

1 **Running head:** *evaluating reintroduced population outcomes*

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

4 MALCOLM A. C. NICOLL^{1*}, CARL G. JONES^{2,3}, JIM G. GROOMBRIDGE⁴, SION HENSHAW², KEVIN
5 RUHOMAUN⁵, VIKASH TATAYAH², NICOLAS ZUEL^{2,6} & KEN NORRIS^{1,7}.

6 ¹*Institute of Zoology, Zoological Society of London, Regent's Park, London, NW14RY, UK.*

7 ²*Mauritian Wildlife Foundation, Grannum Road, Vacoas, Mauritius.*

8 ³*Durrell Wildlife Conservation Trust, Les Augres Manor, Trinity, Jersey, UK.*

9 ⁴*Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, Marlowe building,*
10 *University of Kent, Canterbury, CT2 7NR, UK.*

11 ⁵*National Parks and Conservation Service (Government of Mauritius) Reduit, Mauritius.*

12 ⁶*Current address: Ebony Forest Reserve Chamarel, Seven Coloured Earth road, Chamarel 90409, Mauritius.*

13 ⁷*Current address: The Natural History Museum, Cromwell road, London, SW7 5BD, UK.*

14

15 *Corresponding author.

16 Email: malcolm.nicoll@ioz.ac.uk

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18 Conservation translocations are commonly used in recovery programmes for threatened
19 species from a wide range of taxa, but outcomes can vary considerably both within and
20 between programmes, and the causes of success or failure are often unclear. Central to
21 understanding translocation success is the implementation of an accompanying monitoring
22 programme, enabling the drivers of population establishment and persistence to be explored
23 within a population ecology framework. Here we review and assess the outcome of a
24 translocation programme for the Endangered Mauritius Kestrel, which involved the initial
25 translocation of captive-reared kestrels into four isolated populations and long-term nest-site
26 management and monitoring. We show that after 20 years these four populations have

27 different recovery trajectories including, local extinction, recent decline and comparative
28 stability. We explore the demographic drivers behind these trajectories and how they have
29 been influenced, and could potentially be manipulated, by conservation management actions.
30 Metrics of breeding performance differed between populations and in part this was driven by
31 nest-site selection, with kestrels nesting more frequently, laying larger clutch sizes and
32 rearing larger broods in nestboxes. We found no compelling evidence for inter-population
33 variation in survival rates. Simulating population trajectories under a range of conservation
34 management scenarios, including further conservation translocations or a scaling up of nest-
35 site management, suggested that the latter would be a more effective, practical long-term
36 solution for the population currently in decline. Our findings provide valuable insights into
37 the merits of monitoring, population demographic reviews and the challenges associated with
38 identifying and mitigating for the drivers of rarity in threatened species.

39

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

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43 Conservation translocations are a widely used management tool as part of species and
44 ecosystem restoration programmes across many taxa (Hale & Koprowski 2018, Soorae
45 2018). This management tool includes: reintroductions to establish a species in part of its
46 previous historical range; reinforcement (supplementation) where individuals are added to an
47 existing population of conspecifics and conservation introductions to areas outside of a
48 species' historical range (IUCN 1998). However, the resulting outcomes of conservation
49 translocations (hereafter referred to as translocations) and our understanding of the drivers
50 behind this, are hugely variable, both within (Stanley-Price 1991, Cade 2000, Jule *et al.* 2008,

51 Ewen *et al.* 2014, Harding *et al.* 2016, Jourdan *et al.* 2018) and between taxa (Wolf *et al.*
52 1996, Fischer & Lindenmayer 2000, Pérez *et al.* 2012, Berger-Tal *et al.* 2020).

