SURVIVAL RATES OF A TROPICAL ISLAND ENDEMIC FOLLOWING CONSERVATION INTRODUCTION ON A REHABILITATED ISLAND: THE CASE OF THE ENDANGERED SEYCHELLES WHITE-EYE

Elvina HENRIETTE^{1, 3*} & Gérard ROCAMORA^{2, 3}

RÉSUMÉ.— Taux de survie d'un endémique insulaire tropical après introduction pour la conservation sur une île réhabilitée : le cas de l'Oiseau-lunettes des Seychelles, espèce en danger.— L'Oiseau-lunettes des Seychelles Zosterops modestus est une espèce endémique hautement menacée des Seychelles, confinée à l'origine dans les deux îles de Mahé et Conception. Ses populations ont subi au cours du XX^e siècle un déclin drastique, vraisemblablement lié à l'introduction du Rat noir Rattus rattus et peut-être aussi à la destruction ou dégradation des forêts indigènes, et comptaient seulement 300 oiseaux environ en l'an 2000. Pour sauver cette espèce en danger critique d'extinction. 37 individus ont été transférés sur l'île de Frégate entre 2001 et 2003, et depuis, cette population a été suivie régulièrement chaque année. À partir de 206 données de recaptures visuelles nous avons estimé les taux de survie de ces oiseaux à l'aide du logiciel MARK 5.1 en utilisant les modèles de Cormack-Jolly-Seber (CJS), et présentons ici les premières estimations robustes des taux annuels de survie adulte publiés pour cette espèce. Nous avons aussi tenté d'estimer les taux de survie pour les oiseaux de première année. La probabilité de survie des adultes (φ) était de 76 %, et fut constante sur la période étudiée. Ce taux de survie annuel des adultes ne fut pas notablement différent entre les oiseaux-luneîtes transférés ($\varphi = 72$ %, n = 31) et ceux nés sur Frégate ($\varphi = 78$ %, n = 175), ni entre les mâles ($\varphi = 77$ %, n = 117) et les femelles ($\varphi = 74$ %, n = 86). Il n'a pas été possible de modéliser le taux de survie des juvéniles faute de données suffisantes sur les poussins bagués au nid ou juste après l'envol. Cependant, 24 sur 27 (89 %) de ceux-ci ont survécu à leur première année, ce qui indiquerait un taux de survie élevé et comparable à celui des adultes. Nous recommandons que l'on poursuive la collecte des données démographiques sur ces oiseaux à travers un protocole bien défini et aussi de façon empirique, et qu'une attention plus particulière soit donnée à l'estimation de la survie des juvéniles afin de permettre des évaluations démographiques plus précises sur cette population. Le suivi rapproché d'oiseaux menacés réintroduits dans des petites îles offre aussi l'opportunité de mieux comprendre les principes fondamentaux régissant la dynamique et l'écologie des populations en général.

SUMMARY.— Survival rates of the endemic Seychelles White-eye *Zosterops modestus* were investigated in a small transferred population on Frégate Island, Seychelles. The population has been studied since the first conservation introduction of 37 Seychelles White-eyes in 2001-2003, in an attempt to secure the long term future of this critically endangered species. Re-sighting data of 206 birds from direct systematic surveys were analysed with Cormack-Jolly-Seber (CJS) models using the software MARK 5.1. Here we present the first robust estimates of adult annual survival published for this species. We also attempted to provide a preliminary survival rate of first-year birds. Adult survival probability (φ) was found to be 76 % in our best-supported model, and survival was constant over time. Annual adult survival rate did not differ significantly between the transferred white-eyes ($\varphi = 72$, n = 31) and the Frégatois (those born on Frégate) ($\varphi = 78$, n = 175), nor did it between males ($\varphi = 77$, n = 117) and females ($\varphi = 74$, n = 86). Juvenile survival rate could not be modelled due to insufficient data on chicks marked at the nest or shortly after fledgling. However, 24 out of 27 (89 %) white-eyes marked as chicks/fledglings on Frégate between 2002 and 2008

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¹ Department of Environment, Botanical Gardens, Mahé, Seychelles

² Island Conservation Society, PO Box 775, Pointe Larue, Seychelles

³ Centre de Recherche sur la Biologie des Populations d'Oiseaux, UMR 7204, Muséum National d'Histoire Naturelle de Paris, 55 rue Buffon, 75005, Paris, France

^{*} Corresponding author's e-mail: elvinahenr@gmail.com

survived to one year old, indicating potentially high juvenile survival rates, comparable to the adults. More data are needed on marked chicks/fledglings to determine reliable and robust juvenile survival rates through modelling. Our study revealed the importance of having good monitoring design, regular, systematic and long-term data collection for such transferred populations, which will aid in the estimation of reliable survival rates along with other demographic and ecological parameters. We recommend the continued collection of both protocol-driven and empirical data, as well as an increased effort to estimate juvenile survival rates which will lead to more accurate assessments of population status. Close monitoring of transferred threatened birds on small islands offers further opportunities to better understand fundamental principles of population dynamics and ecology in these environments.

