

JOURNAL OF AVIAN BIOLOGY

Research article

First demographic insights reveal high extinction risk of an endemic raptor species: the Reunion harrier

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Journal of Avian Biology

2023: e03112

doi: 10.1111/jav.03112

Subject Editor: Wesley Hochachka

Editor-in-Chief: Jan-Åke Nilsson

Accepted 8 May 2023



Gathering demographic information on rare species is critical to understanding their population dynamics and implementing efficient conservation measures. Using integrated models, we jointly analyzed multiple data sets, including capture–recapture, GPS tracking and nest monitoring data collected over the last 10 years, to provide the first demographic insights for one of the world's rarest raptors, the endemic Reunion harrier *Circus maillardi*. We estimated key demographic rates including annual survival and breeding parameters (clutch size, hatching and fledging success), and used population projection models to assess population growth rate and quasi-extinction risk. In order to guide future conservation actions for the population, we evaluated the effects of different management scenarios that improve survival, fecundity, or both, on population growth and quasi-extinction risk. Comparison of the estimated annual survival (juvenile and subadult survival: 0.66; adult survival: 0.71) and breeding parameters (clutch size: 2.3; hatching success: 0.45; fledging success: 0.83) with those of other harrier species suggests that adult survival and breeding parameters of Reunion harriers are low. A small data set collected 40 years ago suggests that the probability of an egg producing a fledgling was higher and has declined to the current low level. The population models project that the Reunion harrier population is declining and faces a high risk of quasi-extinction in the next 40 years. Only management measures that simultaneously improve adult survival and fecundity could lead to a recovery of the population. These alarming results call for immediate conservation action aimed at rapidly improving the demographic rates.

Keywords: *Circus maillardi*, extinction, fledging success, hatching success, population growth rate, population viability, survival

Introduction

Raptors are iconic bird species with half of the 557 species showing declining population trends and 18% of them is classified as 'Vulnerable', 'Endangered' or 'Critically



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Endangered' on the IUCN red list (McClure et al. 2018). The vulnerability of raptors to extinction is linked to their large body size and slow life history strategy, resulting in smaller population sizes and longer generation times than other bird species such as passerines. These life history characteristics make them particularly sensitive to global change and especially to increasing mortality (Lee and Jetz 2011, Chichorro et al. 2019). Unfortunately, these top predators are still subject to persecution because they are often perceived as competing with humans for game species, and can prey on small livestock (McClure et al. 2018). Raptor species with small distribution ranges and reliance on tropical forests are often of greatest conservation concern (McClure et al. 2018). However, these species are the least studied to date (Buechley et al. 2019), compromising our ability to develop targeted conservation plans (Sutherland et al. 2004, Martin et al. 2012).

Collecting demographic data that allow the estimation of demographic rates (e.g. survival and reproductive success) is particularly important for building population models to understand population dynamics (Caswell 2001, Fay et al. 2019). These models allow researchers to assess the current population status and to predict future population trends (Weimerskirch et al. 1997, Schaub et al. 2010, Wilson et al. 2016). Furthermore, they enable study of demographic mechanisms underlying population changes and the projection of populations under different management scenarios, which is critical to making smart management decisions (Beissinger and Westphal 1998). However, collecting the robust demographic information needed to inform population models is often challenging, particularly for rare and inconspicuous species such as certain raptors. For such species, it is typical that only small datasets are available, collected over a short period of time and limited to a few demographic rates. Recently, the development of integrated analyses provides new opportunities to study population dynamics in these situations (Zipkin and Saunders 2018, Schaub and Kéry 2022). They allow an efficient use of the available data, such as reproductive data, GPS tracking or capture–mark–recapture, by analyzing them jointly in a single model. Advantages of integrated analyses are that they properly account for uncertainty in parameter estimates, increase the precision of parameter estimates and allow the estimation of additional demographic parameters for which data have not been explicitly collected (Schaub and Kéry 2012).

This study aims to better understand the demography and population dynamics of the Reunion harrier *Circus maillardi*, one of the world's rarest raptors (IUCN 2022). This originally forest-dwelling species is endemic to the tropical island of La Reunion and has declined sharply over the last century as a result of anthropogenic mortality and habitat loss (Bretagnolle et al. 2000, Grondin and Philippe 2011). The Reunion harrier is currently listed as endangered on the IUCN red list due to its small but stable population size (IUCN 2022). A recent study has shown that this harrier is highly exposed to pesticides (anticoagulant rodenticides), which are found in 93% of harrier carcasses examined

(Coeurdassier et al. 2019). Recent population surveys have also questioned the stability of the breeding population, suggesting that the population may have been declining over the past 20 years (Villers et al. unpubl.). If the small harrier population is indeed declining, it may deserve a higher red list status (critically endangered). Unfortunately, the species is poorly studied and we urgently need more information, especially on its demography and population dynamics.

Here we have attempted to clarify the current status of the Reunion harrier population by estimating demographic rates, which are used to assess the viability of the population. Three different sets of demographic data (capture–mark–recapture, GPS tracking, breeding monitoring) have been collected over the last decade. We jointly analyzed these fragmentary data to build up a population model and better understand population dynamics. Our aim was to fill the gaps in our understanding of the dynamics of the Reunion harrier population by achieving three objectives: 1) to estimate survival and reproductive rates, 2) to assess population growth rates and the risk of quasi-extinction and 3) to identify the possible effects of different management scenarios aimed at improving demographic rates on population trends.

