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Contrasting recovery trajectories of four reintroduced populations of the Endangered Mauritius Kestrel (*Falco punctatus*)

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Conservation translocations are commonly used in recovery programmes for threatened species from a wide range of taxa but outcomes can vary considerably both within and between programmes, and the causes of success or failure are often unclear. Central to understanding translocation success is the implementation of an accompanying monitoring programme, enabling the drivers of population establishment and persistence to be explored within a population ecology framework. Here we review and assess the outcome of a translocation programme for the Endangered Mauritius Kestrel, which involved the initial translocation of captive-reared Kestrels into four isolated populations and long-term nest-site management and monitoring. We show that after 20 years these four populations have different recovery trajectories including local extinction, recent decline and comparative stability. We explore the demographic drivers behind these trajectories and how they have been influenced, and could potentially be manipulated, by conservation management actions. Metrics of breeding performance differed between populations and in part this was driven by nest-site selection, with Kestrels nesting more frequently, laying larger clutch sizes and rearing larger broods in nestboxes. We found no compelling evidence for inter-population variation in survival rates. Simulating population trajectories under a range of conservation management scenarios, including further conservation translocations or a scaling up of nest-site management, suggested that the latter would be a more effective, practical long-term solution for the population currently in decline. Our findings provide valuable insights into the merits of monitoring, population demographic reviews and the challenges associated with identifying and mitigation for the drivers of rarity in threatened species.

Keywords: artificial nest-site, captive breeding, conservation management, island endemic, nestbox, raptor, threatened species, tropical bird.

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Conservation translocations are a widely used management tool as part of species and ecosystem restoration programmes across many taxa (Hale & Koprowski 2018, Soorae 2018). This management tool includes: reintroductions to establish a species in part of its previous historical range; and reinforcement (supplementation) where individuals

are added to an existing population of conspecifics and conservation introductions to areas outside of a species' historical range (IUCN 1998). However, the resulting outcomes of conservation translocations (hereafter referred to as translocations) and our understanding of the drivers behind this are hugely variable, both within (Stanley-Price 1991, Cade 2000, Jule *et al.* 2008, Ewen *et al.* 2014, Harding *et al.* 2016, Jourdan *et al.* 2018) and between taxa (Wolf *et al.* 1996, Fischer & Lindenmayer 2000, Pérez *et al.* 2012, Berger-Tal *et al.* 2020).

Central to the process of assessing and understanding the drivers of translocation success is the implementation of an accompanying monitoring programme, which delivers data enabling relevant questions to be asked relating to population establishment and persistence (i.e. population dynamics) (Fischer & Lindenmayer 2000, Armstrong & Seddon 2008). This can be challenging due to the often long-term nature of translocations and the timescale over which they need to be monitored and assessed (Robert *et al.* 2015). However, by their very nature, long-term species restoration programmes (Sarrazin & Legendre 2000, Schaub *et al.* 2004, Martin-Hugues & Christian 2012, Samojlik *et al.* 2018), involving translocations, afford an ideal opportunity to explore the drivers of success or failure. Since 1973 the Mauritius Kestrel *Falco punctatus* has been the subject of one of the longest running avian restoration programmes, recovering from four known wild individuals in 1974 (Jones *et al.* 1991, Jones *et al.* 2002), based on captive breeding and translocations (reintroductions and reinforcements) to create populations in four discrete mountainous areas of Mauritius (Jones *et al.* 1995) (Fig. 1). The establishment of these four populations, between 1984 and 1994, was supported by brood and clutch manipulation, supplementary feeding and nest-site management (Jones *et al.* 1995, Jones & Merton 2012). By 1995 intensive population management had stopped and the focus shifted to a sustainable programme of long-term monitoring and management. The latter was based around the provision of artificial nest-sites (nestboxes), which had been used as a management tool to benefit other kestrel species (Hamerstrom *et al.* 1973, Kostrzewa & Kostrzewa 1997) and more recently shown to be beneficial for population recovery and persistence in other raptors and owls

(Lambrechts *et al.* 2012, Altwegg *et al.* 2014, Fay *et al.* 2019).

According to population ecology theory, the dynamics of closed populations (i.e. where no immigration or emigration occurs) are driven by the key demographic rates – reproduction and mortality (or survival), which are in turn influenced by a range of intrinsic (e.g. density-dependent) and extrinsic (e.g. habitat, weather) factors, including conservation management actions (Newton 1998). Hence, understanding the role that conservation management actions play in the persistence (and thus success) of (translocated) populations is complex, as the influence of these various factors on key demographic rates must be considered in combination rather than in isolation. To do this comprehensively requires detailed individual-based long-term ecological data and the well-documented implementation of conservation management actions. Mauritius Kestrels exhibit restricted dispersal typically breeding within ~ 1 km of their natal nest-site (Burgess *et al.* 2008); this, coupled with no evidence for any natural interchange of wild individuals between the four populations, suggests strongly that each population is closed, i.e. there is no emigration or immigration (Nevoux *et al.* 2013). Therefore, the translocations, long-term management and intensive monitoring associated with the recovery of the Mauritius Kestrel provide an ideal opportunity to explore this across four closed populations, inform long-term management recommendations for the species and contribute to translocation best practices.

Using > 30 years of demographic data from the long-term population-based monitoring programme, capture–mark–recapture methods and population viability analyses, we: (1) document the trajectories of four translocated populations, (2) explore whether key demographic rates vary over time within populations and differ among populations, (3) examine the impact of conservation management (in this case the use of artificial nest-sites by Mauritius Kestrels) specifically on breeding performance, (4) explore population-specific long-term viability under observed demographic rates, (5) based on our findings, explore each population's viability under a range of potential conservation management scenarios, and (6) provide recommendations to secure the long-term future of the Mauritius Kestrel and contributions to translocation best practices.