Estimation of reliable survival rates requires several years of data typically analysed by capture–recapture modelling (Lebreton *et al.*, 1992). Furthermore, robust survival estimates, in addition to other parameters such as productivity are needed for assessing bird population status and for understanding the relationship between population growth and population limiting factors. Survival, being a component of individual fitness in animal populations is also an important factor in population structure and population dynamics (Dietrich *et al.*, 2003). The conservation introduction of 37 Seychelles White-eyes (31 in 2001 and 6 in 2003) to Frégate Island (Seychelles) and the long-term monitoring of the resulting new population between 2001 and 2010 provided 9 years of data for estimation of reliable survival rates.

The Seychelles White-eye is a small passerine endemic to the Seychelles, an archipelago of 115 islands (455 km²) in the Indian Ocean (Collar *et al.*, 1994; Birdlife International, 2000). It was formerly known and widespread on Mahé (Newton, 1867; Nicoll, 1906; Vesey-Fitzgerald, 1936) and was believed to have become extinct (Crook, 1961) until it was rediscovered in 1961 (Lousteau-Lalanne, 1962). The population was estimated at less than 100 individuals in the mid 1970s (Collar & Stuart, 1985) and at 35–45 individuals in 1996 (Rocamora, 1997; Rocamora & Richardson, 2003).

In 1997 a previously unknown population, estimated at 279 individuals (242-327; P < 0.05) using a capture-mark-relocate method (Rocamora & François, 2000, 2001), was discovered on Conception Island, bringing the global population estimate to c.300 individuals.

After identifying nest predation by introduced arboreal rats (*Rattus rattus*) as the main threat to the species survival (Rocamora & François, 2000, 2001), and given the vulnerability of small island populations, it became imperative to translocate some individuals to suitable rehabilitated predator free islands in order to secure the long-term survival of this species. As a consequence, 37 Seychelles White-eyes were transferred from Conception (69 ha) to Frégate (219 ha, Fig. 1) between 2001 and 2003 (Rocamora *et al.*, 2003; Rocamora & Henriette Payet, 2008). Frégate is free of rats and cats (Beaver & Mougal, 2009) and the area of broad-leaf woodland and forest, which represents the main potential suitable habitat available for the Seychelles White-eye, covered c.60 ha at the time of the transfer in 2001 (Rocamora *et al.*, 2001).

The continued conservation and management of the species and its habitat (Rocamora & Henriette, 2009) led to the downlisting of the species from Critically Endangered to Endangered in 2005 (IUCN, 2006; Birdlife International 2007).

Continuous post-transfer monitoring of the abundance of the Seychelles White-eye on Frégate Island has provided descriptions of its population trends (Henriette, 2007; Rocamora & Henriette Payet, 2008; Henriette, 2011). However, the understanding of the life-history stages that have influenced these trends and the proximate or ultimate factors driving them is lacking.

Here, we present the first robust estimates of adult annual survival rates of the Seychelles White-eye on Frégate Island and compare them with the source population, Conception Island. We also present a conservative estimate of first-year bird survival rate and discuss survival of juveniles based on our observations. We analyse the variability in survival rates and determine whether there is any differences in survival rates between the transferred individuals and those born on the island 'Frégatois' (referred to as group effect), and between males and females (referred to as sex effect). We compare these survival rates with that of other passerines and discuss our results in relation to the conservation of the species.

METHODS

The methods consist of marking and relocation of birds through re-sightings each year during the breeding season, generally from January to March, for the years 2002 to 2010, throughout most of the island (Fig. 1). However, logistical and human resource constraints, resulted in poor re-sighting efforts in January-March of 2004 and 2005, and hence re-sighting data of May-June and June-August respectively were analysed giving a total of 10 % of the re-sightings outside of the main survey period. This meant that the time interval between the main survey occasions varied for the years 2003 to 2006. All 37 individuals transferred from Conception were already marked.

CAPTURE-MARK-RELOCATE

Catching and colour ringing of Seychelles White-eyes is regularly undertaken as part of the post-release monitoring programme. This allows for individual identification, but also maintains a high proportion of marked birds in the population (between 50 and 90 %). Birds were captured using mist-nets set in the territories or communal foraging areas. The Seychelles White-eyes were attracted by playing back a tape-recorded song of the species ('tape luring'). Each bird caught was marked using a unique combination of a numbered metal ring from the Museum National d'Histoire Naturelle (Paris) and one to three plastic colour rings. Morphometric measurements and blood samples (for determination of sex based on DNA analysis) were taken for all birds captured. After sampling and examination, the birds were released at the same site.