Material and methods

Study species and study area

The Reunion harrier *C. maillardi* is the last breeding raptor on the island of La Reunion, a volcanic tropical island that forms part of the Mascareignes archipelago in the south-west Indian Ocean. Reunion harriers occupy a wide range of habitats from open or semi-open landscapes, including degraded forests, shrublands, savannah, cultivated (sugar cane) fields and pastures, but also denser native forests of steep ravines (Clouet 1978, Bretagnolle et al. 2000). Their original diet probably consisted only of birds, reptiles and insects, but now includes a large proportion of introduced small mammals, especially rats *Rattus rattus* and mice *Mus musculus* (Clouet 1978), which may be the predominant prey in some locations (Augiron 2022). Reunion harriers build nests on the ground, hidden in the vegetation. Two to three eggs are laid and incubated for 33–36 days by the female, who is fed by the male during incubation. Both partners participate in the rearing of the chicks. The young fledge at the age of about 45 days, and usually, are fed by the male for at least two more months.

We monitored Reunion harriers at two study sites located in the municipalities of Bras-Panon (21°01'S, 55°40'E) and Saint-Benoit (21°04'S, 55°41'E), in the north-east of Reunion Island. These two sites, which together support an average of 12 pairs per year, are composed of a mosaic of natural and agricultural (mainly sugar cane) vegetation, including many areas of wasteland and degraded native and secondary forests at altitudes between 30 and 350 m. The breeding density of the harrier is one of the highest recorded on the island, suggesting that the study sites provide relatively favorable habitats for the species (Augiron 2022).

Data collection

We collected data on breeding ecology across 10 years (2013–2022). Each year, we located breeding pairs and their nests, which were visited repeatedly, usually once every two or three weeks, on foot or by drone to record clutch size and the numbers of hatchlings (brood size) and fledglings. We found a total of 65 active nests (i.e., nests with at least one egg or one chick). The information collected allowed the estimation of clutch size, hatching success (number of eggs hatched/number of eggs laid) and fledging success (number of fledglings/number of eggs hatched). Each year, most nestlings were ringed at a minimum age of 30–40 days ($n=24$) with an aluminium ring on the tarsus and a wing-tag attached to each patagium. In addition, a total of 13 subadults and 12 adults were captured using clap traps, pole traps or whoosh nets, and marked with rings and wing tags. These marked individuals were visually resighted over the years. From 2017 to 2021, 25 individuals (11 juveniles, 3 subadults and 11 adults) were tagged with GPS transmitters (OrniTrack-20 gr – solar powered GPS-GSM/GPRS transmitter ©Ornitela) that were affixed using wing harnesses. Seven of these birds had been previously marked. Individuals with GPSs were either followed until their death ($n=8$), or their data were right censored because they were still alive at the end of the study period ($n=10$) or because of tag failure and unknown fate ($n=7$). Chicks and individuals in their first plumage were sexed based on their mass and size, and adults were sexed based on their plumage coloration. In total, we have marked 36 males (21 and 15 for wing-tags only and GPS trackers, respectively) and 30 females (20 and 10).

Data analysis

We built an integrated model to jointly analyze capture–mark–recapture data, GPS tracking and breeding monitoring. We did not include abundance data, and therefore did not fit a more complex integrated population model (IPM, Schaub and Kéry 2022), because of the relatively large uncertainty in the number of breeding pairs (the breeding status of pairs is often uncertain) and of the lack of knowledge of several key parameters (age at first reproduction and annual breeding probabilities). Furthermore, the sample sizes were modest, making the estimation of hidden parameters (e.g. immigration and emigration), which would be conceptually possible by using an IPM, highly uncertain and possibly even biased (Paquet et al. 2021, Plard et al. 2021). We have therefore preferred to keep our integrated model relatively simple assuming a population closed to immigration and emigration. We discussed the potential effect of immigration and emigration on our results.

Estimation of survival

We estimated survival from a joint analysis of capture–resighting data and GPS encounter data. We fitted the model in a Bayesian framework because it allows for the joint modeling of different data sets in a convenient way (Schaub and Kéry 2022).

The capture–resighting data were analysed with a Cormack–Jolly–Seber model (Lebreton et al. 1992), where apparent survival was modelled with a Bernoulli distribution as:

$$Z_{it} \sim \text{Bernoulli}(S_{it}^{\text{CMR}} \times Z_{it-1})$$

$$S_{it}^{\text{CMR}} = \text{logit}^{-1}(\Phi_{\text{age} \times \text{sex}})$$

where Z_{it} is the latent survival state of individual i from year $t-1$ to year t ($0 = \text{dead}$, $1 = \text{alive}$), S_{it}^{CMR} is the survival probability from year $t-1$ to year t and $\Phi_{\text{age} \times \text{sex}}$ is the age- and sex-specific logit transformed annual survival probability. We distinguished three age classes for survival: juvenile (from fledging to one-year-old, S_0), subadult (one- to two-years-old, S_1) and adult ($\geq$ two-years-old, S_2). Conditional on survival, individual i can be resighted in year t modelled with an additional Bernoulli process:

$$R_{it} | (Z_{it} = 1) \sim \text{Bernoulli}(\text{logit}^{-1}(p_{t+\text{sex}}))$$

where R_{it} is the resighting data of individual i in year t and $p_{t+\text{sex}}$ is the logit transformed resighting probability. The resighting probabilities were assumed to be different during the two time periods 2013–2015 and 2016–2022 corresponding to two levels of sampling effort. During the first period, resightings were opportunistic, whereas from 2016 onwards, observations were made monthly from fixed points distributed across the study area. We also assessed an additive sex effect on resighting probability, as sex-specific coloration and behavior may generate sex-specific detection probability.

The GPS encounter data W were converted to individual encounter histories on a monthly basis ($0 = \text{dead}$, $1 = \text{alive}$, $\text{NA} = \text{censored}$). We assumed an encounter probability of one, and modelled survival with a Bernoulli distribution:

$$W_{it} \sim \text{Bernoulli}(S_{it}^{\text{GPS}} \times W_{it-1})$$

$$S_{it}^{\text{GPS}} = \text{logit}^{-1}(\Phi'_{\text{age} \times \text{sex}})$$

where S_{it}^{GPS} is the survival probability from month $t-1$ to month t and $\Phi'_{\text{age} \times \text{sex}}$ is the age- and sex-specific logit transformed monthly survival probability. The annual survival probabilities were calculated from the monthly survival probabilities as $S_{it}^{\text{CMR}} = S_{it}^{\text{GPS}^{12}}$. We did not consider temporal variation in survival due to the small sample size.