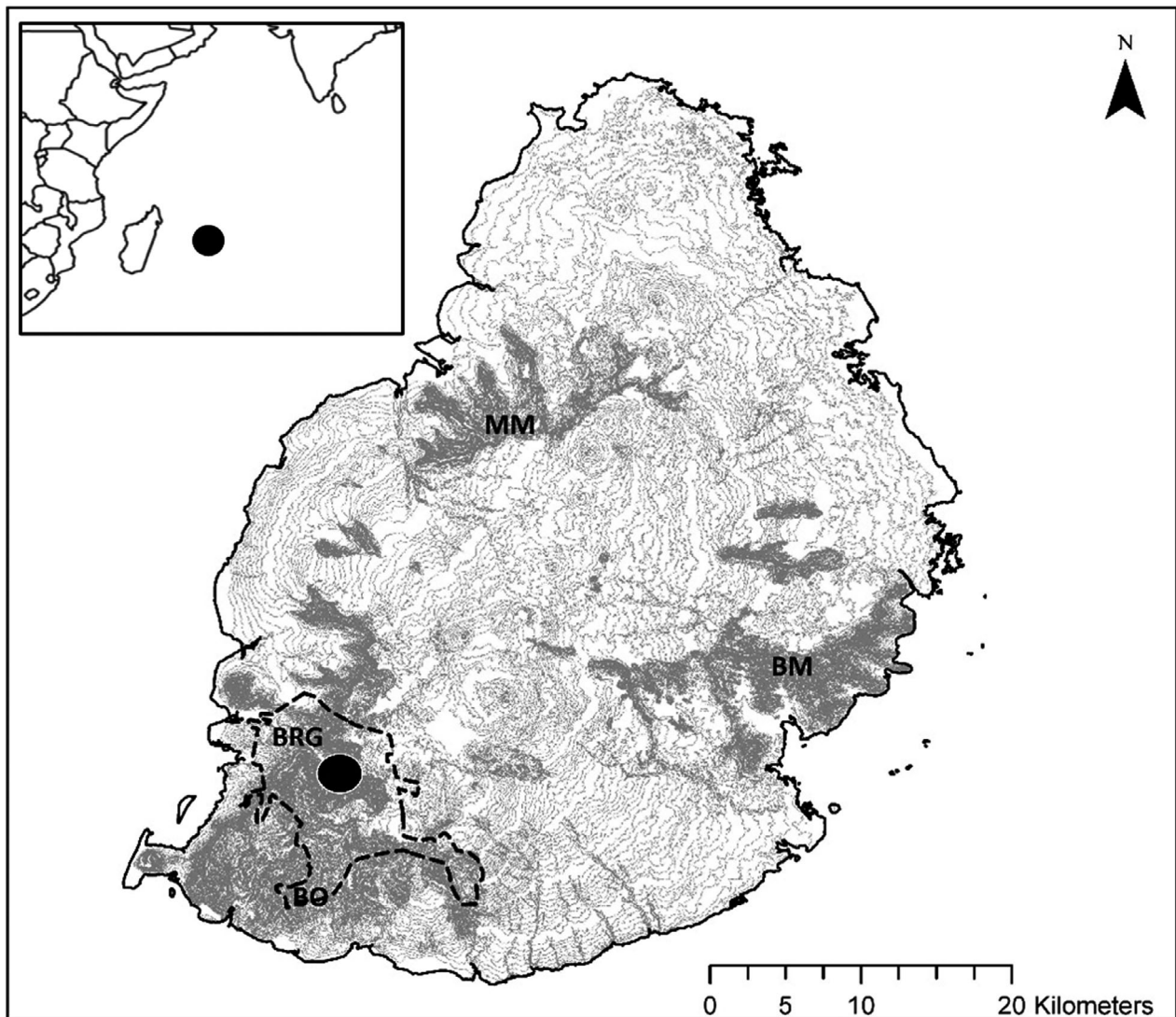


Figure 1. The remnant (black-filled oval) and translocated population locations of the Mauritius Kestrel: Black River Gorges (BRG) in the West; Bambou Mountain (BM) range in the East; Moka Mountain (MM) range in the North; and the Bel Ombre region (BO) in the South. The boundary of the Black River Gorges National Park is shown as a dashed line. The inset map shows the approximate location (black dot) of Mauritius in the Indian Ocean.

METHODS

Study species

The Mauritius Kestrel is a small, endemic falcon found on the Indian Ocean island of Mauritius. It is a territorial species, typically forming monogamous pairs. The breeding season spans two calendar years during the southern hemisphere summer, with the earliest eggs (clutch size: 2–5) laid in early September and the latest fledglings (brood size: 1–4)

leaving the nest in late February. Breeding seasons are thus referred to by the first calendar year, e.g. 1991/1992 would be labelled 1991. Mauritius Kestrels fledge at around 35 days old, achieve independence at around 85 days and are capable of breeding at 1 year (Nicoll *et al.* 2003).

Species recovery programme

Prior to the human colonization of Mauritius, the Mauritius Kestrel was widely distributed across the

island. However, following extensive habitat loss and transformation and the widespread application of DDT, it was restricted to the remote Black River Gorges (Fig. 1) by the late 1950s and had reached a population low of four known birds in the wild in 1974 (Jones *et al.* 1991, 1995, 2002).

Following a successful restoration programme, the Mauritius Kestrel population grew to an estimated 500–800 individuals by 2000 (Jones *et al.* 2002), although this peak population estimate was later revised to 350–400 individuals (Jones *et al.* 2013) and was downlisted to Vulnerable on the IUCN Red List of Threatened Species. The programme involved the management of the remnant wild population, captive breeding and translocations (Jones *et al.* 1991, 1995, Jones & Merton 2012). Translocations included the reinforcement of the remnant wild population in the Black River Gorges (hereafter referred to as West); reintroduction into the Bambou Mountain range (hereafter referred to as East); reintroduction into the Moka Mountain range (hereafter referred to as North); and reintroduction into the Bel Ombre region (hereafter referred to as South). These four populations are all discrete, with no evidence of any natural interchange of wild-bred Kestrels (Nevoux *et al.* 2013); their locations are shown in Figure 1. Between 1984 and 1993, a total of 327 Kestrels were released: 140 in the West (1984–1993), 120 in the East (1987–1993), 40 in the North (1990–1991) and 27 in the South (1993) (Jones *et al.* 1995).