Direct systematic surveys (detailed below) were used to collect re-sighting data through relocating birds using binoculars.

DIRECT SYSTEMATIC SURVEYS

Annual survival rate was estimated by re-sighting marked individuals through one main direct systematic survey per year over 9 years, normally during the period January-March. Surveys of 8-13 days were undertaken in all territories and communal foraging areas of the Seychelles White-eye at 07:00–11:00 and 14:00–18:00. The duration of each survey depended on the number and locations of territories each year. Territories and foraging areas were identified through island-wide surveys along a network of nine transects, and early morning song census conducted at dawn (0530–0630 hrs) to detect singing males and breeding territories. Direct systematic survey is used to census the population by thoroughly checking all known territories and the group composition (identity and sex of each individual). Tape luring was also used to attract birds to the observer and facilitate their identification. Direct systematic surveys are accurate but usually extremely time consuming. Each survey was undertaken by 2 persons; one person note-taking and the other doing the re-sighting using a pair of binoculars. All marked and unmarked individuals that were seen as well as their respective activities, time and location were noted. Direct systematic surveys were also undertaken outside the main annual surveys, as part of the Seychelles White-eye post-release monitoring programme. Generally, monthly re-sighting of 2-7 days was conducted in 2001-2002 and 2009, and 3 to 6 annual visits of 2-7 days were done between 2003 and 2008 and in 2010.

DATA ANALYSIS

Re-sighting data of 206 adult birds from direct systematic surveys were analysed with Cormack-Jolly-Seber (CJS) models using the software MARK 5.1 (White & Burnham, 1999). The matrix of re-sighting histories predominantly consisted of sightings with less than a dozen recaptures. More than 2000 sightings were recorded between 2001 and 2010.

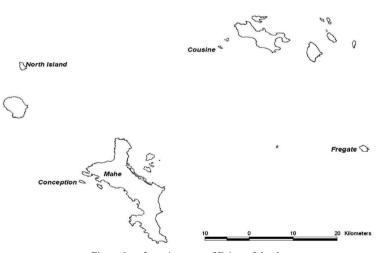


Figure 1.- Location map of Frégate Island.

Unequal time interval was taken into account in the data analysis, as in some years data was collected at other periods than January-March. Models estimated annual survival (ϕ) and recapture (p) probabilities. We fitted models with different parameterizations for survival and recapture probabilities. We modelled these parameters as being constant over time (.), varying with year (t), or depending on group (g), that is, either transferred birds or 'Frégatois'. To reduce the number of parameters in the model, we first modelled group effects (Transferred versus Frégatois), followed by sex effects on survival and recapture probabilities.

Model selection was based on Akaike's information criterion (AIC). Models with lower AIC values are assumed to best explain the variation in the data whilst using fewer parameters.

In addition to the use of the AIC value, the level of significance in the temporal variation of survival, and group effects were investigated using the Likelihood Ratio test (LR test) between nested models.

Insufficient data meant that survival rate of juveniles (birds under 1 year of age) could not be modelled. Few Seychelles White-eyes were marked at the nest as chicks or as newly fledged chicks due to inaccessibility of the nests or chicks (often remaining very high up the tree guarded by an adult and not responding to tape luring even when a distress call was played). We observed that independent juveniles were attracted to distress calls, but not young fledglings accompanied by parents. Instead, we provided and discussed empirical data on the fate of 27 White-eye chicks/fledglings marked between 2002 and 2008.

RESULTS

We analysed 206 recapture histories from 117 males, 86 females and 3 birds of unknown sex captured, marked and re-sighted from 2001 to 2010. Data were fitted to 16 models with different parameterisation of survival and recapture. First, we estimated the average annual survival rate for the entire population, next we estimated differences in survival between the transferred individuals and the Frégatois, and lastly we estimated survival of males versus females. Probability of recapture was also assessed.

SURVIVAL RATE

Two CJS models for annual survival and recapture (Tab. 1) had strong statistical support (that is, $\Delta AICc \le 2$). Seychelles White-eye survival in the most parsimonious model $\varphi(.)$ p(t) where survival was constant over time with temporal variation in recapture rates was 75.9 %, (SE = 2.3; 95 % CI = 71.2-80.0). There were not enough data to calculate a statistically meaningful value for the survival of one year old adult 'Fregatois' obtained from the model $\varphi(g^*t)$ p(t), which provided a survival rate of 96.3 %, (SE = 12.7; 95 % CI = 2.4-100) when in fact the observed value was 86 %.