Estimation of breeding parameters

We estimated the mean clutch size (CS) and present the frequency distribution of the collected data. Hatching success (HS) and fledging success (FS) were each modelled with a binomial distribution:

$HS_i \sim \text{Binomial}(n_i, \alpha)$ with $\text{logit}(\alpha) = \mu_{HS} + \varepsilon_{\text{nest}}$ and $FS_i \sim \text{Binomial}(HS_i, \gamma)$ with $\text{logit}(\gamma) = \mu_{FS} + \varepsilon_{\text{nest}}$. Here HS_i and FS_i are the number of eggs hatched and of chicks fledged, respectively, in brood i , n_i is the clutch size of brood i , μ_{HS} and μ_{FS} are the estimated mean hatching and fledging success, respectively, on the logit scale, and $\varepsilon_{\text{nest}}$ and $\varepsilon_{\text{nest}}$ are the nest random effects. As for survival, we did not account for temporal variation in breeding parameters due to the small sample size. We did not use the Mayfield method (Dinsmore et al. 2002) to estimate nest success because the nest status (i.e. active or failed) was often uncertain. Indeed, failed nests often contained unhatched eggs (see discussion) making it difficult to determine the nest status during visits. Moreover, as nests were usually monitored from the time of pair formation, nest failures prior to nest discovery are likely to be rare and therefore the estimates of breeding success are unlikely to be greatly overestimated.

Finally, we compared current breeding parameters with historical data collected 40 years ago. Clouet (1978) reported on the monitoring of seven nests of Reunion harriers in 1975 and 1976 at the Montagne Saint-Denis site, approximately 30 km from our study site. The information collected was clutch size and the number of fledglings. We compared the mean clutch size and egg success, i.e. the probability that an egg will produce a fledgling (i.e. $HS \times FS$), between our study and this historical dataset to assess a change in reproductive performance (Supporting information).

Matrix population model

Based on the estimated demographic rates, we parameterized a pre-breeding female-based census matrix population model (Caswell 2001). The model included two age classes corresponding to sub-adult (one-year-old) and adult ($\geq$ two-years-old) individuals and considered a one-year time step. Recruitment was calculated as the product of clutch size, hatching success, fledging success and juvenile survival, assuming a balanced sex ratio (0.5). Age at first reproduction could not be accurately estimated from our data. Based on information from the closely related marsh harrier *Circus aeruginosus* (Bavoux et al. 1995), we assumed that one-year old individuals do not yet reproduce, but once females are two years old, they may reproduce each year. Field observations show that replacement clutches are rare in Reunion harriers and we therefore assumed that there is only one breeding attempt per year. Field observations also suggest that the breeding probability (BP) may be less than one. Unfortunately, our data do not allow a formal estimate of breeding probability. However, a rough minimum estimate of breeding probability is the proportion of pairs that are known to have laid a clutch out of all identified breeding pairs in the same year. We found that the breeding probability in the study population was unlikely to be less than 0.6. In our population model, we therefore included different breeding probabilities ranging from 0.6 to one, assuming that the true (unknown) value is within this range. Finally, we did not include emigration and immigration hence we assumed that this population was geographically closed. We discuss some

of the necessary assumptions and their potential impact on our results in the discussion section.

The final matrix projection model was:

$$\begin{bmatrix} N_1 \\ N_2 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & BP \times CS \times HS \times FS \times S_0 / 2 \\ S_1 & S_2 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}_t \quad (1)$$

Using standard methods presented in Caswell (2001), we computed several demographic metrics from the population matrix model: asymptotic deterministic population growth rate (λ), net reproductive rate (R0, defined as the mean number of female offspring produced by a female over her lifetime), generation time (mean age of mothers that reproduce) and the stable age distribution (proportion of each age class). We also conducted a prospective perturbation analysis to assess the impact of changes in the demographic parameters on the population growth rate. We calculated the elasticity of the asymptotic deterministic growth rate to each demographic parameter, which assesses the effect of a proportional change in one demographic parameter on λ when the other demographic parameters are held constant (Caswell 2001). We have calculated posterior distributions of all these derived demographic metrics from the posterior distributions of the demographic parameters. Their uncertainties therefore reflect the uncertainties in our estimated demographic parameters. As we did not have an accurate estimate of breeding probability which is a key component of fecundity, we also assessed the sensitivity of the demographic metrics to changes in breeding probability.

Quasi-extinction risk and management scenarios

To assess the viability of the studied population, we simulated population dynamics based on the matrix model described above. The initial population size was 200 females, which corresponds to the most recent estimates of the breeding population size (2017–2019, Villers et al. unpubl.). Due to the small size of the studied population, we incorporated demographic stochasticity by assuming a Poisson distribution for fecundity (i.e. for the total number of one-year-old females produced) and a Binomial distribution for survival. We ran 1000 independent simulations, each projecting 100 years of population dynamics. We recorded the probability of quasi-extinction over these 1000 simulations using a threshold of < 4 females. This is an arbitrary threshold suggesting that a demographically closed population of three or fewer females is doomed to extinction in the short term. We found it more relevant to assess the quasi-extinction risk than strict extinction risk, as the latter tends to overestimate population persistence.

We evaluated the effects of different management scenarios on the asymptotic deterministic growth rate and quasi-extinction risk to guide future management of the population. The management scenarios considered focused on adult survival and hatching success. This focus is motivated by the high elasticity of the population growth rate to changes in adult survival and by the very low hatching success (see results and discussion). We considered management scenarios that increased adult survival only, hatching success only or both simultaneously. According to

the allometric relationship for survival in diurnal raptors (Newton 2016), we can expect an average annual adult survival of about 0.77 for the Reunion harrier. However, given the slow life history of this species and its tropical location, a higher survival value of around 0.8 seems equally plausible (see discussion). We therefore used two survival values, 0.77 and 0.83, which we will refer to as medium and high, respectively. For hatching success, we considered two values, 0.70 and 0.90, to reflect the range of values published in the literature for other harrier species (Curtis et al. 2004, Sternalski et al. 2013, Wiącek 2015).

