richardson and Hammers 2011). Importantly, in the 2013 post-translocation assessment of Frégate Island, Seychelles Warblers were found only in native broad-leafed woodlands, and it was thought that the majority of Frégate Island's habitat was unsuitable (Pettersen 2013). If the population is confined exclusively to native broad-leafed woodland, Frégate Island's final potential carrying capacity would be smaller than expected and may impact the species' International Union for Conservation of Nature status.

This study uses occupancy modelling to identify which habitat features are important to the Seychelles Warbler, while also testing the validity of the territory quality measure used within the pre-translocation assessment (Richardson and Hammers 2011). We hypothesise that territory quality will better predict Seychelles Warbler presence than the other habitat features, as it measures the abundance of food available to the birds and is positively associated with fledgling production on Cousin Island (Hammers et al. 2012). Next, we use these results to estimate Seychelles Warbler carrying capacity and produce a habitat suitability map to guide restoration on Frégate Island. Finally, we compare post-translocation population growth on Frégate Island with that of all the other islands with Seychelles Warblers, and assess the longer-term status of this translocation.

Method

Data collection

We performed a census (20 April 20 to 8 July 2016) identifying Seychelles Warblers using unique combinations of a British Trust for Ornithology metal ring and three colour rings, following methods detailed by Wright et al. (2014). Each territory was visited repeatedly (mean number of visits = 7; standard error = 0.2 visits) throughout the field season, and was mapped with minimum convex polygon modelling using observations of resident individuals (Barg et al. 2005).

Vegetation and insect sampling

We sampled vegetation and insects in all Seychelles Warbler territories and a random selection of control areas. Control areas were assigned by overlaying a 73.8-m^2 (mean area of southwest territories on Frégate Island after we visited each territory three times; standard error = 3.1-m^2) grid onto a map of Frégate Island. Squares overlapping territories or areas dominated by bare rock were discounted. From the remaining grid, 60 control areas were randomly selected. When control areas were conjoined, one random control area was removed, creating a distance lag around each control area of 73.8 m, reducing the chance of spatial autocorrelation (Plant 2012). This reduced the number of control areas to 29.

We sampled vegetation once over 5 days in mid-May, recording plant species between 0 and 20 m at 20 random locations in each territory and control area. Our random locations were chosen by standing in the centre of each territory and walking ten paces in a random direction; this position was then sampled. From this point, ten more paces were taken in a random direction towards a previously unsampled place, remaining within the territory boundary at all times. This was repeated 20 times. We sampled insects twice over 3 days in both late May and late June, counting the number of insects on the underside of 50 leaves. Seychelles Warblers source most of their food by gleaning insects from the underside of leaves (Komdeur and Pels 2005). Insects were counted on the dominant plant species (accounting for more than 80% of relative plant abundance) in each territory and control area. Vegetation and insect survey methods are detailed in Brouwer et al. (2009). We extracted nine habitat features from these vegetation and insect surveys, each capturing an important aspect of Seychelles Warbler ecology (Table 1).

Island management and restoration

We calculated habitat suitability by comparing the values of important habitat predictors in suitable and active territories with those in unused control areas:

$$h = \sum_{i=1}^{c}\left(1 - \frac{\Sigma\sqrt{(\bar{a}_i - x_i)^2}}{\mathrm{MAX}}\right) \times 100,$$

where h is habitat suitability, $\bar{a}$ is the mean value of a predictor across all active territories [the mean value was used, as the optimal occupancy (presence or absence) predictor value is unknown], i denotes the predictors to include in the calculation (only predictors with an effect in occupancy modelling were included), x is the predictor value in each control point, c is the number of predictors with an effect, and MAX is the maximum value from the equation in the numerator, used to scale habitat suitability between 0 and 1. This was multiplied by 100 to create a percentage. This equation creates a scale, from suitable (100% in active territories) to unsuitable (0% in the most unsuitable control area); all control areas fell within this scale. We squared the numerator and then obtained the square root to ensure a positive suitability value.