53 Central to the process of assessing and understanding the drivers of translocation success is
54 the implementation of an accompanying monitoring programme, which delivers data
55 enabling relevant questions to be asked relating to population establishment and persistence
56 (i.e. population dynamics) (Fischer & Lindenmayer 2000, Armstrong & Seddon 2008). This
57 can be challenging due to the often long-term nature of translocations and the timescale over
58 which they need to be monitored and assessed (Robert *et al.* 2015). However, by their very
59 nature long-term species restoration programmes (Sarrazin & Legendre 2000, Schaub *et al.*
60 2004, Martin-Hugues & Christian 2012, Samojlik *et al.* 2018), involving translocations,
61 afford an ideal opportunity to explore the drivers of success or failure. Since 1973 the
62 Mauritius Kestrel *Falco punctatus* has been the subject of one of the longest running avian
63 restoration programmes, recovering from four known wild individuals in 1974 (Jones *et al.*
64 1991, Jones *et al.* 2002), based on captive breeding and translocations (reintroductions and
65 reinforcements) to create populations in four discrete mountainous areas of Mauritius (Jones
66 *et al.* 1995) (Fig. 1). The establishment of these four populations, between 1984 and 1994,
67 was supported by brood and clutch manipulation, supplementary feeding and nest-site
68 management (Jones *et al.* 1995, Jones & Merton 2012). By 1995 intensive population
69 management had stopped and the focus shifted to a sustainable programme of long-term
70 monitoring and management. The latter was based around the provision of artificial nest-sites
71 (nestboxes), which had been used as a management tool to benefit other kestrel species
72 (Hamerstrom *et al.* 1973, Kostrzewa & Kostrzewa 1997) and more recently shown to be
73 beneficial for population recovery and persistence in other raptors and owls (Lambrechts *et*
74 *al.* 2012, Altwegg *et al.* 2014, Fay *et al.* 2019).

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

92 Using >30 years of demographic data from the long-term population-based monitoring
93 programme, capture-mark-recapture methods and population viability analyses we: (i)
94 document the trajectories of four translocated populations, (ii) explore if key demographic
95 rates vary over time within populations and differ among populations, (iii) examine the
96 impact of conservation management (in this case the use of artificial nest-sites by Mauritius
97 Kestrels) specifically on breeding performance, (iv) explore population-specific long-term
98 viability under observed demographic rates, (v) based on our findings explore each
99 population's viability under a range of potential conservation management scenarios and (vi)

100 provide recommendations to secure the long-term future of the Mauritius Kestrel and
101 contributions to translocation best practices.

102

103 ***Materials & Methods***

104 *Study species*

105 The Mauritius Kestrel is a small, endemic falcon found on the Indian Ocean island of
106 Mauritius. It is a territorial species, typically forming monogamous pairs. The breeding
107 season spans two calendar years during the southern hemisphere summer, with the earliest
108 eggs (clutch size: 2-5) laid in early September and the latest fledglings (brood size: one-four)
109 leaving the nest in late February. Breeding seasons are thus referred by the first calendar year,
110 e.g., 1991/1992 would be labelled 1991. Mauritius Kestrels fledge at around 35 days old,
111 achieve independence at around 85 days old and are capable of breeding at one year old
112 (Nicoll *et al.* 2003).

113 *Species recovery programme*

114 Prior to the human colonisation of Mauritius, the Mauritius Kestrel was widely distributed
115 across the island. However, following extensive habitat loss and transformation and the
116 widespread application of DDT it was restricted to the remote Black River Gorges (Fig. 1)
117 by the late-1950s and reached a population low of four known birds in the wild in 1974
118 (Jones *et al.* 1991, Jones *et al.* 1995, Jones *et al.* 2002).

119 Following a successful restoration programme, the Mauritius Kestrel population grew to an
120 estimated 500-800 individuals by 2000 (Jones *et al.* 2002), although this peak population
121 estimate was later revised to 350-400 individuals (Jones *et al.* 2013) , and was downlisted to
122 Vulnerable on the IUCN Red List of Threatened Species. The programme involved; the

123 management of the remnant wild population, captive breeding and translocations (Jones *et al.*
124 1991, Jones *et al.* 1995, Jones & Merton 2012). Translocations included: the reinforcement of
125 the remnant wild population in the Black River Gorges (hereafter referred to as West);
126 reintroduction into the Bambou Mountain range (hereafter referred to as East); reintroduction
127 into the Moka Mountain range (hereafter referred to as North); and reintroduction into the Bel
128 Ombre region (hereafter referred to as South). These four populations are all discrete, with no
129 evidence of any natural interchange of wild-bred kestrels (Nevoux *et al.* 2013); their locations
130 are shown in Figure 1. Between 1984 and 1993 327 kestrels were released: 140 in the West
131 (1984-1993), 120 in the East (1987-1993), 40 in the North (1990-1991), and 27 in the South
132 (1993) (Jones *et al.* 1995).