Model implementation

Analyses were conducted in R (www.r-project.org) and JAGS (Plummer 2003) via the R package jagsUI (Kellner 2016). For parameter estimation, we specified weakly informative priors for all estimated parameters. We used the uniform distribution on the interval [0, 1] as priors for all demographic parameters. We confirmed parameter convergence by visual inspection of trace plots and by using the Gelman–Rubin statistic (Brooks and Gelman 1998). We report posterior means and 95% credible intervals. To determine the most parsimonious survival model, we compared models using the widely applicable information criterion (WAIC, Watanabe 2010), a fully Bayesian information criterion used to measure the predictive accuracy of a model. Matrix population metrics were calculated using the R package ‘popbio’ (Stubben and Milligan 2007).

Results

Survival and breeding parameters

Model selection suggested that subadult survival was indistinguishable from juvenile survival and did not support sex effects for either survival or resighting probabilities (Table 1). Mean resighting probabilities were 0.55 and 0.82 depending on the level of monitoring effort. Mean annual survival probabilities were estimated to be 0.66 [0.50, 0.80] for juveniles and subadults, and 0.71 [0.56, 0.84] for adults. Survival estimated from CMR data tended to be lower than survival estimated from GPS data: 0.61 [0.46, 0.77] and 0.67 [0.52, 0.81] vs 0.69 [0.47, 0.88] and 0.83 [0.63, 0.94] for juveniles and subadults, and adults, respectively. We note that considering the GPS data independently of CMR data may have resulted in a slight overestimation of adult survival due to censored histories.

The mean clutch size was 2.3 eggs ($n=46$ nests) and ranged from one to three eggs. The most common clutch size was two (48%), followed by three (41%) and one (11%). The average hatching and fledging success were 0.45 [0.31, 0.59] ($n=38$ nests and 92 eggs) and 0.83 [0.67, 0.96] ($n=40$ nests and 63 chicks), respectively (Table 2). Focusing on successful clutches and broods, i.e. those where at least one hatchling or one fledgling was observed, the mean hatching and fledging success were 0.63 [0.50, 0.75] ($n=26$ nests and 68 eggs) and 0.89 [0.78, 0.96] (34 nests and 53 chicks), respectively.

Table 1. Model selection to assess the effect of age and sex on annual survival of Reunion harriers (2013–2022). The number of mathematical parameters (k), the widely applicable information criterion (WAIC) and the difference in WAICs between the current and the best model within each sub-set of models (Δ WAIC) are shown. The final selected model is highlighted in bold. Model notations: ‘juv’: juvenile, ‘subad’: subadult, ‘ad’: adult, ‘=’ equal survival, ‘/’ different survival, ‘+’: additive effect, ‘*’ interactive effect.

Model	k	WAIC	Δ WAIC
Resighting process			
p_{time}	8	599.4	0
$p_{\text{time+sex}}$	9	604.3	4.9
Survival process: age effect			
$\Phi_{(\text{juv}=\text{subad},\text{ad}) \times \text{sex}}$	6	593.1	0
Φ	6	595.6	2.5
$\Phi_{(\text{juv},\text{subad},\text{ad}) \times \text{sex}}$	8	599.4	8.3
Survival process: sex effect			
$\Phi_{\text{juv}=\text{subad},\text{ad}}$	4	587.9	0
$\Phi_{(\text{juv}=\text{subad}) \times \text{sex}+\text{ad}}$	5	589.7	1.8
$\Phi_{(\text{juv}=\text{subad},\text{ad})+\text{sex}}$	5	590.4	2.5
$\Phi_{(\text{juv}=\text{subad},\text{ad})+\text{ad} \times \text{sex}}$	5	591.1	3.2
$\Phi_{(\text{juv}=\text{subad},\text{ad}) \times \text{sex}}$	6	593.1	5.2

The mean number of hatchlings in successful clutches was 1.6 ($n=40$ nests) and the mean number of fledglings in successful broods was 1.4 ($n=34$ nests). Finally, the probability of an initiated clutch resulting in at least one fledgling was 0.46 [0.32, 0.60].

The mean clutch size observed 40 years ago (Clouet 1978) was slightly higher than that observed during our study period (2.7 vs 2.3). Given the frequency of clutch sizes in our population, the probability of observing a mean clutch size equal to or greater than 2.7 based on the sample size of Clouet was 0.08. During our study period, the probability of an egg producing a fledgling was 0.25 [0.14, 0.36], whereas in 1975 it was 0.53 [0.24, 0.80] (Fig. 1). Hence, these results suggest that current clutch size is slightly lower and current breeding success substantially lower than in the past.

Population models

Assuming a breeding probability of 0.9, which is in the upper range of likely values (i.e. an optimistic value), the population grew at an average annual rate of 0.89 and achieved a net lifetime reproductive rate of 0.57 offspring per female (Table 2). The median generation time was five years and the population consisted of 22% subadults and 78% adults at the start of the breeding season. Perturbation analyses showed that the population growth rate was about four times more sensitive to a change in adult survival than to the same relative change in fecundity or juvenile and subadult survival (Table 2). Population growth rate and all other demographic characteristics were weakly affected by the assumed value of breeding probability (Supporting information). Population projections showed that the observed survival and breeding parameters were too low to support a viable population. Assuming that our study population is representative of the total population (see discussion), the projected total population size declines sharply and faces a high risk of quasi-extinction (Fig. 2). After 30 years,

Table 2. Posterior means, posterior SD and 95% credible intervals (CRI) of demographic traits estimated for the Reunion harrier (2013–2022).