Next we applied kriging interpolation to the habitat suitability scale, working on a fine scale of a maximum of four neighbouring points and a raster resolution of 5 m × 5 m (Stein 2012). We categorised this habitat suitability scale into quartiles: suitable habitat (100% to more than 75%), moderately suitable habitat (75% to more than 50%), poor habitat (50% to more than 25%) and unsuitable habitat (25% to 0%). We converted these into categories to calculate the area of the island represented by each quartile and identify the broad sections of Frégate Island that

Table 1 Habitat features extracted from vegetation and insect surveys used for the comparison of Seychelles Warbler territories and control areas

Habitat feature	Description/citation of formula	Justification
Tree diversity (*H*)	Shannon–Wiener index of tree diversity (Shannon 1949)	Knops et al. (1999)
Tree species richness	Number of tree species	Knops et al. (1999)
Native vegetation (%)	Native broad-leafed vegetation compared with exotic broad-leafed vegetation (excluding all narrow-leafed trees, e.g. coconut)	Ikin et al. (2013)
Broad-leafed vegetation (%)	Broad-leafed vegetation compared with narrow-leafed vegetation	Komdeur and Pels (2005)
Lower-storey density (%)	Vegetation present or absent at 60 points between 0 and 4 m	Huang et al. (2014)
Middle-storey density (%)	Vegetation present or absent at 100 points between 4 and 14 m	Huang et al. (2014)
Upper-storey density (%)	Vegetation present or absent at 60 points between 14 and 20 m	Huang et al. (2014)
Mean insect count (dm^2)	Insect count on dominant plant species (Brouwer et al. 2009)	Lindström (1999)
Territory quality	Territory quality measure (broad-leafed vegetation × insects) adapted from Komdeur (1992), removing territory size from the equation	Komdeur (1992)

The units shown next to the habitat feature underwent mean and standard deviation standardisation in occupancy modelling to allow comparison of parameter estimates. A description of the habitat feature and citation of the formula are included (if published), along with a citation to justify the inclusion of the habitat feature required the most and least restoration. We then calculated the carrying capacity within each habitat suitability quartile by multiplying the mean suitability value (converted to a proportion) within the quartile by the maximum population estimate for each area:

$$k = \sum_{i-1}^{4} a_i \times d \times \left(100/c_i\right)^3,$$

where k is carrying capacity, a is the surface area of the habitat suitability quartile (in hectares), i is the habitat quality quartile (i.e. suitable, moderately suitable, poor, unsuitable), d is the mean Seychelles Warbler density on Cousin Island (11.7 birds per hectare; standard error = 0.1 birds per hectare), and c is the mean value of 'suitability' in each quartile (i), divided by 100 to make a proportion. We cubed the mean suitability value to provide a conservative carrying capacity estimate, where highly unsuitable values will be further depreciated. For example, suitable habitat will decrease only marginally (e.g. $0.9^3 = 0.729$), but unsuitable habitat will decrease considerably (e.g. $0.2^3 = 0.008$). This is necessary as bird density and habitat suitability are unlikely to show a linear relationship, given that birds do not occupy areas of particularly poor-quality habitat, for example, coconut plantation (Komdeur and Pels 2005). The number of years required to reach carrying capacity was calculated with the exponential growth equation (Reece et al. 2011).

Population growth

We compared the growth rate of the Frégate Island population with the post-translocation growth rates on all other islands where Seychelles Warblers reside. We followed the same methods as those used to calculate growth rates on other islands (Brouwer et al. 2009).

Statistical analyses

All analyses were conducted in R 3.2.3 (R Core Team 2015), unless otherwise stated.

Occupancy modelling

Nine habitat features (Table 1) were assessed as predictors of the occupancy response variable (territories, $N = 56$, versus control areas, $N = 29$) in a model fitted with a binary logistic family error distribution. Covariates with a high variance inflation factor (less than 3) were removed (upper-storey density and tree species richness) from the analysis to reduce collinearity (Zuur et al. 2010). We used glmulti 1.0.7 (Calcagno and Mazancourt 2010) to exhaustively search all possible combinations of the remaining habitat features and ranked these using Akaike's corrected information criterion (AICc). Next, we performed model averaging using MuMIn 1.15.6 (Bartoń 2013), averaging all 'plausible' models with a delta AICc less than 7 (Burnham et al. 2011). Natural averaged parameter estimates were calculated (Symonds and Moussalli 2011) as well as relative variable importance (RVI). We did not detect spatial autocorrelation within the global model residuals using a spatial correlelogram and Moran's I test in ncf 1.1–7 (Bjornstad 2009). We tested model averaged goodness of fit (specificity and sensitivity) using the receiver operating characteristic and area under the curve (0.97), achieving a good fit in pROC 1.8 (Robin et al. 2011). Predictors with an effect were used in the habitat suitability equation.