133 *Population monitoring*

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

144 In the West, population translocations ceased in 1994. Population-level monitoring, and the
145 provision of a small number of nestboxes (7% of known nest-sites are nestboxes) continued
146 until 1997 when the recovering population exceeded the programme's capabilities and

147 resources. Between 1998 and 2001 monitoring was conducted at a limited number of nest-
148 sites (~20), then suspended until 2007 when it resumed on an annual basis.

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

153 In the North the kestrel was reintroduced between 1990 and 1991 and the population was
154 monitored for a further three years. In 2001 two surveys were conducted and these were
155 followed by further surveys in 2007 and 2008.

156 The kestrel was reintroduced into the South in 1993 and comprehensively monitored until
157 1998. Since 1998, except for 2004 and 2005 (no monitoring), this nestbox-based population
158 was partially monitored each year resulting in limited annual data on breeding metrics.

159 Further details of the topography and habitat for each population are provided in the
160 supporting online information.

161 *Population demography*

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

169 During 1991-2016, 583 breeding attempts were monitored in the West population with 296
170 occurring between 2007 and 2016; of these 6% were in nestboxes and 94% in natural nest-
171 sites. In comparison 462 breeding attempts were monitored in the East population during
172 2007-2016 with 75% in nestboxes and 25% in natural nest-sites. From these we estimated the
173 following parameters of annual breeding performance: nesting rate (proportion of territorial
174 pairs laying eggs), clutch size (number of eggs), brood size (number of fledglings), and egg
175 success (proportion of eggs becoming fledglings). We used these to explore differences in
176 breeding performance between specific periods in the West population and between the West
177 and East populations.

178 Through the ringing and re-sighting of individual Mauritius Kestrels during the 6-month
179 breeding season the monitoring programme generated an extensive capture-mark-recapture
180 (CMR) data set for both populations (for details see Nicoll *et al.* 2003, Nicoll *et al.* 2004).
181 Data span the period 1991-2016 and include, 395 (West) and 1138 (East), wild-bred kestrels
182 ringed as nestlings. No ringing was conducted, or re-sightings made of kestrels from 2002-
183 2006 in the West population. We used these data to explore differences in survival rates
184 between specific periods in the West population and between West and East populations.

185 *Statistical analyses*

186 To evaluate the demographic drivers behind the observed trends in population trajectories we
187 conducted a set of analyses to explore if rates of breeding performance and survival (i) varied
188 in the West population between 1991 and 2016 and (ii) between the West and East
189 populations for the period 2007-2016. We then used population viability analyses (PVA) to
190 understand how demographic rates and historical management affected population
191 trajectories and how management options might affect future conservation outcomes.

192 Breeding performance

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

197 Using data from 2007-2016 we explored if any of the four metrics of breeding performance
198 varied between the East and West populations and if this was influenced by historical
199 management actions, specifically the provision of nestboxes. We performed this analysis in
200 three steps. First, to test for population-level differences, we compared a null model for each
201 metric of breeding performance with a model including population as a two-level factor.
202 Second, to test if any of the variation observed between populations (in step one) was
203 attributable to nest-site type, we initially fitted a model including nest-site type as a two-level
204 factor (nestboxes or natural cavities), and then added population as a two-level factor to this
205 model. If nest-site type explained most (or all) of the variation in breeding performance
206 between populations then we would expect no significant improvement in the fit of the model
207 to the data when population was added to it. Conversely if breeding performance varied
208 between populations in addition to the effect of nest-site type, then adding population to the
209 model containing nest type should significantly improve the fit of the model. Lastly, we
210 included an interaction term between nest-site type and population to test whether differences
211 in breeding performance metrics between nest-site types were consistent between
212 populations.

213 We used general linear mixed models (GLMM) with territory ID as a random factor to
214 account for repeated measures. All model comparisons were made using likelihood-ratio tests
215 (LRT; chi-squared test statistic). Initially, we tested for overdispersion in the data following
216 Harrison (2014). Overdispersion was found in the egg success data (OD estimate: 1.38) and
217 models were run using 'glmmadmb' in the package glmmADMB (Fournier *et al.* 2012) with

218 a betabinomial error distribution. No overdispersion was found in the other breeding
219 performance metrics, and models were run using ‘glmer’ in the package lme4 (Bates *et al.*
220 2015), with a binomial error distribution for nesting rate and Poisson error distribution for
221 clutch size and brood size. All models were implemented in the statistical programme R
222 (version 3.3.1) (R Core Team 2008).