Demographic traits	Mean	SD	95% CRI
<i>Parameters estimated from population monitoring</i>			
Juvenile and sub-adult survival	0.66	0.08	0.50, 0.80
Adult survival (> two-year-old)	0.71	0.07	0.56, 0.84
Clutch size	2.30	NA	NA
Hatching success	0.45	0.07	0.31, 0.59
Fledging success	0.83	0.08	0.67, 0.96
<i>Parameters derived from the matrix population model (assuming a breeding probability of 0.9)</i>			
Deterministic population growth rate	0.89	0.07	0.75, 1.04
Net reproductive rate	0.57	0.25	0.27, 1.22
Generation time	5.02	0.94	3.79, 7.40
Scaled stable age distribution: subadults	0.22	0.03	0.16, 0.28
Scaled stable age distribution: adults	0.78	0.03	0.72, 0.84
Elasticity: juvenile survival and fecundity*	0.17	0.03	0.11, 0.24
Elasticity: subadult survival	0.17	0.03	0.11, 0.24
Elasticity: adult survival	0.65	0.07	0.52, 0.78

*Note that the elasticity of fecundity and of all breeding parameters (breeding probability, clutch size, hatching success and fledging success) are equal since the former is defined as the product of the latter.

the quasi-extinction risk is > 0.2 and reaches 0.9 after 50 years (Fig. 2). Considering the case of a local population, the immigration needed to maintain the population is very important. Each year, between 10 and 20% of the breeding females should be new immigrants which means that in the long-term between 40 and 60% of the local breeding females in the population are originally immigrants (Supporting information).

Management scenarios

Increasing only adult survival or only hatching success is unlikely to reverse the negative population trend (Fig. 3). In most of these scenarios, the quasi-extinction risk over 100 years was high (> 0.5) (Fig. 3). The only scenarios compatible with population persistence over the next 100 years were those with very large increases in survival (from 0.71 to 0.83) or hatching success (from 0.45 to 0.90), coupled with high

breeding probability (> 0.80). Only simultaneous increases in survival and of hatching success resulted in population growth rates greater than one and significantly reduced quasi-extinction risks, regardless of the value of breeding probability. Furthermore, the increases in survival and hatching success must be substantial as a 50% increase in hatching success (increase from 0.45 to 0.70) combined with an increase in adult survival from 0.71 to 0.77 is not sufficient to achieve positive population growth when breeding probability is < 0.80 .

Discussion

We jointly analyzed capture-recapture, GPS tracking and nest monitoring to study, for the first time, the demography and population dynamics of the endangered and endemic Reunion harrier. Controlling for the uncertainties in

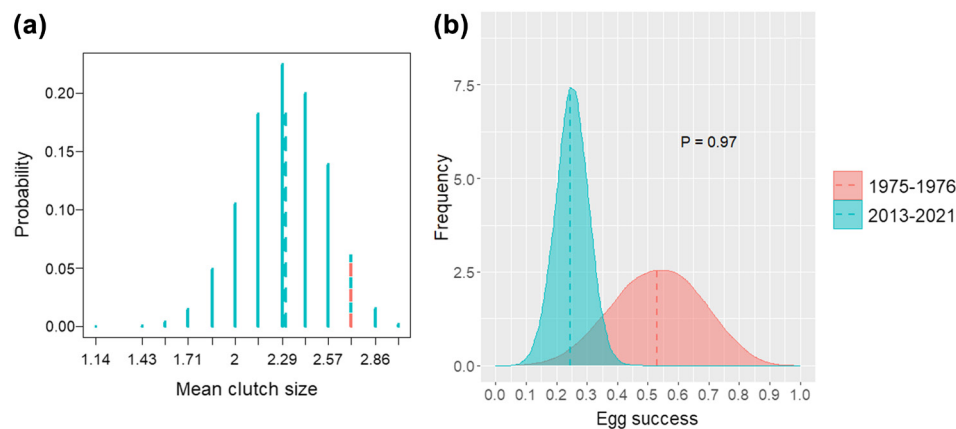


Figure 1. Comparison of mean clutch size and egg success between two periods: 1975–1976 (Clouet 1978) and 2013–2022 (this study). (a) Simulated mean clutch size distribution based on the clutch size frequency observed in our study and the sample size of Clouet (1978). (b) Posterior distribution of the mean egg success probability (i.e. probability that an egg will produce a fledgling) in the two periods. P is the probability that the egg success observed in our study was lower than that reported by Clouet (1978). For both plots, the dashed red and blue lines indicate the average reproductive trait during the two periods.

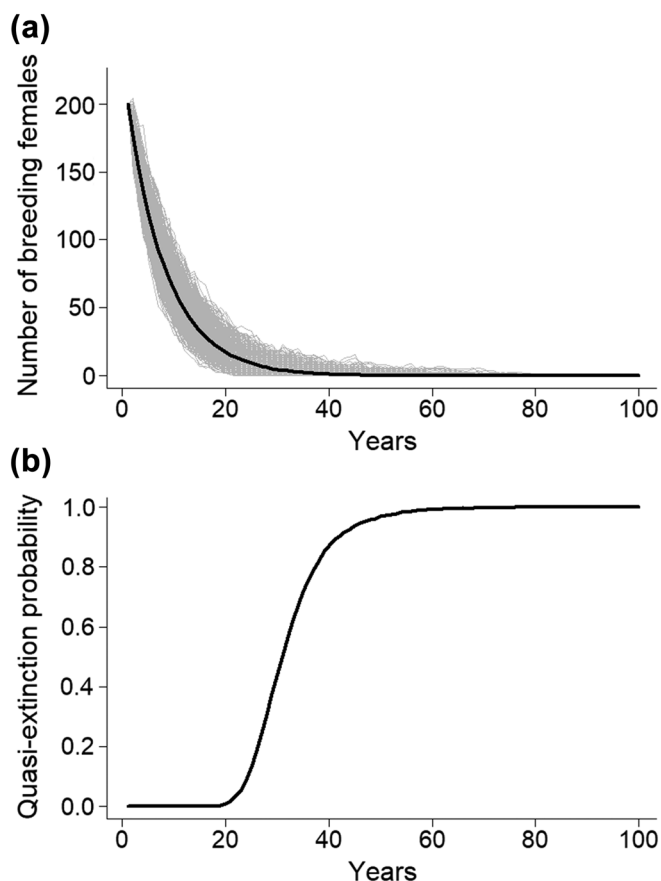


Figure 2. Population projections over 100 years (a) and quasi-extinction probability (population size < 4) (b) for the Reunion harrier population. For these projections, we assumed a breeding probability of 0.9. For panel a, dark solid lines show the mean number of females over 1000 simulations and gray lines show all the population projections.