TABLE 1

Models of annual survival (φ) and recapture (p) probabilities for adult introduced Seychelles White-eyes and birds born on Frégate Island ('Frégatois'), for the period 2002 – 2010. Columns give model notation, Akaike's Information Criterion values (AICc), AICc variation (Δ AICc), AICc weights, the Model Likelihood, number of estimable parameters (Num. Par) and the deviance. Results for the most parsimonious model are in bold. Subscripts describe parameterisations of φ and p: (g) = group, (t) = annual variation and (.) constant

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
Phi(.) p(t)	711.84	0.00	0.57	1.00	9	154.53
Phi(g) p(t)	712.96	1.13	0.33	0.57	10	153.56
Phi(t) p(t)	716.88	5.05	0.05	0.08	15	146.83

ANNUAL VARIABILITY IN SURVIVAL RATES OF THE POPULATION

Annual variation in survival rates of the Seychelles White-eye was obtained using our 3^{rd} most parsimonious model (Fig. 2). We observed some variations in survival probabilities over time, which increased from 72 % in 2003 (SE = 11.9, 95 % CI = 44.6-88.9) to 89 % in 2006 (SE = 7.1, 95 % CI = 66.2-97.2). A decrease was observed in 2007 (down to 66 %) and was followed with more fluctuations thereafter.

There was no evidence of significant annual variation in survival probabilities (Likelihood Ratio test between two nested models φ (t) p(t) where survival is allowed to vary over time and φ (.) p(t) where it does not (Chi² = 7.70, p = 0.26).

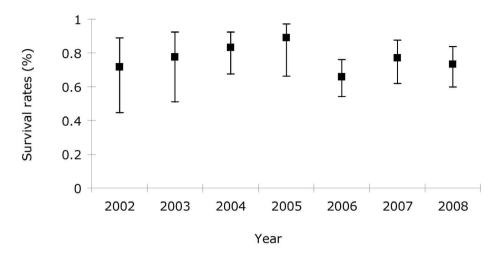


Figure 2.— Annual variability in survival rates of the Seychelles White-eye on Frégate Island.

INFLUENCE OF ORIGIN ON SURVIVAL RATES

Our 2nd best supported model $\varphi(g)$ p(t) was used to obtain the survival rate of the transferred Seychelles White-eyes (72.7 %, SE = 4.1; 95 % CI = 64.6-80.0) and the 'Frégatois' (77.4 %, SE = 2.7; 95 % CI = 71.8-82.2). A Likelihood Ratio test between the reduced model $\varphi(.)$ p(t) and the general model $\varphi(g)$ p(t) indicated no evidence of a significant difference in survival rate between the two groups (Chi² = 0.97, p = 0.32). The 'Frégatois' exhibited a greater fluctuation in survival rates (Fig. 3a) over time (64 % to 96 %) than the transferred birds (62 % to 78 %).

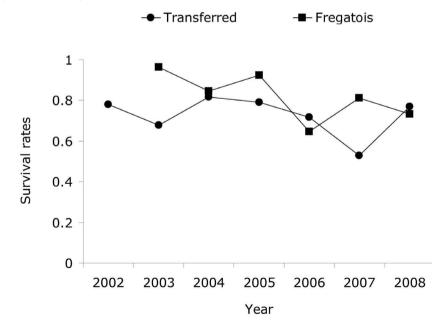


Figure 3a.— Annual variability in survival rates of the transferred Seychelles White-eye and the birds born on Frégate Island ('Frégatois')

SEX-SPECIFIC EFFECTS ON SURVIVAL RATES

The second set of modelling tested for the influence of sex on survival and recapture probabilities. Male survival (76.6 %, SE = 2.9; 95 % CI = 70.5-81.8) was slightly higher than female survival (74.2 %, SE = 3.5; 95 % CI = 66.9-80.4), although there were no significant sex-specific differences (Chi² = 0.31, p = 0.58).

Analysis of survival probabilities over time (Fig. 3b) showed no significant differences between males and females ($\text{Chi}^2 = 20.02$, p = 0.09). Greater fluctuations in female survival were observed whereas male survival probabilities were stable over time. Initially (2002-2003), females survived better than males, but the following year they suffered a steep decline in survival. Another dramatic reduction was observed between 2006 and 2007 (98 % to 53 %). Male survival rates increased from a low 57.0 % (SE = 12.4, 95 % CI = 33.0-78.1) in 2002 to 91.6 % (SE = 12.2, 95 % CI = 34.0-99.6) in 2003 and remained relatively stable over time.