Results

Occupancy modelling

Active territories had more broad-leafed vegetation (RVI = 1), greater tree diversity (RVI = 1), and higher middle-storey density (RVI = 0.95) than control areas (Fig. 1). There was no difference between active territories and control areas in any other predictor, including territory quality. The index of territory quality ranged from 2 to 37 in active territories, and from 0 to 14 in control areas.

Island management and restoration

Active territories were characterised by the mean values ($\bar{x}$) and standard errors (SE) of important predictors in occupancy modelling, specifically, tree diversity (H:$\bar{x}$ = 1.74, SE = 0.11), broad-leafed vegetation ($\bar{x}$ = 88.7%, SE = 0.05%), and middle-storey density ($\bar{x}$ = 56.5%, SE = 0.11%). Without any further restoration, the island

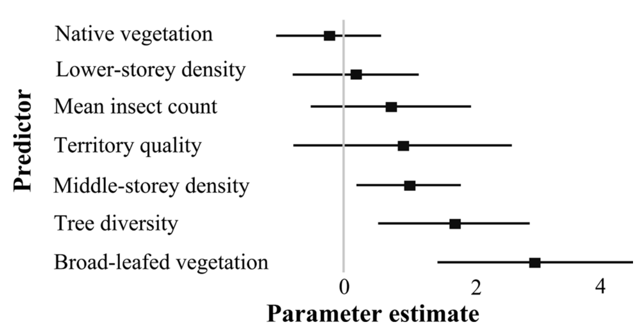

Fig. 1 Forest plot displaying standardised model averaged parameter estimates and 95% confidence intervals for active Seychelles Warbler territories compared with unused control areas (located at zero). Parameter estimates are ranked in ascending order. Middle-storey density, tree diversity, and broad-leafed vegetation estimates do not overlap with zero. Model averaging resulted in 19 plausible models

currently provides 138 ha of suitable habitat, 58 ha of moderately suitable habitat, 10 ha of poor habitat, and 5 ha of unsuitable habitat (Fig. 2). We estimate Frégate Island's carrying capacity will reach 1722 individuals (suitable habitat 1533, moderately suitable habitat 179, poor habitat 10, unsuitable habitat 0) by September 2029. Restoring habitat quality is predicted to increase carrying capacity by 502 birds for moderate to high quality (nine birds per hectare), 113 birds for poor to high quality (11 birds per hectare), and 60 birds for unsuitable to high quality (12 birds per hectare). As a result, if the entire island were restored, carrying capacity would rise to 2397, an increase of 675 birds.

Population growth

A total of 141 Seychelles Warblers were observed. The estimated population on Frégate Island has increased 2.4 fold (from 59 to 141 birds) in the 5 years since the translocation. In comparison, the population on Denis Island increased 3.4 fold (from 58 to 198), that on Cousine Island increased 4.1 fold (from 29 to 119), and that on Aride Island increased 14.2 fold (from 29 to 413) in the 5 years after the respective translocations (Fig. 3).