estimating demographic parameters and future population size, our analyses clearly indicate that the Reunion harrier population is at high risk of quasi-extinction in the medium term. Below, we compare our demographic estimates with those of other harrier species and discuss the robustness of our conclusions. We also discuss possible causes of the observed population decline and management actions that could be taken to improve the population status of the Reunion harrier.

Demographic rates

The results show that the Reunion harriers have a low fecundity, with an average of 0.9 chicks produced per breeding attempt (i.e. per clutch laid). Fecundity is made up of several components and each of these could have contributed to this low value. The average clutch size of Reunion harriers was low, typically two or three eggs, much lower than the clutch sizes of other harrier species, which are typically between three and five eggs (Table 3). The low clutch size of Reunion harriers could be interpreted as an evolution towards a slower pace

of life, a recurrent pattern for insular species also observed in the very close relative, the endemic Madagascar harrier *Circus macrosceles* (Covas 2012, René de Roland et al. 2004). The hatching success of 0.45 for Reunion harriers is low compared to all other harrier species (Table 3). Even in successful clutches, the hatching success of an egg was only 0.63, which is much lower than typical hatching successes observed in birds (0.9 based on eggs incubated to term, Spottiswoode and Möller 2004, Hemmings and Evans 2020). Unhatched eggs were frequently found with no sign of embryonic development (Augiron 2022), suggesting that either infertile eggs or early embryonic mortality are the main reasons for the low hatching success. Unfortunately, we are currently unable to determine which of the two is the main cause. Finally, the observed fledging success of 0.83 is within the range of values observed for other harriers (Table 3) as well as other raptors (McDonald et al. 2004, Nägeli et al. 2022) indicating that the current low fecundity of Reunion harriers is mainly due to the low hatching success. Comparison with the historical data shows that past and current clutch size distributions are close, but the breeding success used to be higher and declined to the current low levels over the past 40 years (Fig. 1).

Our estimate of juvenile survival (0.66) was within the higher range of juvenile survival observed for other medium-sized raptors, such as the red kite *Milvus milvus* (mean = 0.55, min = 0.37, max = 0.80, Sergio et al. 2021, Pfeiffer and Schaub 2023). In contrast, adult survival (0.71) appeared to be lower than expected based on an allometric relationship (Newton et al. 2016). Based on their weight (500–700 g), a survival probability of around 0.77 would be expected for Reunion harriers. Given the slow life history of this species, an even higher survival probability of around 0.80 seems plausible, as has been observed for other medium-sized raptors with similar fecundity (i.e. typical clutch size of two or three eggs, snail kite *Rostrhamus sociabilis* (0.86, Reichert et al. 2010), Swainson's hawks *Buteo swainsoni* (0.84, Schmutz et al. 2006), red kite *M. milvus* (0.84, Sergio et al. 2021)). Thus, our results suggest that both hatching success and adult survival are lower than would be expected.

Population growth rate and viability

Population models based on current estimates of fecundity and survival suggest that the Reunion harrier population is not viable. The population is predicted to decline by 11% per year, even assuming an optimistically high breeding probability of 0.9. Considering the potential rescue effect of immigration for a local population, we found that the number of immigrants would have to be unrealistically high (10–20% of annual breeding females should be immigrants) to maintain a population with such demographic parameters. This means that the studied population is either in decline or at best, a strong sink. The predicted decline is consistent with the observed decline in breeding pairs over the last 20 years for the whole Reunion Island (Villers et al. unpubl.). We estimated that each female produces on average only 0.57