Population monitoring

Since the early 1980s the Mauritius Kestrel has been subjected to intensive monitoring, whereby territorial pairs were identified in each breeding season, their breeding performance was monitored during repeated visits throughout the breeding season and the following data were recorded: clutch size, brood size, Territory (i.e. where it occurred) and nest-site type (i.e. nestbox or natural – cliff/tree) (for details see Nicoll *et al.* 2003, 2004). Kestrels were ringed primarily as nestlings (aged 12–28 days) with a unique combination of colour rings on one tarsus and a numbered aluminium ring on the other, which allowed identification in the field during each breeding season throughout their lifetime. All released individuals were ringed in a similar fashion. Where colour rings were lost or had faded, individuals were trapped and

identified and colour rings were replaced (Nicoll *et al.* 2003).

In the West, population translocations ceased in 1994. Population-level monitoring and the provision of a small number of nestboxes (7% of known nest-sites are nestboxes) continued until 1997 when the recovering population exceeded the programme's capabilities and resources. Between 1998 and 2001, monitoring was conducted at a limited number of nest-sites (~20) and then suspended until 2007, after which it was resumed on an annual basis.

In the East, the population has been monitored since the initial reintroduction in 1987 (Nicoll *et al.* 2003, 2004) with over 93% of wild-bred fledglings ringed while still in the nest (Nevoux *et al.* 2013, Cartwright *et al.* 2014b). Due to a limited number of natural nest-sites, an extensive network of nestboxes has been maintained (65% of nest-sites).

In the North, the Kestrel was reintroduced between 1990 and 1991 and the population was monitored for a further 3 years. In 2001, two surveys were conducted, followed by further two surveys in 2007 and 2008.

The Kestrel was reintroduced into the South in 1993 and comprehensively monitored until 1998. Since 1998, except for 2004 and 2005 (no monitoring), this nestbox-based population has been partially monitored each year, resulting in limited annual data on breeding metrics.

Further details of the topography and habitat for each population are provided in the Supporting Information, Appendix S1.

Population demography

The monitoring programme collected data that could document population size (number of monitored pairs during each 6-month breeding season) and provide insight into the demographic parameters driving population establishment and persistence. Population size was measured in all four populations, whereas demographic parameters were only assessed in the West and East populations. The North population did not become established, and the South population remained small, experienced inconsistent monitoring effort and generated limited data.

During 1991–2016, a total of 583 breeding attempts were monitored in the West population with 296 occurring between 2007 and 2016; of

these, 6% were in nestboxes and 94% in natural nest-sites. In comparison, 462 breeding attempts were monitored in the East population during 2007–2016, with 75% in nestboxes and 25% in natural nest-sites. From these we estimated the following parameters of annual breeding performance: nesting rate (proportion of territorial pairs laying eggs), clutch size (number of eggs), brood size (number of fledglings) and egg success (proportion of eggs becoming fledglings). We used these to explore differences in breeding performance between specific periods in the West population and between the West and East populations.

Through the ringing and re-sighting of individual Mauritius Kestrels during the 6-month breeding season, the monitoring programme generated an extensive capture–mark–recapture (CMR) dataset for both populations (for details see Nicoll *et al.* 2003, 2004). Data span the period 1991–2016 and include 395 (West) and 1138 (East) wild-bred Kestrels ringed as nestlings. No ringing was conducted or re-sightings were made of Kestrels from 2002 to 2006 in the West population. We used these data to explore differences in survival rates between specific periods in the West population and between the West and East populations.

Statistical analyses

To evaluate the demographic drivers behind the observed trends in population trajectories, we conducted a set of analyses to explore whether rates of breeding performance and survival varied in the West population between 1991 and 2016, and between the West and East populations between 2007 and 2016. We then used population viability analyses (PVAs) to understand how demographic rates and historical management affected population trajectories and how management options might affect future conservation outcomes.

Breeding performance

To test for changes in breeding performance metrics during 1993–2016 in the West population, we conducted Mann–Kendall Tau tests on annual mean data for each breeding success metric using the Kendall package (v2.2) (McLeod 2011). No data on wild-bred fledglings were available for 1991 or 1992, and hence those years were excluded.

Using data from 2007–2016, we explored whether any of the four metrics of breeding performance varied between the East and West

populations and whether this was influenced by historical management actions, specifically the provision of nestboxes. We performed this analysis in three steps. First, to test for population-level differences, we compared a null model for each metric of breeding performance with a model including population as a two-level factor. Secondly, to test whether any of the variation observed between populations (in step one) was attributable to nest-site type, we initially fitted a model including nest-site type as a two-level factor (nestboxes or natural cavities) and then added population as a two-level factor to this model. If nest-site type explained most (or all) of the variation in breeding performance between populations, then we would expect no significant improvement in the fit of the model to the data when population was added to it. Conversely, if breeding performance varied between populations in addition to the effect of nest-site type, then adding population to the model containing nest type should significantly improve the fit of the model. Lastly, we included an interaction term between nest-site type and population to test whether differences in breeding performance metrics between nest-site types were consistent between populations.

We used general linear mixed models (GLMMs) with territory ID as a random factor to account for repeated measures. All model comparisons were made using likelihood-ratio tests (LRTs; chi-square test statistic). Initially, we tested for over-dispersion in the data following Harrison (2014). Over-dispersion was found in the egg success data (OD estimate: 1.38) and models were run using ‘glmmadmb’ in the package glmmADMB (Fournier *et al.* 2012) with a betabinomial error distribution. No over-dispersion was found in the other breeding performance metrics, and models were run using ‘glmer’ in the package lme4 (Bates *et al.* 2015), with a binomial error distribution for nesting rate and Poisson error distribution for clutch size and brood size. All models were implemented in the statistical program R (version 3.3.1) (R Core Team 2008).

Survival

First, we compared the survival rates of Kestrels in the West population during 1991–2001 with those from 2007–2016; secondly, we explored whether survival rates differed between the East and West populations. In each step, we used a series of single-state Cormack–Jolly–Seber (CJS) models

implemented in program MARK 6.2 (White & Burnham 1999). Model notation follows Lebreton *et al.* (1992): apparent survival (Φ), recapture probability (P), time dependence (t) and constant ($.$). For each dataset (West and East/West combined) we tested the fit of our fully time-dependent global model ($\Phi_{(t)} P_{(t)}$) to the data using a goodness-of-fit test in U-CARE 2.3.2 (Choquet *et al.* 2009) and, where necessary, Akaike's information criterion (AIC) was corrected for over-dispersion (QAICc). In both the West and the combined population recapture datasets there was evidence for trap-dependence and transience in our global model and we applied an over-dispersion coefficient (\hat{c}) of 1.26 in each case in program MARK. Model selection was based on the corrected Akaike's information criterion (QAIC) using a difference in QAIC threshold of ≥ 2 (Burnham & Anderson 2002). Additional details are provided in the Supporting Information, Appendix S1.