223 Survival

224 Firstly, we compared the survival rates of kestrels in the West population during 1991-2001
225 with those from 2007-2016; secondly, we explored if survival rates differed between the East
226 and West populations. In each step, we used a series of single-state Cormack-Jolly-Seber
227 (CJS) models implemented in Program MARK 6.2 (White & Burnham 1999). Model
228 notation follows Lebreton *et al.* (1992); apparent survival (Φ), recapture probability (P), (t)
229 time dependence and (.) constant. For each data set (West and East/West combined) we tested
230 the fit of our fully time-dependent global model ($\Phi_{(t)} P_{(t)}$) to the data using a goodness-of-fit
231 test in U-CARE 2.3.2 (Choquet *et al.* 2009) and where necessary Akaike’s Information
232 Criteria (AIC) was corrected for over-dispersion (QAICc). In both the West and combined
233 populations recapture data sets there was evidence for trap-dependence and transience in our
234 global model and we applied an over-dispersion coefficient (\hat{c}) of 1.26 in each case in
235 Program MARK. Model selection was based on corrected Akaike’s Information Criteria
236 (QAIC) using a difference in QAIC threshold of ≥ 2 (Burnham & Anderson 2002).
237 Additional details are provided in the supporting online information.

238 To determine if survival rates in juveniles (< one year old) and/or adults (> one year old)
239 differed between the two periods in the West population, we initially constructed a time-
240 dependent two-age class model, based on prior information on Mauritius Kestrel survival
241 indicating that juvenile survival < adult survival and that recapture rates differed between

242 juveniles and adults (Nicoll *et al.* 2003, Nevoux *et al.* 2011) (Table S6a, model 1). We then
243 explored the evidence for: time-dependent survival in both age classes, constant survival in
244 both age classes (Table S6a, model 2) and time-dependent survival in each age class
245 separately (Table S6a; models 3 and 4). Recapture remained time-dependent in both age
246 classes in these models. The most parsimonious age-structured survival model was then used
247 to examine the influence of time-dependence in each recapture age class (Table S6a; models
248 5, 6 and 7). Finally, the most parsimonious model resulting from this was then used to
249 explore any differences in survival rates between the two periods in each age class (Table
250 S6a; models 8 and 9).

251 To determine if survival rates differed between the two populations during 1991-2016, we
252 merged the two populations' CMR data and assigned each kestrel to either population
253 accordingly. Prior survival analyses of the East population show that juvenile survival is
254 negatively density-dependent, while adult survival is constant as are recapture probabilities
255 for each age class (Nicoll *et al.* 2003, Nevoux *et al.* 2011). In contrast juvenile and adult
256 survival in the West population are different but consistent from year to year (see results
257 section and Table S6a). We therefore specified the following starting model $\Phi_{j(E:t, W:t), a(E:, W:)}$
258 $P_{j(E:, W:t), a(E:, W:t)}$ (Table S6b, model 1). To test for population differences in adult survival we
259 compared the starting model with a reduced model (Table S6b, model 2) where adult survival
260 did not differ between populations. To generate an estimate of juvenile survival in the East
261 during the period 2007-2016, which we could use in population viability analysis (see
262 methods section below), we ran a model where juvenile survival in the East was split into two
263 periods 1991-2006 and 2007-2016, with time-dependent survival in the first period and
264 constant in the second period.

265 *Population viability analysis*

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

$$272 \quad N_{t+1} = cb s_0 N_t + s N_t \quad \text{eq(1)}$$

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

279 We initially ran each baseline model to estimate population growth (λ) and viability (the
280 probability of extinction) for each population. Next, we ran scenarios for each population that
281 assumed (i) all birds nested in boxes and (ii) all birds nested in natural cavities. This was
282 because the vital rates differ considerably between nest-site types across both populations and
283 the proportion of pairs nesting in boxes is much higher in the East population (see Results).

284 To explore the impact of historical releases on the West population, we supplemented the
285 West baseline model with additional birds in the early (years 1-8) of each simulation. In each
286 of these years, we assumed 18 birds (9 males, 9 females) were released, which approximates
287 the duration and intensity of actual releases into the West population during the early years of
288 the restoration programme. Demographic rates were considered equal to those for wild-bred

289 birds based on prior research findings (Nicoll *et al.* 2004, Nicoll *et al.* 2006, Butler *et al.*
290 2009).