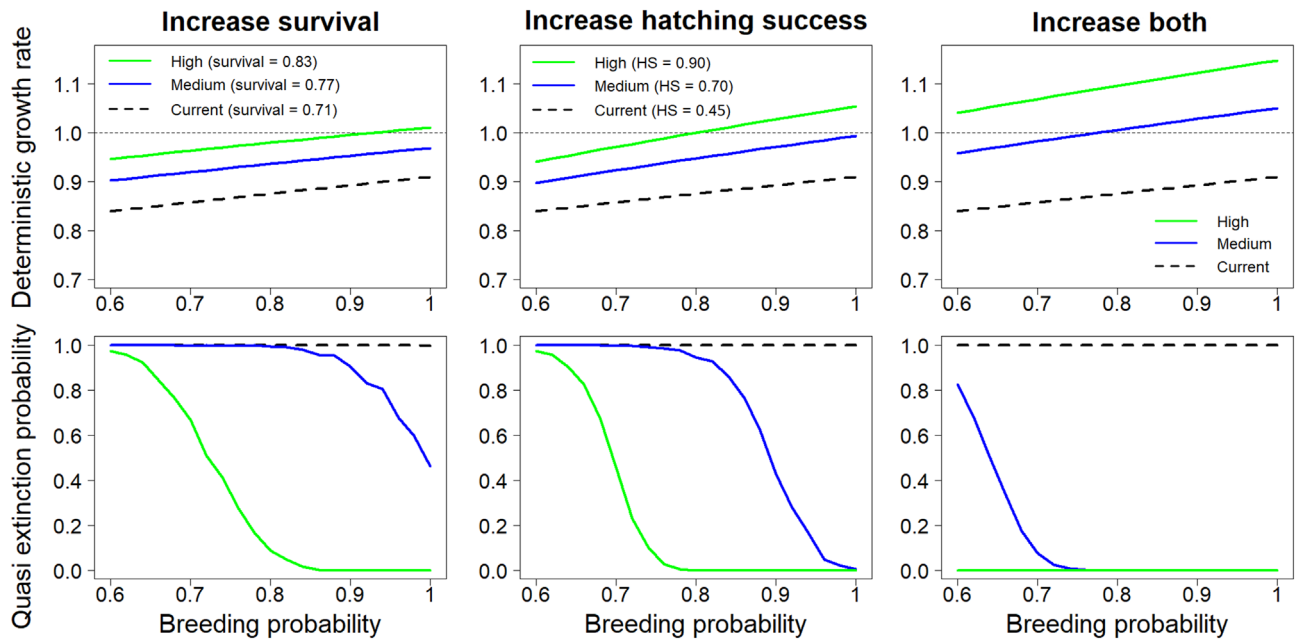


Figure 3. Effects of different management scenarios on the asymptotic deterministic population growth rate and on the risk of quasi-extinction (population size < 4) within 100 years. Management scenarios considered increasing adult survival only, increasing hatching success only and increasing of both adult survival and hatching success simultaneously.

female offspring during her lifetime that are recruited to the breeding population (net reproductive rate), which is far too low for a population to be stable. Consequently, our population projections showed a very high risk of quasi-extinction within the next 30–50 years (Fig. 2). At the current fecundity

levels, it is very unlikely that any biologically realistic increase in adult survival would result in a stable population, despite the high sensitivity of the population growth rate to changes in adult survival. This result highlights the fact that current breeding rates, in particular hatching success, are abnormally

Table 3. Breeding parameters observed in different Harrier species. For clutch size, we give mean and range of common clutch sizes. Hatching success is the proportion of eggs laid that hatched successfully. Fledging success is the percentage of hatchlings that successfully fledged. Fecundity is the number of fledglings per breeding attempt (i.e. per clutch).

Species	Clutch size	Hatching success	Fledging success	Fecundity	References
Reunion harrier	2.3 (1–3)	0.45	0.83	0.9	This study
<i>Circus maillardi</i>					
Spotted harrier	2.8 (2–4)	NA	NA	1.3	Baker-Gabb (1983), Olsen and Marples (1993)
<i>Circus assimilis</i>					
Madagascar harrier	2.9 (2–4)	0.61	0.50	0.9	René de Roland et al. (2004)
<i>Circus macroscleus</i>					
Long-winged harrier	3.2 (3–4)	0.85	0.86	2.2	Segura and Bó (2018)
<i>Circus buffoni</i>					
Black harrier	3.5 (3–4)	0.63	0.88	1.9	Curtis et al. (2004)
<i>Circus maurus</i>					
Montagu's harrier	3.5 (3–5)	0.73	0.64	1.6	Corbacho et al. (1997)
<i>Circus pygargus</i>					
Swamp harrier	3.6 (2–5)	NA	NA	2.3	Baker-Gabb (1983), Olsen and Marples (1993)
<i>Circus approximans</i>					
African marsh harrier	3.6 (3–4)	NA	NA	NA	Simmons (1994)
<i>Circus ranivorus</i>					
Cinereous harrier	3.7 (3–5)	0.78	0.82	2.3	Segura and Bó (2018)
<i>Circus cinereus</i>					
Pied harrier	4.3 (4–5)	0.97	0.67	2.8	Neufeldt (1967)
<i>Circus melanoleucos</i>					
Western marsh harrier	4.9 (4–6)	0.65	0.85	2.5	Witkowski (1989)
<i>Circus aeruginosus</i>					
Pallid harrier	5.1 (4–6)	0.61	NA	2.2	Terraube et al. (2012)
<i>Circus macrourus</i>					

low. The population projections also showed that improving the breeding parameters alone is unlikely to halt the negative population trend. Therefore, a simultaneous improvement in adult survival and breeding parameters is required to reverse the negative population trend.

Possible reasons for the low demographic rates

Current evidence suggests that exposure to anticoagulant rodenticides (ARs) is a serious threat to Reunion harriers. The outdoor use of ARs on Réunion island is motivated by the need to control rat and mouse populations, both to prevent leptospirosis and to minimize crop losses (Grollier and Soufflet 2011). Coeurdassier et al. (2019) found that Reunion harriers are highly exposed to ARs. The reported exposure levels are among the highest currently reported in raptors (Coeurdassier et al. 2019). AR were found in 93% of all harrier carcasses ($n=58$), and in 62% of these the concentration was compatible with a decline in physiological functions and demographic rates. Exposure of non-target wildlife to ARs is a widespread conservation concern and has been associated with declines in predator populations (Jacquot et al. 2013, Fernandez-de-Simon et al. 2019, Roos et al. 2021). Acute exposure of predators to ARs has a toxic effect, potentially leading to death (Coeurdassier et al. 2014, Niedringhaus et al. 2021). Furthermore, accumulating evidence suggests that sub-lethal concentrations have complex effects on individual health, such as delayed blood clotting (Rattner et al. 2020), disruption of the immune system (Fraser et al. 2018) and reduction in body condition (Martínez-Padilla et al. 2017), which may ultimately reduce survival and reproductive performance (Salim et al. 2014, Serieys et al. 2015). A sub-lethal effect may also lead to a reduction in agility and vigilance, which in turn may affect hunting success, as well as increase the risk of collision (motor vehicles, power lines), the latter being a major source of mortality in Reunion harriers (Augiron 2022).