To determine whether survival rates in juveniles (< 1 year old) and/or adults (> 1 year old) differed between the two periods in the West population, we initially constructed a time-dependent two-age-class model, based on prior information on Mauritius Kestrel survival indicating that juvenile survival $<$ adult survival and that recapture rates differed between juveniles and adults (Nicoll *et al.* 2003, Nevoux *et al.* 2011) (Supporting Information Table S6a, model 1). We then explored the evidence for time-dependent survival in both age-classes, constant survival in both age-classes (Table S6a, model 2) and time-dependent survival in each age-class separately (Table S6a; models 3 and 4). Recapture remained time-dependent in both age-classes in these models. The most parsimonious age-structured survival model was then used to examine the influence of time-dependence in each recapture age-class (Table S6a; models 5, 6 and 7). Finally, the most parsimonious model resulting from this was used to explore any differences in survival rates between the two periods in each age-class (Table S6a; models 8 and 9).

To determine whether survival rates differed between the two populations during 1991–2016, we merged the two populations' CMR data and assigned each Kestrel to either population accordingly. Prior survival analyses of the East population show that juvenile survival is negatively density-dependent, whereas adult survival is constant, as are recapture probabilities for each age-class

(Nicoll *et al.* 2003, Nevoux *et al.* 2011). In contrast, juvenile and adult survival in the West population are different but consistent from year to year (see Results section and Table S6a). We therefore specified the following starting model: $\Phi_{j(E:t, W:.)} a_{(E:., W:.)} P_{j(E:., W:.)} a_{(E:., W:t)}$ (Table S6b, model 1). To test for population differences in adult survival, we compared the starting model with a reduced model (Table S6b, model 2) where adult survival did not differ between populations. To generate an estimate of juvenile survival in the East during 2007–2016 which we could use in population viability analysis (see Methods section below), we ran a model where juvenile survival in the East was split into two periods, 1991–2006 and 2007–2016, with time-dependent survival in the first period and constant survival in the second period.

Population viability analysis

Our PVA aimed to address two main issues. First, we wished to understand the observed population trajectories for the West and East populations in terms of vital rates and historical releases of captive-reared birds. Secondly, we wished to understand the extent to which management options might be used to improve future population growth and viability. To do this, we constructed a simple demographic model in VORTEX10 (Lacy & Pollak 2014) in the form:

$$N_{t+1} = cbs_0 N_t + sN_t \quad (1)$$

where N = the number of adult females (≥ 1 year of age), b = the mean number of female offspring fledged per breeding female per year (i.e. brood size), c = nesting rate, s_0 = the annual survival probability of birds from fledging to 1 year of age, s = the annual survival probability of birds from 1 year of age onwards, and t = time in years. We constructed separate models for each population. These formed the baseline models for all modelling scenarios.

We initially ran each baseline model to estimate population growth (λ) and viability (the probability of extinction) for each population. Next, we ran scenarios for each population that assumed that all birds nested in boxes or that all birds nested in natural cavities. This was because the vital rates differ considerably between nest-site types across both populations and the proportion

of pairs nesting in boxes is much higher in the East population (see Results).

To explore the impact of historical releases on the West population, we supplemented the West baseline model with additional birds in the early part (years 1–8) of each simulation. In each of these years, we assumed 18 birds (nine males, nine females) were released, which approximates the duration and intensity of actual releases into the West population during the early years of the restoration programme. Demographic rates were considered equal to those for wild-bred birds based on prior research findings (Nicoll *et al.* 2004, 2006, Butler *et al.* 2009).

Lastly, we wished to explore the extent to which the provision of nestboxes might improve population growth and viability in the West population. To do this, we created two additional scenarios in which we combined vital rates from the two populations. The first used the West baseline model but with values for parameters c and b in Equation 1 derived from the East nestbox data and the second used the East baseline model but with values for c and b derived from the West nestbox data. In this way, we could explore the effects of nestbox provision on population growth and viability against different background demographic rates and make use of more precise estimates of reproductive rates from nestboxes using the more extensive East data.

For each modelling scenario, we ran 1000 iterations over a period of 25 years. It was not our intention to explicitly model population dynamics over a specific period of time, but to explore more generally the population dynamics consequences of variation in vital rates between populations, between nest types and in relation to management interventions (i.e. the release of captive-reared birds) over a standardized period of time. Full details of each modelling scenario, including demographic rates (and between-year variation in rates) and model structures are provided in the supporting online information (Tables S1–S4).

In some iterations, population size reached zero and the population was considered extinct. We estimated lambda ($\lambda = N_{t+1}/N_t$) for each pair of years within each iteration until the population went extinct or the simulation reached the end of the 25-year period. We then averaged lambda across each time series, and then across the 1000 iterations to generate a mean value for each scenario. For each scenario, we ordered the 1000

lambda values from lowest to highest and used the 25th and 975th values as estimates of the 95% confidence limits of mean lambda. The probability of extinction (p) was calculated as the proportion of the 1000 iterations in which the population reached an abundance of zero within the 25-year period. We estimated the approximate 95% confidence limits of p as: $p \pm 2[\sqrt{p(1-p)/n}]$, where n = the number of iterations ($n = 1000$).

RESULTS

Population trajectories

The four Mauritius Kestrel populations showed markedly different population trajectories (Fig. 2). Whereas the East population became well established and appeared relatively stable after 2008 at > 50 monitored pairs, the North population had become extinct by 2007. A small population of fewer than eight monitored pairs persisted in the South and, at least since 2007, the West population declined, with ~ 20 monitored pairs in 2016, resulting in the species being up-listing to Endangered in 2014 (<https://www.iucnredlist.org/species/22696373/93557909>). Recent data from the ongoing monitoring programme (2018) suggested that there are now < 15 monitored pairs in this population, and the current population in Mauritius is < 250 individuals (this study).