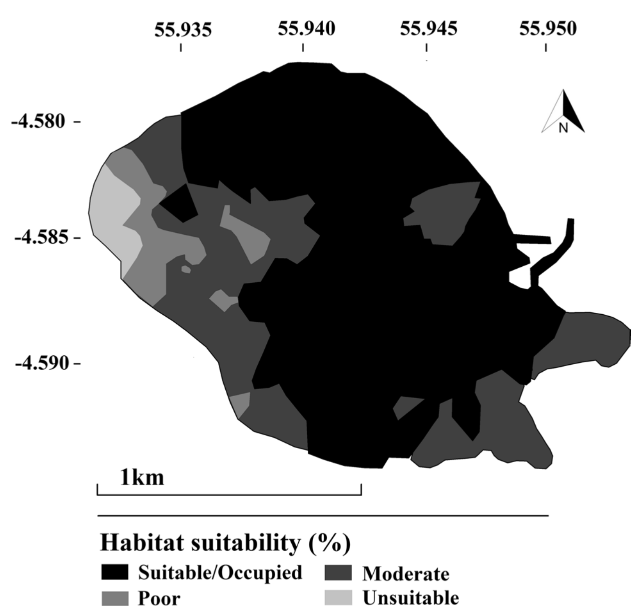

Fig. 2 The suitability of habitat for the Seychelles Warbler on Frégate Island (2017). High-quality habitat (occupied by birds) is shown in black and lower-quality habitat is shown in increasingly lighter shades of grey. Habitat quality is calculated using tree diversity, middle-storey density, and broad-leafed vegetation density. Coordinates are in decimal degrees

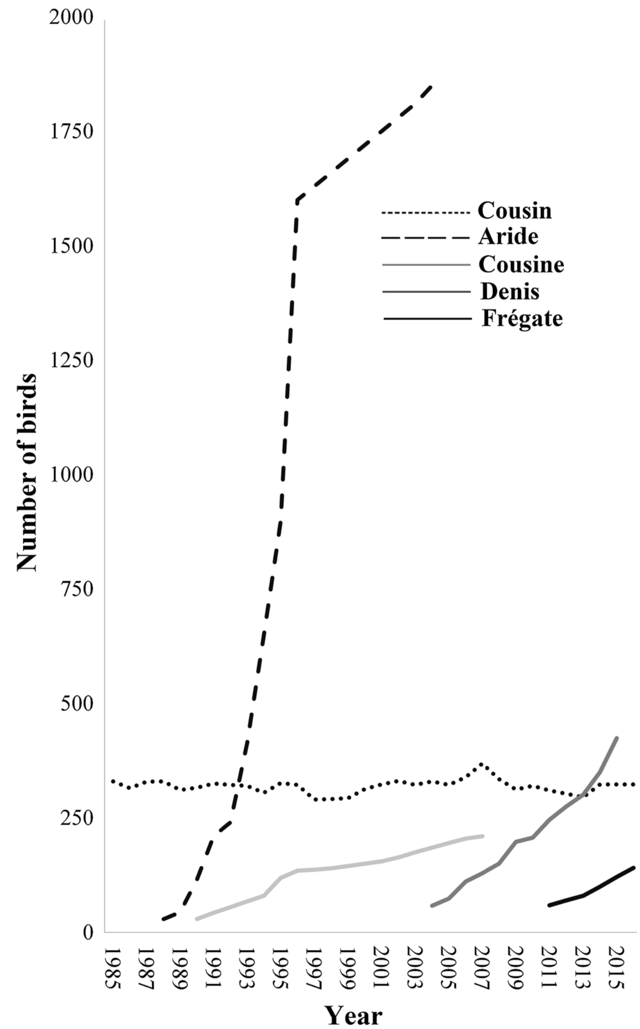

Fig. 3 Post-translocation population growth of Seychelles Warblers on Frégate, Denis, Cousine, and Aride Islands. The growth is plotted alongside the growth of the founder population on Cousin Island, which was at carrying capacity over the timescale displayed

Discussion

The territory quality index based on insect prey availability (Brouwer et al. 2009) was a poor predictor of Seychelles Warbler presence on Frégate Island. This was unexpected as the territory quality index influences fitness on Cousin Island (Hammers et al. 2012). Although Seychelles Warblers occupied habitat with the highest index of territory quality on Frégate Island, they also occupied habitat with a low index of territory quality. Rather than an index of territory quality, Seychelles Warbler presence was best predicted by a habitat with a greater tree diversity, denser middle storey, and more broad-leafed vegetation. These predictors measured habitat at a finer scale than the index of territory quality, and were more sensitive towards detecting desirable habitat traits on Frégate Island, helping to inform future conservation management decisions.