ANNUAL VARIABILITY IN RECAPTURE RATES

Our most parsimonious model $\varphi(.)$ p(t) fitted the data well (Fig. 4). Recapture rates increased over time from 55.7 % in 2003 (SE = 11.2, 95 % CI = 34.1-75.3) to 84.5 % in 2010 (SE = 7.4, 95 % CI = 64.2-94.3). The lowest annual recapture rate was 45 % in 2004 and the highest rate was 94 % in 2006 and 2009. Recapture probabilities were above 90 % for 2006, 2007 and 2009. There was no evidence of any significant differences in recapture probabilities between the sexes or between the transferred birds and the 'Frégatois'.

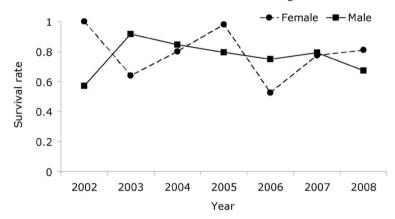


Figure 3b.— Annual variability in survival rates of male and female Seychelles White-eye on Frégate Island.

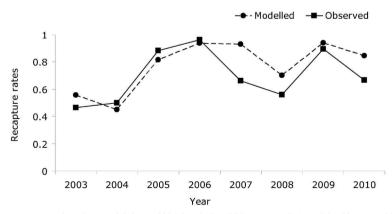


Figure 4.— Recapture rates based on re-sightings of 206 Seychelles White-eyes on Frégate Island between 2001 and 2010.

DISCUSSION

This paper presents the first robust estimates of adult annual survival published for this species. Here, we discuss our survival estimates and compare them with the source population on Conception and with those from other passerines. We also discuss the effects of origin and sex on survival rates, the conservation implications and elements for further research. The influence of survival probabilities on population growth rate (λ) will be examined in another paper.

ADULT SURVIVAL

The adult survival rate calculated for the Seychelles White-eye on Frégate was high (76 %) and constant over time. It compares to values obtained for the species on Conception 81 % (Rocamora & Julliard, unpublished), to other Seychelles passerines as well as reintroduced tropical island birds (over 77 %; Tab. IIa; Brooke, 1985; Currie et al., 2002; Nicoll et al., 2003; Brouwer et al., 2006; Brouwer et al., 2009; A. Cristinacce & Mauritius Wildlife Foundation, pers. comm.) and some other tropical forest passerines from around the world (60 to 82 %; Tab. IIa, Thrine, 1998; Mcgregor et al., 2007; Ricklefs & Shea, 2007; Blake & Loiselle, 2008). The Seychelles White-eye survival rate on Frégate is clearly higher than values for temperate passerines and some tropical continental species like the Yellow White-eye Zosterops senegalensis (Tab. IIa, Chase et al., 1997; Siriwardena et al., 1998; Porneluzi & Faaborg, 1999; Jones et al., 2004; Tinbergen & Sanz, 2004; Mcgregor et al., 2007). Higher survivals recorded for tropical birds as opposed to temperate ones (see reviews in Karr et al., 1990, which challenge this widely accepted concept, and Johnston et al., 1997 which support it) can be linked to the absence of contrasting climatic conditions and to particular life history traits (Martin, 1996; Arnold & Owens, 1998; Russell et al., 2004). High survival rates are also not a surprise for an island bird like the Seychelles White-eye, this being a well known characteristic of the insularity syndrome (MacArthur & Wilson, 1967; Blondel, 1979, 1986). Being both a tropical bird and an island endemic, the Seychelles White-eye clearly fits into these two tendencies. Its high adult survival rate reflects the total absence of introduced mammalian predators, such as cats and rats, which were eradicated from Frégate Island in 1982 and 2000 respectively (Beaver & Mougal, 2009).

The apparent regular increase in survival rates for the Seychelles White-eye on Frégate during the first four years, as the population grew, suggests a density dependent factor but may just be an artefact, as for the drop observed in 2007, since the annual variations recorded were not statistically significant. Other reintroduced populations have shown stability in adult survival rates over the years, like the Mauritius Kestrel *Falco punctatus* (Nicoll *et al.*, 2003), or a decrease like the Seychelles Warbler *Acrocephalus sechellensis* on Aride from an initial 100 %, possibly linked to the increase in density (Komdeur, 1997; Brouwer *et al.*, 2009).

Due to the closed nature of our population (219 ha island isolated by 20 km from the nearest island) we were not faced with the difficulty of separating mortality from permanent emigration since it was realistic for us to assume no dispersal to nearby islands, and we can confidently state that our calculated survival rates are reliable. Hence, an adult survival rate of 76 % appears favourable and suggests that ecological conditions encountered on Frégate Island are suitable for the establishment and long term survival of the introduced Seychelles White-eye population. Also, with the exception of feather mites that we regularly observe when conducting body examination during capture operations on both source and transferred populations, no evidence of any particular disease or other parasites were observed.