Population demography

Breeding performance

In the West population we found no evidence that the four metrics of breeding performance had changed over the course of the population's recovery and subsequent decline: nesting rate $T = -0.29$, $P = 0.092$; clutch size $T = -0.131$, $P = 0.461$; brood size $T = -0.018$, $P = 0.94$; and egg success $T = 0.212$, $P = 0.219$.

The West population exhibited lower levels than the East population in three of the four breeding performance metrics: nesting rate (null vs. population model) $\chi^2_1 = 21.78$, $P < 0.001$; clutch size (null vs. population model) $\chi^2_1 = 9.82$, $P = 0.002$; brood size (null vs. population model) $\chi^2_1 = 7.74$, $P = 0.005$; egg success (null vs. population model) $\chi^2_1 = 0.91$, $P = 0.339$. Population-specific mean annual estimates (2007–2016) for all four metrics are shown in Figure 3.

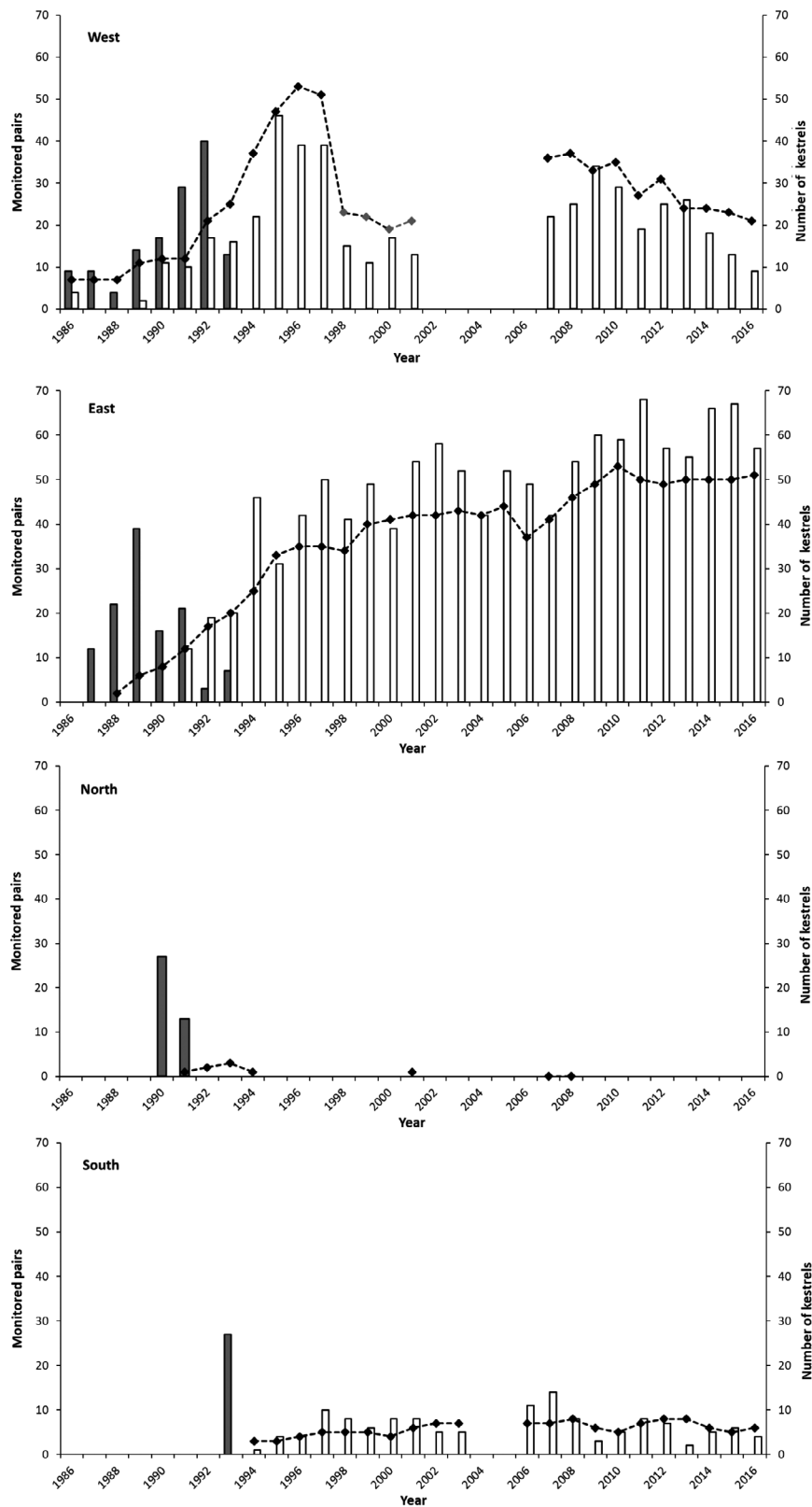


Figure 2. Mauritius Kestrel population-specific metrics from 1986 to 2016: number of monitored pairs (territorial pairs) observed each year during the 6-month breeding season (dashed line/black diamonds and primary y-axis); number of Kestrels released each year (grey bars and secondary y-axis); and number of wild-bred fledglings recorded each year (white bars and secondary y-axis). Years of partial population monitoring in the West are denoted by grey diamonds. No monitoring was conducted in this population between 2002 and 2006, and in the South between 2004 and 2005. Five Mauritius Kestrels were released as a trial between 1984 and 1985 in the West and are not shown on the relevant chart.

Three of the four breeding performance metrics varied between nest-site type, being greater in nestboxes than in natural nest-sites: nesting rate (null vs. nest-site model) $\chi^2_1 = 24.70$, $P < 0.001$; clutch size (null vs. nest-site model) $\chi^2_1 = 12.83$, $P < 0.001$; brood size (null vs. nest-site model) $\chi^2_1 = 5.97$, $P = 0.015$; egg success (null vs. nest-site model) $\chi^2_1 = 1.18$, $P = 0.278$. Additional population-level variation in breeding performance was only evident in nesting rate (nest-site vs. nest-site + population model $\chi^2_1 = 4.03$, $P = 0.044$). No additional population-level variation was evident in either clutch size (nest-site vs. nest-site + population model $\chi^2_1 = 0.45$, $P = 0.51$) or brood size (nest-site vs. nest-site + population model $\chi^2_1 = 2.93$, $P = 0.087$). The variation in nesting rate between nest-site type was consistent between populations (nest-site + population vs. nest-site + population + nest-site * population model $\chi^2_1 = 0.78$, $P = 0.376$). All additive and interaction models are shown in Supporting Information Table S5a,b; Table 1a provides mean metrics by population and/or nest-site type where relevant.