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

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

307 In some iterations, population size reached zero and the population was considered extinct.
308 We estimated lambda ($\lambda = N_{t+1}/N_t$) for each pair of years within each iteration until the
309 population went extinct or the simulation reached the end of the 25-year period. We then
310 averaged lambda across each time series, and then across the 1000 iterations to generate a
311 mean value for each scenario. For each scenario, we ordered the 1000 lambda values lowest
312 to highest and used the 25th and 975th values as estimates of the 95% confidence limits of

313 mean lambda. The probability of extinction (p) was calculated as the proportion of the 1000
314 iterations in which the population reached an abundance of zero within the 25-year period.
315 We estimated the approximate 95% confidence limits of p as: $p \pm 2[\sqrt{(p(1 - p)/n)}]$, where
316 n = the number of iterations ($n = 1000$).

317

318 **Results**

319 *Population trajectories*

320 The four Mauritius Kestrel populations show markedly different population trajectories (Fig.
321 2). While the East population became well established and appeared relatively stable since
322 2008 at > 50 monitored pairs, the North population became extinct by 2007. A small
323 population of < 8 monitored pairs persisted in the South, while the West population declined
324 since at least 2007, with ~20 monitored pairs in 2016 resulting in the species up-listing to
325 Endangered in 2014 (<https://www.iucnredlist.org/species/22696373/93557909>). Recent data
326 from the ongoing monitoring programme (2018) suggested that this population is now < 15
327 monitored pairs and the current population in Mauritius is < 250 individuals (this study).

328 *Population demography*

329 Breeding performance

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

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

340 Three of the four breeding performance metrics varied between nest-site type, being greater
341 in nestboxes than natural nest-sites: nesting rate (null vs nest-site model) $\chi^2_1 = 24.70$, $p <$
342 0.001 ; clutch size (null vs nest-site model) $\chi^2_1 = 12.83$, $p < 0.001$; brood size (null vs nest-site
343 model) $\chi^2_1 = 5.97$, $p = 0.015$; egg success (null vs nest-site model) $\chi^2_1 = 1.18$, $p = 0.278$.
344 Additional population-level variation in breeding performance was only evident in nesting
345 rate (nest-site vs nest-site + population model $\chi^2_1 = 4.03$, $p = 0.044$). No additional
346 population-level variation was evident in either clutch size (nest-site vs nest-site + population
347 model $\chi^2_1 = 0.45$, $p = 0.51$) or brood size (nest-site vs nest-site + population model $\chi^2_1 = 2.93$,
348 $p = 0.087$). The variation in nesting rate between nest-site type was consistent between
349 populations (nest-site + population vs nest-site + population + nest-site * population model
350 $\chi^2_1 = 0.78$, $p = 0.376$). All additive and interaction models are shown in Table S5a and b, and
351 Table 1a provides mean metrics by population and/or nest-site type where relevant.

352 Survival

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

356 There was no compelling statistical support for any between population difference in annual
357 adult survival (1992-2016): West (0.726) and East (0.775) (Table 1b and Table S6b, Model 1

358 v Model 2,). However, estimates of adult annual survival differed between populations by
359 ~6% and was accounted for in the PVA analyses.

360 *Population viability analysis*

361 The baseline models revealed contrasting population dynamics; the West population was
362 declining at ~18% p.a. and has a high probability of extinction within 25 years, whereas the
363 East population was approximately stable with a very low probability of extinction (Table
364 2a). The additional simulations that explored the impact of nest type on dynamics show that
365 population growth was low and extinction risk high for birds nesting in natural cavities in the
366 West population (Table 2a). In contrast, population growth was higher and extinction risk
367 lower across both populations for birds using nestboxes.

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

374

375 *Discussion*

376 The recovery of the Mauritius Kestrel from a wild population of just four birds in 1974 is a
377 remarkable conservation success and an example of what can be achieved through
378 translocations in conjunction with suitable levels of long-term commitment and management.
379 However, the four reintroduced populations exhibit very different trajectories, despite being
380 established using the same suite of management techniques. While this is not unique in small

381 falcon recovery programmes, as shown by the mixed success with the reintroduction of the
382 Aplomado Falcon *Falco femoralis* in to south and west Texas (USA) (Hunt *et al.* 2013), our
383 long-term monitoring programme allowed us to comprehensively explore the reasons behind
384 these different trajectories.