SURVIVAL OF JUVENILES

We were not able to realistically model juvenile survival (from fledgling to their first year) due to insufficient data on birds marked at the nest or shortly after fledgling. There is a general belief that juveniles survive less well than adults (Anders & Marshall, 2005; Berkeley *et al.*, 2007). However, empirical data suggests that juvenile Seychelles White-eyes tend to have high survival rates. On Frégate, 24 out of 27 (89 %) White-eyes marked as chicks/fledglings between 2002 and 2008 were re-sighted at one year old, confirming survival to the end of their first year.

Species common name	Species scientific name	Location	Survival rate (%)	Method	Source
Tropical Island birds					
Seychelles Fody	Foudia sechelllarum	Cousin Island, Seychelles 79-83	79-83	Re-sighting probability, Lincoln Index	Brooke, 1985
Seychelles Paradise Flycatcher	Terpsiphone corvina	La Digue, Seychelles	79	Re-sighting probability, unspecified method	Currie et al., 2005
Mauritius Kestrel	Falco punctatus	Mauritius	78	Re-sighting probability, programme MARK	Nicoll et al., 2003
Seychelles Warbler	Acrocephalus sechellensis	Cousin Island, Seychelles	84	Re-sighting probability, programme MARK	Brouwer et al., 2006
Seychelles Warbler	Acrocephalus sechellensis	Cousin Island, Seychelles	83	Re-sighting probability, programme MARK	Brouwer et al., 2009
Seychelles Warbler	Acrocephalus sechellensis	Aride Island, Seychelles	77	Re-sighting probability, programme MARK	Brouwer et al., 2009
Mauritius Fody	Foudia rubra	Ile aux Aigrettes, Mauritius	86-100	Re-sighting probability, direct count	A. Cristinacce & Mauritius Wildlife Foundation, pers. comm.
Tropical passerines					
Variable Sunbird	Cinnyris venustus	Nigeria	96	Re-sighting probability, programme MARK	Mcgregor et al., 2007
Crimson-backed Tanager	Ramphocelus dimidiatus	Central America	82	Ratio method based on Museum collections	Ricklefs & Shea, 2007
Spot-backed Antbird	Hylophylax naevius	Ecuador	73	Capture-recapture, programme MARK	Blake & Loiselle, 2008
Yellow White-eye	Zosterops senegalensis	Nigeria	34	Re-sighting probability, programme MARK	Mcgregor et al., 2007
Scarlet-chested Sunbird	Chalcomitra senegalensis	Nigeria	39	Re-sighting probability, programme MARK	Mcgregor et al., 2007
Temperate passerines					
Wilson's Warbler	Wilsonia pusilla	California, USA	50	Capture-recapture	Chase <i>et al.</i> , 1997
Wood Thrush	Hylocichla mustelina	Southern Illinois, USA	02-09	Capture-recapture	Thrine, 1998
Chiffchaff	Phylloscopus collybita	Great Britain	38	Ring recoveries, programme MARK	Siriwardena et al., 1998
Wren	Troglodytes troglodytes	Great Britain	31	Ring recoveries, programme MARK	Siriwardena et al., 1998
Ovenbird	Seiurus aurocapillus	Central Missouri, USA	52	Re-sighting probability, programme JOLLY	Porneluzi & Faaborg, 1999
Cerulean Warbler	Dendroica cerulean	Ontario, Canada	54	Re-sighting probability, programme MARK	Jones <i>et al.</i> , 2004
Great Tit	Parus major	Netherlands	41	Canture-recanture programme MARK	Tinhergen & Sanz 2004

TABLE IIA

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Species common name	Species scientific name	Location	Survival rate (%)	Method	Source
Tropical birds					
Brown Thornbills	Acanthiza pusilla	Australia	64 (during first 6 weeks)	Re-sighting probability, mixed models	Green & Cockburn, 2001
White-throated Robin	Turdus assimilis	Costa Rica	67 (during first 3 weeks)	Radiotelemetry	Cohen & Lindell, 2004
Seychelles Warbler	Acrocephalus sechellensis	Cousin Island, Seychelles	61 (during first year)	Re-sighting probability, programme MARK	Brouwer et al., 2006
White-throated Tree-creeper Cormabates leucophaea	Cormabates leucophaea	Australia	100 (during first 4 weeks)	Re-sighting, hierarchical generalized	Doerr & Doerr, 2006
linear models					
Puff-throated Bulbul	Alophoixus pallidus	Thailand	61 (during first 8 weeks)	Re-sighting probability, programme MARK	Sankamethawee <i>et al.</i> , 2009
Temperate passerines					
Great Tit	Parus major	Switzerland	53 (during first 3 weeks)	Radiotelemetry, observation probability,	Naef Daenzer et al., 2001
programme MARK					
Swainson's Thrush	Catharus ustulatus	California, USA	25 (during first year)	Re-sighting probability, programme MARK Gardali et al., 2003	Gardali <i>et al.</i> , 2003
Spotted Flycatcher	Muscicapa striata	United Kingdom	46-47 (during first year)	Ring recoveries, programme MARK	Freeman & Crick, 2003
Ortolan Bunting	Emberiza hortulana	Norway	32.2 (during first year)	Capture-recapture	Steifetten & Dale, 2006
Dickcissel	Spiza americana	North America	33 (during first 4 weeks)	Radiotelemetry, Kaplan-Meier procedure	Berkeley et al., 2007