Survival

There was no evidence that survival rates in the West differed for juveniles (see Tables 1b and Table S6a, Model 8 vs. Model 7) or adults between 1991–2001 and 2007–2016 (see Tables 1b and Table S6a, Model 9 vs. Model 7).

There was no compelling statistical support for any between-population difference in annual adult survival (1992–2016): West (0.726) and East (0.775) (Tables 1b and Table S6b, Model 1 vs. Model 2). However, estimates of adult annual survival differed between populations by ~ 6% and were accounted for in the PVAs.

Population viability analysis

The baseline models revealed contrasting population dynamics; the West population was declining at ~ 18% p.a. and had a high probability of extinction within 25 years, whereas the East population

was approximately stable with a very low probability of extinction (Table 2a). The additional simulations that explored the impact of nest type on dynamics showed that population growth was low and extinction risk was high for birds nesting in natural cavities in the West population (Table 2a). In contrast, population growth was higher and extinction risk was lower across both populations for birds using nestboxes.

Our simulations suggest that the initial releases of captive-reared birds into the West population were enough to cause the population to grow until releases had ended (Supporting Information Fig. S1). In effect, this pulse of releases masked the underlying dynamics of this population. The simulations exploring the impact of increasing the proportion of Kestrels breeding in nestboxes on the West population (Table 2b) showed this is likely to improve population growth and reduce extinction risk.

DISCUSSION

The recovery of the Mauritius Kestrel from a wild population of just four birds in 1974 is a remarkable conservation success and an example of what can be achieved through translocations in conjunction with suitable levels of long-term commitment and management. However, the four reintroduced populations are exhibiting very different trajectories, despite being established using the same suite of management techniques. Although this is not unique in small falcon recovery programmes, as shown by the mixed success with the reintroduction of the Aplomado Falcon *Falco femoralis* in south and west Texas (USA) (Hunt *et al.* 2013), our long-term monitoring programme allowed us comprehensively to explore the reasons behind these different trajectories.

Population trajectories

Through a standardized monitoring programme, we documented the trajectory of each population

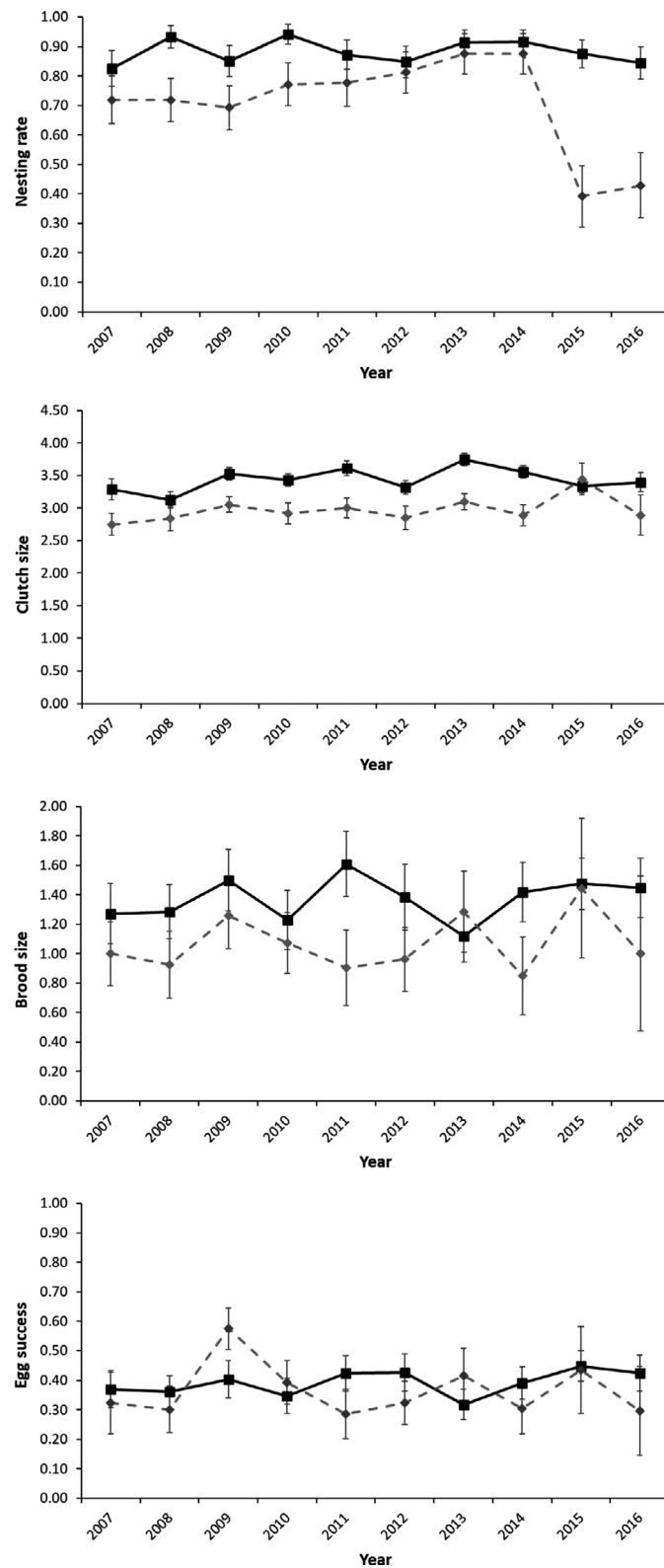


Figure 3. Mauritius Kestrel population-specific breeding performance metrics (2007–2016), from top to bottom: nesting rate, clutch size, brood size and egg success. Values are annual means with standard errors. Solid lines/squares are for the East population and dashed lines/diamonds are for the West population.