385 *Population trajectories*

386 Through a standardised monitoring programme, we documented the trajectory of each
387 population following their reintroduction or reinforcement. However, it was not implemented
388 systematically as shown by the infrequent surveys of the North population, missed seasons in
389 the South population and a hiatus in the West population. This was largely due to limited
390 financial and logistical resources, particularly during the period 1997-2007, a reason often
391 cited as one of the primary causes underpinning a lack of long-term monitoring post
392 reintroduction (Wolf *et al.* 1996, Fischer & Lindenmayer 2000, Berger-Tal *et al.* 2020). In
393 contrast monitoring of the East population has been continuous and intensive since the initial
394 reintroduction. This has been achieved through a combination of support from local and
395 international conservation NGOs; and academic institutions recognising the unique value of
396 this tropical study system for scientific research as evidenced by publications in the
397 disciplines of population ecology (Nevoux *et al.* 2011, Senapathi *et al.* 2011, Nevoux *et al.*
398 2013, Cartwright *et al.* 2014b, Cartwright *et al.* 2014a) and small population management
399 (Nicoll *et al.* 2003, Nicoll *et al.* 2004, Nicoll *et al.* 2006, Ewing *et al.* 2008, Butler *et al.*
400 2009). In addition, this has facilitated regular population demographic reviews, which have
401 the potential to identify declines in key population-level metrics and the implementation of
402 suitable management actions should the need arise.

403 It is unclear how the intermittent monitoring affected the outcome of the other kestrel
404 population reintroductions, but at least it could have provided evidence to initiate the

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

418 *Population demography*

419 In comparison to the relatively stable East population, it appeared that lower levels of
420 breeding investment, i.e., nesting rate and clutch size, and smaller brood sizes led to overall
421 lower levels of breeding success and hence population decline in the West. While there were
422 other intrinsic and extrinsic factors (currently unquantifiable across both populations) that
423 could be driving the observed inter-population variation in breeding performance, the
424 provision of nestboxes and kestrel nest-site selection was clearly influential. Mauritius
425 Kestrels were more likely to attempt to breed and lay larger clutches in artificial than in
426 natural nest-sites as seen with the American Kestrel *Falco sparverius* (Hamerstrom *et al.*
427 1973), the Lesser Kestrel *Falco naumanni* (Catry *et al.* 2009), the European Kestrel *Falco*
428 *tinnunculus* (Fay *et al.* 2019) and other raptors, owls and passerines (Lambrechts *et al.* 2012,
429 Altwegg *et al.* 2014, Møller *et al.* 2014). Of course, it is possible that kestrels using nestboxes

430 were more likely to be detected early on in a breeding attempt than those using natural nest-
431 sites, due to the known location and ease of access that nestboxes afford. This might have
432 biased our findings in relation to nesting rate but, we believe that this is unlikely to be the
433 case as we found that nest-site choice influences nesting rate in both populations and in the
434 East population all nest-sites (irrespective of type) were well-documented and visited
435 regularly throughout the breeding season. However, it is possible that this may at least
436 partially explain the inter-population variation in nesting rate.

437 While the Bambou Mountains and Black River Gorges environments are very different in
438 terms of habitat (Vaughan & Wiehe 1937) and land-use (hunting lands vs protected area)
439 there was no evidence to suggest that the ability of pairs to rear fledglings (i.e., egg success)
440 differed. Brood size for Mauritius Kestrels was on average lower than that recorded for the
441 American Kestrel (Hamerstrom *et al.* 1973), similar to the lower estimates for the European
442 Kestrel (Village 1991), but comparable with the Seychelles Kestrel *Falco area* (Watson
443 1992). Additional analyses, using the same model structure (see methods), indicated that
444 clutch size had a strong positive influence on egg success ($\chi^2_1 = 7.18, p = 0.007$), irrespective
445 of population or nest cavity type. This suggests that while clutch size in the West was on
446 average smaller (due to the predominance of nests in natural cavities) than those in the East,
447 if it was possible to increase these to a comparable level then this would result in larger brood
448 sizes. Facilitating this would be a logical step in reversing the decline of the West population.
449 Our PVA models allowed us to explore the population dynamic consequences of variation in
450 vital rates between populations and nest-sites, and in relation to the release of captive-reared
451 birds. Our results showed that the West population is declining and has a much higher
452 extinction risk than the East population. This was predominantly driven by differences in
453 reproductive performance between nestboxes and natural nest-sites – reproductive
454 performance was typically higher in nestboxes and far fewer birds breed in nestboxes in the