TABLE IIB

Preliminary analysis of juvenile survival rates on the source population (Conception), using similar analytical techniques as the current study, and based on re-sightings and recaptures of 30 Seychelles White-eyes marked as chicks or fledglings between 1998 and 2002, revealed a survival probability as high as for the adults (79 %, Rocamora & Julliard, *unpublished data*) although this result is very imprecise due to extremely high confidence intervals.

Relatively high annual survival rates of fledglings (over 61 %) have been reported for other tropical birds (Tab. IIb; Green & Cockburn, 2001; Cohen & Lindell, 2004; Brouwer *et al.*, 2006; Doerr & Doerr, 2006; Sankamethawee *et al.*, 2009). Juvenile survival rates reported for temperate passerines are much lower than for tropical species (25 to 53 %; Table IIb; Naef Daenzer *et al.*, 2001; Freeman & Crick, 2003; Gardali *et al.*, 2003; Steifetten & Dale, 2006; Berkeley *et al.*, 2007). There is sufficient evidence to support the increased survivorship of tropical juvenile birds, often explained by their life history traits such as prolonged parental care and natal philopatry (Martin, 1996; Russell *et al.*, 2004). The Seychelles White-eye is a cooperative breeder and fledglings remain dependent on adults for up to 6 weeks (Rocamora *et al.*, 2002) which may contribute to their increased survivorship.

Juvenile survival of tropical birds after a reintroduction has been reported in some cases to increase with time, as for the Mauritius Fody *Foudia rubra* (33 %, 61 % and 75 % during the first three years; Cristinacce *et al.*, 2009), and the Mauritian Olive White-eye *Zosterops chloronothos* on Ile aux Aigrettes: 56 %, 67 % and 100 %, (Mauritius Wildlife Foundation Passerine reports; MWF, *pers. comm*); or either to decrease over the years as for Seychelles Warbler on Aride (68 % on average, higher during the first three years; Brouwer *et al.*, 2009) or for the Mauritius Kestrel due to climatic variations or density dependence (60-73 % down to c.35-45 %; Nicoll *et al.*, 2003).

More monitoring data are needed on marked chicks/fledglings to determine reliable and robust juvenile Seychelles White-eye survival rates through modelling, but such data collection is logistically difficult on Frégate Island, where a combination of high closed-canopy forests, difficult terrain and the cryptic and passive nature of fledglings render it difficult to access nestlings or attract fledglings into mist-nets.

INFLUENCE OF ORIGIN AND SEX ON ADULT SURVIVAL RATES

The 'Frégatois' seem to survive better than the transferred birds although this difference is not significant. The greater fluctuations observed in survival rates of the 'Frégatois' stabilized over time to a level similar to the transferred birds. Both groups survive well on Frégate where ecological conditions are suitable (ample space, 90 ha of favourable habitats, low avian interspecific competition, lack of introduced predators). High survival values recorded during the first three years of the 'Fregatois' adult life and the subsequent drop may reflect the fact that all the 'Frégatois' were young during that period and hence less prone to mortality, compared to after the first four years, when relatively old Frégatois appeared in the population.

Generally, survival in birds is thought to be higher in males than in females (Breitwisch, 1989; Donald, 2007) but this was not supported by our data where no significant difference in sex-specific survival was observed. On the source population of Conception, there were no significant differences between male and female survival between 1999 and 2002 (Rocamora & Julliard, unpublished). Survival probabilities also did not differ between sexes for the Seychelles Warbler on Cousin between 1986 and 2004 (Brouwer et al., 2006). Female survival appeared to fluctuate more over time compared to males, possibly because having to lay the eggs, they spend more time incubating (Rocamora & François, 2000) and may be more sensitive to adverse external factors such as higher predation risks. Initially, female white-eyes survived better than males on Frégate. Such a high survival (90 % due to 9 out of 10 females that survived) has been of extreme importance since only a small number of females were initially transferred to Frégate. However, the steep decline to 64 % and 53 % in 2003 and 2006 respectively and the observed fluctuations in survival rates (although not significant) are of concern because even small differences in survival may have serious consequences on population dynamics. This highlights the potential very negative effects that mortality linked to stochastic events may have on small transferred populations at early stages of colonization. Interestingly, a further addition of 6 females in 2003 to balance the sex ratio did not change the female survival rates (modelling was done with and without the 6 females). Contrarily, a higher mortality rate was observed for the males during the first year after the transfer. A total of nine males died compared to only one female by the end of 2002. We have no evidence of the causes of such a higher mortality amongst males.