Table 1. Mauritius Kestrel key demographic rates for the West (Black River Gorges) and East (Bambou Mountains) populations. (a) Mean population (or global) values (\pm sd) by nest-site type for the breeding performance metrics: nesting rate, clutch size, brood size and egg success. (b) Survival estimates and 95% confidence intervals (CI) by age-class, population and period.

(a) Breeding metric	Nest-site type	East	West
Nesting rate	Box	0.91 (0.281)	0.76 (0.437)
Nesting rate	Natural	0.79 (0.409)	0.71 (0.453)
Clutch size*	Box	3.51 (0.67)	
Clutch size*	Natural	2.96 (0.78)	
Brood size*	Box	1.40 (1.28)	
Brood size*	Natural	1.12 (1.20)	
Egg success**	na	0.38 (0.015)	

(b) Age-class	Time period	East survival	East 95% CI	West survival	West 95% CI
Juvenile	1991–2016	na	na	0.367	0.289–0.453
Juvenile	2007–2016	0.348	0.296–0.403	na	na
Adult	1992–2016	0.775	0.750–0.797	0.726	0.658–0.788

*No significant inter-population difference in this breeding performance metric identified. **No significant inter-population or nest-site difference in this breeding performance metric identified.

Table 2. Average population growth (λ) and probability of extinction in relation to (a) population and nest-site type, and (b) simulations exploring the impact of the provision of nestboxes. 95% confidence limits are given in parentheses (see Methods for details of how they were estimated).

		Nest type		
(a)	Population	All nests	Boxes	Natural cavities
Population growth (λ)	West	0.814 (0.69–0.93)	0.905 (0.77–0.99)	0.807 (0.68–0.92)
	East	0.966 (0.91–1.01)	0.976 (0.92–1.02)	0.939 (0.86–0.99)
Probability of extinction	West	0.763 (0.74–0.79)	0.233 (0.20–0.25)	0.79 (0.76–0.82)
	East	0 (0–0)	0 (0–0)	0.006 (0–0.01)

(b) Scenario	λ	Probability of extinction
West baseline model with reproductive rates from East nestboxes	0.915 (0.79–1.00)	0.182 (0.16–0.21)
East baseline model with reproductive rates from West nestboxes	0.966 (0.89–1.01)	0 (0–0)

following its reintroduction or reinforcement. However, this was not implemented systematically, as shown by the infrequent surveys of the North population, missed seasons in the South population and a hiatus in the West population. This was largely due to limited financial and logistical resources, particularly during 1997–2007, a reason often cited as one of the primary causes underpinning a lack of long-term monitoring post-reintroduction (Wolf *et al.* 1996, Fischer & Lindenmayer 2000, Berger-Tal *et al.* 2020). In contrast, monitoring of the East population has been continuous and intensive since the initial reintroduction. This has been achieved through a combination of support from local and international conservation non-governmental organizations (NGOs) and

academic institutions recognizing the unique value of this tropical study system for scientific research, as evidenced by publications in the disciplines of population ecology (Nevoux *et al.* 2011, 2013, Senapathi *et al.* 2011, Cartwright *et al.* 2014a, 2014b) and small population management (Nicoll *et al.* 2003, 2004, 2006, Ewing *et al.* 2008, Butler *et al.* 2009). In addition, this has facilitated regular population demographic reviews, which have the potential to identify declines in key population-level metrics and the implementation of suitable management actions should the need arise.

It is unclear how the intermittent monitoring affected the outcome of the other kestrel population reintroductions, but at least it could have

provided evidence to initiate the examination of a population's decline and justification for (or not) further conservation intervention. In the case of the North population, which appeared to have never exceeded three pairs, it is likely that further intensive conservation action would have been required to support a population that would have been extremely susceptible to both demographic and stochastic processes in an area with potentially very limited habitat. For the West population a continuous monitoring programme would probably have been advantageous as the current population decline may well have been detected earlier, the underlying demographic processes explored, appropriate management actions identified and implemented, and the population decline reversed. However, this was not possible due to limited financial and logistical support available to the Mauritius Kestrel recovery programme from 1997 to 2007. These contrasting population trajectories and associated demographic data clearly demonstrate the value of overcoming one of the principal challenges faced by any reintroduction – effective post-release monitoring (Berger-Tal *et al.* 2020).

Population demography

In comparison with the relatively stable East population, it appeared that lower levels of breeding investment, i.e. nesting rate and clutch size, and smaller brood sizes led to overall lower levels of breeding success and hence population decline in the West. While there were other intrinsic and extrinsic factors (currently unquantifiable across both populations) that could be driving the observed inter-population variation in breeding performance, the provision of nestboxes and Kestrel nest-site selection were clearly influential. Mauritius Kestrels were more likely to attempt to breed and lay larger clutches in artificial than in natural nest-sites, as seen with the American Kestrel *Falco sparverius* (Hamerstrom *et al.* 1973), the Lesser Kestrel *Falco naumanni* (Catry *et al.* 2009), the European Kestrel *Falco tinnunculus* (Fay *et al.* 2019), and other raptors, owls and passerines (Lambrechts *et al.* 2012, Altwegg *et al.* 2014, Møller *et al.* 2014). Of course, it is possible that Kestrels using nestboxes were more likely to be detected early on in a breeding attempt than were those using natural nest-sites, due to the known location and ease of access that nestboxes afford. This might have biased our findings in relation to

nesting rate but we believe that this is unlikely to be the case, as we found that nest-site choice influences nesting rate in both populations, and in the East population, all nest-sites (irrespective of type) were well-documented and visited regularly throughout the breeding season. However, it is possible that this may at least partially explain the inter-population variation in nesting rate.

Although the Bambou Mountains and Black River Gorges environments are very different in terms of habitat (Vaughan & Wiehe 1937) and land-use (hunting lands vs. protected area), there was no evidence to suggest that the ability of pairs to rear fledglings (i.e. egg success) differed. Brood size for Mauritius Kestrels was on average lower than that recorded for the American Kestrel (Hamerstrom *et al.* 1973), similar to the lower estimates for the European Kestrel (Village 1991), but comparable to the Seychelles Kestrel *Falco area* (Watson 1992). Additional analyses, using the same model structure (see Methods), indicated that clutch size had a strong positive influence on egg success ($\chi^2_1 = 7.18$, $P = 0.007$), irrespective of population or nest cavity type. This suggests that although clutch size in the West was on average smaller (due to the predominance of nests in natural cavities) than those in the East, if it were possible to increase these to a comparable level, this would result in larger brood sizes. Facilitating this would be a logical step in reversing the decline of the West population.