455 West population. Although there is slight, but non-significant difference (6%) in adult
456 survival between the two populations, Mauritius Kestrel survival rates are comparable to
457 American and Lesser Kestrels (Prugnolle *et al.* 2003, Hinnebusch *et al.* 2010) and within the
458 range exhibited by other small temperate falcons (Lieske *et al.* 2000, Brown *et al.* 2006).
459 Juvenile survival, at current population levels, is comparable to rates exhibited by other small
460 temperate falcons (Lieske *et al.* 2000, Brown *et al.* 2006), American and European Kestrels
461 (Henny 1972, Village 1991), but lower than the Lesser Kestrel (Prugnolle *et al.* 2003). Our
462 results also showed that the release of captive-bred birds positively contributed to population
463 growth and largely ameliorated the negative effects of low background reproductive
464 performance (see Fig. S1). Although the additional release of captive-reared birds provides an
465 intervention to increase population growth and reduce extinction risk in the West population,
466 this would be very difficult to sustain in practice due to resource demands. Alternatively, our
467 results suggest that population growth and viability could be improved in the West population
468 to levels exhibited in the East by providing a much higher density of nestboxes for the birds
469 to use. Although this would require resources to establish and maintain, a nestbox network is
470 likely to be more sustainable in the long-term than an ongoing captive-rearing and release
471 programme.

472 *Population management*

473 The use of nestboxes to increase avian populations or facilitate scientific research has been
474 successfully applied to a range of species (Catry *et al.* 2009, Lambrechts *et al.* 2012, Altwegg
475 *et al.* 2014, Møller *et al.* 2014, Fay *et al.* 2019), including this study. Our PVA scenarios
476 illustrated how the current West population trajectory might be reversed through increasing
477 the proportion of this population nesting in nestboxes but would require a population-level
478 behavioural shift in nest-site choice. One way to achieve this would be to follow the initial
479 translocation process used to establish the South and East populations; with captive-reared

480 kestrels, creche-reared in boxes, released over multiple years in nestboxes (see Jones *et al.*
481 1995 for details) and the establishment of nestboxes across the potential breeding range.
482 Areas of suitable habitat, currently unoccupied by kestrels, for further translocations can be
483 identified within the Black River Gorges National Park following a habitat mapping and
484 classification process established in the Bambou Mountains (Burgess *et al.* 2009). Currently,
485 these management actions are being implemented; two areas of suitable habitat for
486 translocation in the National Park have been identified – one to the east of the South
487 population and the other on the north-west plateau of the West population; with
488 translocations into both areas currently underway. However, as there are fundamental inter-
489 population differences in some of the breeding performance metrics not associated with nest-
490 site type, and a potentially 6% higher adult survival rate in the East, the implementation of
491 these management actions should be accompanied by a detailed long-term monitoring
492 programme. The data will allow conservation managers to assess if: the predicted gains in
493 breeding performance metrics are realised, adult survival rate in the West is genuinely lower
494 than in the East, and the anticipated change in population trajectory in the West are achieved.

495

496 ***Conclusions***

497 While the recovery of the Mauritius Kestrel from the brink of extinction is a remarkable
498 conservation success, the four populations created as part of the species restoration
499 programme have exhibited very contrasting population trajectories. Documentation of these
500 trajectories has been achieved through the implementation of a long-term monitoring
501 program. However, the monitoring approach was not applied systematically to each
502 population resulting in potential delays in the detection of specific population declines – most
503 notably in the West population. While this approach has not been ideal it has provided data to

504 partially explore the different population trajectories, guide the next steps in the species
505 restoration programme and emphasises the value of implementing a well-designed
506 monitoring programme alongside translocations. The Mauritius Kestrel restoration
507 programme was pioneering in the 1980s and this study shows that there are still valuable
508 lessons to be learnt from species restoration programmes decades after the original
509 translocations took place.

510

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517 reviewer for helpful comments on earlier drafts.

518 **Data availability:** The data that support the findings of this study are available from the
519 corresponding author upon reasonable request.

520

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

681 * No significant inter-population difference in this breeding performance metric identified.