Another issue currently being studied is the potential impact of low genetic diversity and high levels of inbreeding, which threaten small populations (Harrisson et al. 2019). The current size of the breeding harrier population on La Reunion is around 200 pairs (Villers et al. unpubl.), which is likely to be the lowest population size since the arrival of humans on the island 400 years ago with an estimated historical population size of a few thousand pairs (Bourgeois et al. 2022). Low population size is associated with reduced genetic diversity, higher homozygosity and therefore susceptibility to inbreeding depression (Harrisson et al. 2019), which evidence suggests is occurring in Reunion harrier (Bourgeois et al. 2022). Increased hatching failure is a common manifestation of inbreeding depression in captive and wild bird populations (Assersohn et al. 2021). Depressing effects on hatching success have been found in populations that have experienced a severe bottleneck with a minimum population size of about 100–150 individuals (Heber and Briskie 2010), which is lower than the estimated population size of the Reunion harrier. However, inbreeding depression can vary greatly with

environmental conditions and is typically stronger in stressful environments (Fox and Reed 2011). Thus, an interaction between low genetic diversity and exposure to ARs may exacerbate depression of demographic rates.

Robustness of demographic inference

The robustness of the population modeling and quasi-extinction risk assessment depends on the quality of the demographic rate estimates. Our conclusions could be biased if our estimates of survival reflect apparent survival (i.e. the product of true survival and site fidelity) rather than true survival. In our study, survival estimates are based in part on GPS tracking, which ensures perfect detection also outside our study sites and thus controls for permanent emigration. Furthermore, although juveniles may show dispersal movements that takes them outside the study area, we did not observe any breeding dispersal for adults. For these reasons, we believe that our survival estimates, particularly for adults, are representative of true survival. In any case, while an underestimation of survival would lead to an underestimation of the asymptotic population growth rate, this would not change the main conclusion since the population growth rate remains below one and a high risk of quasi-extinction persists for most scenarios, whatever the value of adult survival is used (Fig. 3).

Another important point to consider is whether the estimated demographic rates of our study site, which harbors approximately 5% of all breeding pairs, are representative of the population as a whole. The breeding density at our study site was one of the highest currently known for this species suggesting that the mosaic environment present and the low level of human disturbance at the study sites probably represents the best habitat currently available for the species. We therefore do not expect to find higher demographic rates in other sub-optimal environments. A comparison of the breeding parameters estimated inside and outside our study site supports this statement (Supporting information). However, at the scale of the whole island, the decline of the harrier seems to be more pronounced on the eastern side (where our studied population is located) than on the western side (Villers et al. unpubl.). This geographical differentiation is consistent with the spatial genetic structure of the whole population, suggesting that these two areas can be considered as two functional units (Bourgeois et al. 2022). Thus, the demographic rates we have estimated may be representative of a large part of the population, but not of the complete population.

Finally, our matrix population model relies on simplifying assumptions. We assumed that all individuals breed from their second year. Although breeding has been observed from age two in this species, it is possible that some individuals delay reproduction beyond this age, as observed in other raptors with similar life history traits (e.g. snail kite, Bennetts et al. 1998, red kite, Katzenberger et al. 2021, Pfeiffer and Schaub 2023), and thus that we may have overestimated reproductive output. We also assumed a breeding probability of 0.9 (Fig. 3,

Supporting information for sensitivity analyses) which is again an optimistic value. These assumptions may therefore have led to a slight overestimation of fecundity and hence population growth rate. Our matrix model also ignored temporal variation and covariation in and between demographic rates, which may also have led to an optimistic view of ongoing population dynamics. In fact, temporal variation and covariation, which are predominantly positive (Fay et al. 2022), tend to destabilize population dynamics and reduce the population growth rate (Tuljapourkar 1982). Again, this simplifying assumption may have slightly overestimated the population growth rate and underestimated the quasi-extinction risk.

Conclusion

Our study shows that the demographic situation of the endemic Reunion harrier population is critical. Demographic modelling clearly indicates that this population is in decline and warns of possible extinction within the next four decades. Our findings call for the implementation of immediate and strong conservation measures aimed at rapidly improving demographic rates. Monitoring of declining small populations without the rapid implementation of management actions will only document extinction (e.g. the Christmas Island pipistrelle *Pipistrellus murrayi*, Martin et al. 2012). In our case, one option would be to propose a toolbox of mitigation measures to limit the use of ARs and their exposure to harriers. Rationalizing the outdoor use of ARs, for example prioritizing evidence-based bait deployment rather than prophylactic use, is a pragmatic solution that can be implemented quickly and has been successful elsewhere (Coeurdassier et al. 2014). Gathering additional information, such as the potential interaction between ARs exposure and genetic diversity, is also important to identify all factors depressing demographic rates and to develop future conservation plans. Finally, this study illustrates how fragmentary data collected on a single population can be jointly analyzed using integrated models to provide robust demographic inferences and management recommendations.

Acknowledgements – We would like to thank C. Valette, T. Couturier, N. Laurent, FX. Couzi and F. Rey for their assistance during the field work between 2013 and 2022, as well as all fieldworkers and photographers who have helped to collect the observation data over the years and have spent much time in the field. We also thank Wesley Hochachka, Thomas Riecke and one anonymous reviewer for providing useful comments on this manuscript.

Funding – This work took place within a conservation and research program managed by the SEOR (Société d'études Ornithologique de la Réunion). This research was financially supported by DEAL Reunion and the European Union through a FEDER grant (no. SYNERGIE: RE0027109 and RE0031680).

Permits – This study was conducted under a license delivered by the CRBPO (Museum National d'Histoire Naturelle - France) within no. 577 program coordinated by SA.

Author contributions

Rémi Fay: Conceptualization (equal); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Pierrick Ferret:** Investigation (equal); Data curation (equal); Writing – review and editing (supporting). **Damien Chiron:** Investigation (equal); Data curation (equal); Writing – review and editing (supporting). **Michael Schaub:** Methodology (supporting); Writing – review and editing (supporting). **Steve Augiron:** Conceptualization (equal), Data curation (supporting); Funding acquisition (lead); Project administration (lead); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/jav.03112>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pzgmbsbcv> (Fay et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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