Our PVA models allowed us to explore the population dynamics consequences of variation in vital rates between populations and nest-sites, and in relation to the release of captive-reared birds. Our results showed that the West population is declining and has a much higher extinction risk than the East population. This was predominantly driven by differences in reproductive performance between nestboxes and natural nest-sites – reproductive performance was typically higher in nestboxes, and far fewer birds breed in nestboxes in the West population. Although there is a slight but non-significant difference (6%) in adult survival between the two populations, Mauritius Kestrel survival rates are comparable to those of American and Lesser Kestrels (Prugnolle *et al.* 2003, Hinnebusch *et al.* 2010) and within the range exhibited by other small temperate falcons (Lieske *et al.* 2000, Brown *et al.* 2006). Juvenile survival, at current population levels, is comparable to rates exhibited by other small temperate

falcons (Lieske *et al.* 2000, Brown *et al.* 2006), and American and European Kestrels (Henny 1972, Village 1991) but lower than the rates of Lesser Kestrel (Prugnolle *et al.* 2003). Our results also showed that the release of captive-bred birds positively contributed to population growth and largely ameliorated the negative effects of low background reproductive performance (see Fig. S1). Although the additional release of captive-reared birds provides an intervention to increase population growth and reduce extinction risk in the West population, this would be very difficult to sustain in practice due to resource demands. Alternatively, our results suggest that population growth and viability could be improved in the West population to levels exhibited in the East by providing a much higher density of nest-boxes for the birds to use. Although this would require resources to establish and maintain, a nest-box network is likely to be more sustainable in the long term than an ongoing captive-rearing and release programme.

Population management

The use of nestboxes to increase avian populations or facilitate scientific research has been successfully applied to a range of species (Catry *et al.* 2009, Lambrechts *et al.* 2012, Altwegg *et al.* 2014, Møller *et al.* 2014, Fay *et al.* 2019), including this study. Our PVA scenarios illustrate how the current West population trajectory might be reversed through increasing the proportion of this population nesting in nestboxes, but this would require a population-level behavioural shift in nest-site choice. One way to achieve this would be to follow the initial translocation process used to establish the South and East populations: with captive-reared Kestrels, creche-reared in boxes, released over multiple years in nestboxes (see Jones *et al.* 1995 for details) and the establishment of nestboxes across the potential breeding range. Areas of suitable habitat, currently unoccupied by Kestrels, for further translocations can be identified within the Black River Gorges National Park following a habitat mapping and classification process established in the Bambou Mountains (Burgess *et al.* 2009). Currently, these management actions are being implemented; two areas of suitable habitat for translocation in the National Park have been identified – one to the east of the South

population and the other on the north-west plateau of the West population – with translocations into both areas currently underway. However, as there are fundamental inter-population differences in some of the breeding performance metrics not associated with nest-site type, and a potentially 6% higher adult survival rate in the East, the implementation of these management actions should be accompanied by a detailed long-term monitoring programme. The data will allow conservation managers to assess whether (1) the predicted gains in breeding performance metrics are realized, (2) adult survival rate in the West is genuinely lower than in the East and (3) the anticipated change in population trajectory in the West is achieved.

CONCLUSIONS

While the recovery of the Mauritius Kestrel from the brink of extinction is a remarkable conservation success, the four populations created as part of the species restoration programme have exhibited very contrasting population trajectories. Documentation of these trajectories has been achieved through the implementation of a long-term monitoring programme. However, the monitoring approach was not applied systematically to each population, resulting in potential delays in the detection of specific population declines – most notably in the West population. While this approach has not been ideal, it has provided data to partially explore the different population trajectories and guide the next steps in the species restoration programme, and emphasizes the value of implementing a well-designed monitoring programme alongside translocations. The Mauritius Kestrel restoration programme was pioneering in the 1980s and this study shows that there are still valuable lessons to be learnt from species restoration programmes decades after the original translocations took place.

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AUTHOR CONTRIBUTIONS

Malcolm Nicoll: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Project administration (supporting); Resources (supporting); Writing-original draft (lead); Writing-review & editing (lead). **Carl G. Jones:** Conceptualization (equal); Data curation (supporting); Funding acquisition (lead); Investigation (equal); Methodology (supporting); Project administration (lead); Writing-original draft (supporting); Writing-review & editing (supporting). **Jim Groombridge:** Conceptualization (supporting); Data curation (supporting); Writing-review & editing (supporting). **Sion Henshaw:** Data curation (supporting); Project administration (supporting); Writing-review & editing (supporting). **Kevin Ruhomaun:** Data curation (supporting); Funding acquisition (supporting); Project administration (supporting); Resources (supporting); Writing-review & editing (supporting). **Vikash Tatayah:** Conceptualization (supporting); Data curation (supporting); Funding acquisition (supporting); Investigation (supporting); Project administration (lead); Resources (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Nicolas Zuel:** Data curation (supporting); Investigation (supporting); Project administration (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). **Ken Norris:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (supporting); Resources (equal); Writing-original draft (supporting); Writing-review & editing (supporting).

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Supporting online information.

Table S1. Mauritius Kestrel survival rates used in the population viability analyses.

Table S2. Mauritius Kestrel nesting rates used in the population viability analyses (c).

Table S3. BMauritius Kestrel brood size vales used in the population viability analyses.

Table S4. Input parameters for the different populations and simulations run in VORETEX10.

Table S5. General linear mixed model outputs for the four metrics of breeding performance.

Table S6. Models used to examine survival: (a) in juvenile and adult Mauritius Kestrels in the West population between 1991 and 2016; and (b) differences in juvenile and adult Mauritius Kestrels between the West and East populations.

Fig. S1. The population trajectory of the West Kestrel population following a series of releases of 18 juvenile Mauritius Kestrels each year for 8 years. The population trajectory is derived from the PVA software VORTEX and run with a starting population of 20 female Kestrels.