As territory quality was used to quantify the suitability of Frégate Island for the Seychelles Warbler, it is possible that Frégate Island's carrying capacity was overestimated. However, this is not the case, as our updated carrying capacity estimate (1712 birds in high- and moderate-quality habitat) is greater than the pretranslocation estimate of a minimum of 493 birds (Richardson and Hammers 2011). This increased carrying capacity is probably linked to Richardson and Hammers (2011) using a conservative carrying capacity measure to ensure the minimum population size would still be sufficient for a viable population. However, it is also probable that carrying capacity has increased in response to Seychelles Warblers exploiting exotic broad-leafed vegetation. We lacked detailed fledgling production data to confirm the Cousin Island result that territory quality predicts fitness, and suggest that future post-translocation assessments should model both occupancy and fitness components.

The importance of a high tree diversity and dense middle storey for occupancy was an unexpected finding, as previous research on Cousin Island recorded birds foraging primarily on the lower storey of a small subset of trees (Komdeur 1994). However, our findings are consistent with the wider literature on tropical passerines, where high tree diversity correlates with increased fitness (Lindström 1999). The greater occupancy in areas with a dense middle storey may suggest Seychelles Warblers have changed their niche since the translocation. Alternatively, previous work may have suggested birds forage in the lower storey, as they are harder to detect in the middle and upper stories. The importance of broad-leafed vegetation to Seychelles Warbler occupancy confirms the findings of previous work (Komdeur 1992; Komdeur and Pels 2005).

One of the most important findings was the complete absence of Seychelles Warblers in Frégate Island's old overgrown coconut plantation areas. This finding is consistent with previous studies on the Seychelles Warbler (Komdeur 1992; Komdeur and Pels 2005), confirming predictions made before the translocation (Richardson and Hammers 2011), and emphasises the importance of removing old coconut plantations from islands with Seychelles warblers.

The presence of native broad-leafed vegetation, on its own, was not an important predictor of Seychelles Warbler presence. Rather, both exotic and native broad-leafed vegetation together predicted occupancy. This is important, as restoration can target areas of unsuitable old coconut plantation, rather than removing the abundant broad-leafed exotic trees (cinnamon, cashew), which are found throughout Frégate Island. These old coconut plantations should be replaced with a highly diverse subset of native broad-leafed trees with a dense middle storey. With the Seychelles Warbler occupying a wider range of habitat than expected, this opens up the opportunity to consider translocating the Seychelles Warbler to other islands which may once have been considered unsuitable.

It is unclear why the Seychelles Warbler population growth rate has been lower on Frégate Island compared with Denis, Cousine, and Aride Islands. It is possible that the Frégate Island population has been exposed to new pathogens that are slowing the population growth rate (Fairfield et al. 2016). We advise that research be undertaken to screen the Frégate Island population for pathogens, continuing to monitor the malarial parasite that is becoming less prevalent within Frégate Island's Seychelles Warblers (Fairfield et al. 2016). Additionally, the Common Myna (*Acridotheres tristis*) has been implicated as a causal factor in the slow population growth rate of Seychelles Warblers on Denis Island because it attacks nesting females (Feare et al. 2016). Common Mynas occur on Frégate Island and thus may be a contributing factor to the low Seychelles Warbler growth rate. However, the Common Myna population on Frégate Island is currently very small, so these birds are unlikely to be having a major effect on the Seychelles Warbler population size.

For future translocations of the Seychelles Warbler, and other translocated species, the importance of continued post-release monitoring must not be underestimated. If Frégate island had not been revisited after 2013, this study would not have identified the poor applicability of the territory quality measure in predicting Seychelles Warbler occupancy, and the importance of a diverse broad-leafed tree community with a dense middle storey. This may have led to an ineffective restoration strategy being undertaken across Frégate. In addition, without post-release monitoring, the population's slow growth rate would not have been identified as an area of concern to be investigated in future studies.

Translocations and reintroductions can be a valuable tool within conservation, but only with continued post-release monitoring and habitat assessment, all ensuring the population is, and remains, viable. We recommend all translocation programmes include extended post-release monitoring, assessing all factors that could influence the population's establishment.

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Compliance with ethical standards

Conflict of interest The work did not receive funding, and the authors declare that they have no competing interests.

Human participants and/or animals Nature Seychelles, Frégate Island, the Seychelles Department of Environment, and the Seychelles Bureau of Standards all permitted and authorised the work on Frégate Island. The Ethical Review Committee at the University of East Anglia approved the research.

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