PROBABILITY OF DETECTION

Generally, the probability of detecting a White-eye was high $(80 \% \pm 5 \%)$, indicating that we rarely failed to detect a marked individual present in the study area. Considering that we are studying a small localized population (31 in 2001 to 130 in 2010), recapture through direct surveys provided a robust method to identify and count number of individuals. As we provided a substantial (and apparently sufficient) searching effort (one main survey of 8-13 days between January and March, in addition to 2-3 days of annual island-wide survey, and 3-6 extra annual monitoring visits of 2-7 days each), most birds present in the study area had the same probability of being re-sighted. Although Seychelles White-eyes are small with cryptic colouration, the intensive nature of direct surveys allows for their detection.

CONSERVATION IMPLICATIONS AND FURTHER RESEARCH

Long-term monitoring of the Seychelles White-eye population on Frégate will help to identify any trends in survival probabilities, providing better assessments and insights into limiting factors and their influence on the dynamics of the introduced population. Knowledge of the processes by which such introductions progress is a vital aspect of conservation ecology. This study illustrates that with efficient data collection, analysis of survival can be a good complement to the analysis of population trends, and a useful tool to monitor populations of special conservation concern.

High juvenile and adult survival rates are keys to a successful conservation introduction, but another critical factor in successful establishment of introduced populations of the Seychelles White-eye is the nesting success. This was closely monitored during the first eight months of the establishment phase and was as high as 1.25 fledgling/nest with eggs compared to only 0.42 fledglings/nest with eggs on Conception (Rocamora *et al.*, 2002). Such monitoring could not be continued thereafter although some productivity measurements were done occasionally for some territories between 2003 and 2010.

Future identification of factors that influence nesting success as well as juvenile and adult survival on rehabilitated islands is desirable, depending on the island's species composition (avian, reptiles or invertebrate egg and chick predators).

On Frégate, potential nest predators include native reptiles and large invertebrates (Wolf Snake *Lycognarhophis seychellensis*, House Snake *Boaedon geometricus*, Wright Skink *Mabuya wrightii* and Centipede *Scolopendra subspinipes*) and the invasive Indian Mynah *Acridotheres tristis*. Eradication attempts of the Indian Mynah have been conducted on various islands (Feare, 2011) and it was recently successful on Frégate Island (Canning, 2011).

On Cousine Island where there is another transferred Seychelles White-eye population, potential nest predators also include native birds; the Seychelles Magpie Robin *Copsychus sechellarum* has been reported to kill Seychelles White-eye fledglings and possibly an adult (Jolliffe & Henwood, 2008; Jolliffe *et al.*, 2008) and the Seychelles Fody *Foudia sechellarum* is a known egg-predator of the Seychelles Warbler and seabirds (Komdeur & Kats, 1999) (both birds also present on Frégate boot at much lower densities). On Conception, suspected nest predators include the Seychelles Kestrel *Falco araea* and the Green-backed Heron *Butorides striatus* (Rocamora & François, 2000 and *pers. obs*). Identification of factors that influence nest success and survival rates (juvenile and adult) in transferred populations could play an important part in selecting islands for future translocations; in addition to assessing potential nest predators or species competitors from the composition of the island's faunal community.

For future research, we recommend the continued collection of data through direct systematic surveys in territories plus opportunistic re-sightings by trained personnel conducting other monitoring activities to detect floating individuals, along with increased efforts to estimate juvenile survival rates which will lead to more accurate assessments of population status. This greater accuracy will facilitate the identification of factors limiting the population and will provide a better understanding of where we should focus our conservation efforts. We also recommend carefully designed monitoring protocols which will allow for proper and timely data collection, easing data treatment and analysis. Similar efforts to calculate adult and juvenile survival rates of other tropical passerines will contribute to the apparent deficit of knowledge on life history traits of tropical island birds. As evidenced with other threatened island birds requiring similar conservation management (see for example Nicoll *et al.*, 2003; Brouwer *et al.*, 2009 and other case-studies in Soorae, 2008, 2010), close monitoring of transferred populations of the Seychelles White-eye offers further opportunities to serve as a model for future passerine reintroduction projects and to better understand fundamental principles of population dynamics and ecology.

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