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

(b) Age class	Time period	East Survival	East 95% CIs	West Survival	West 95% CIs
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

683

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

(a)	Population	All nests	Nest type 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)

687

(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)

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

695

696 Figure 2. Mauritius Kestrel population-specific metrics from 1986 to 2016: number of monitored pairs
697 (territorial pairs) observed each year during the 6-month breeding season (dashed line/black diamonds and
698 primary y-axis); number of kestrels released each year (grey bars and secondary y-axis); number of wild-bred
699 fledglings recorded each year (white bars and secondary y-axis). Years of partial population monitoring in the
700 West are denoted by grey diamonds, and no monitoring was conducted in this population between 2002 and
701 2006 and in the South between 2004 and 2005. NB: five Mauritius Kestrels were released as a trial between
702 1984 and 1985 in the West and are not shown on the relevant chart.

703

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

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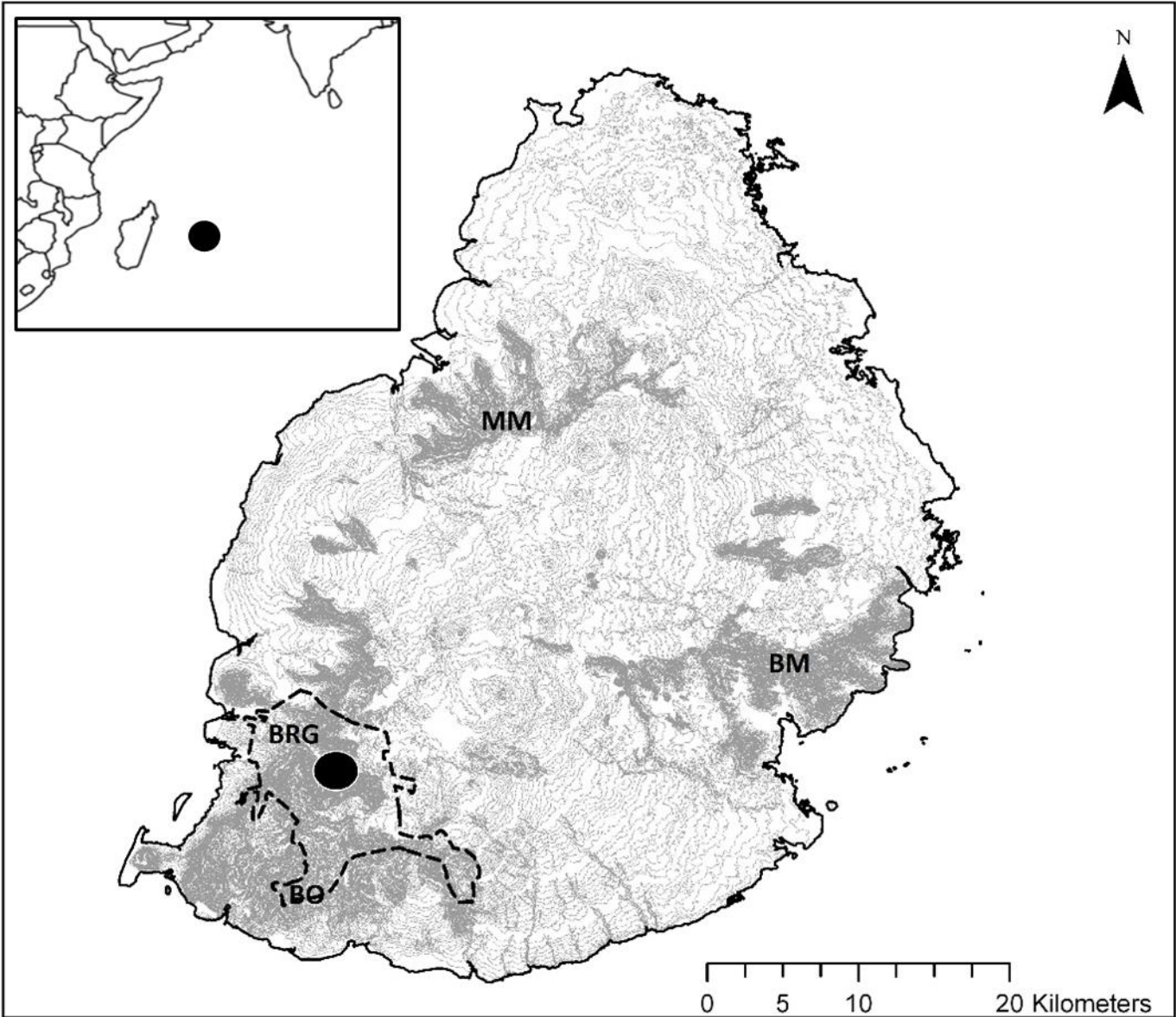
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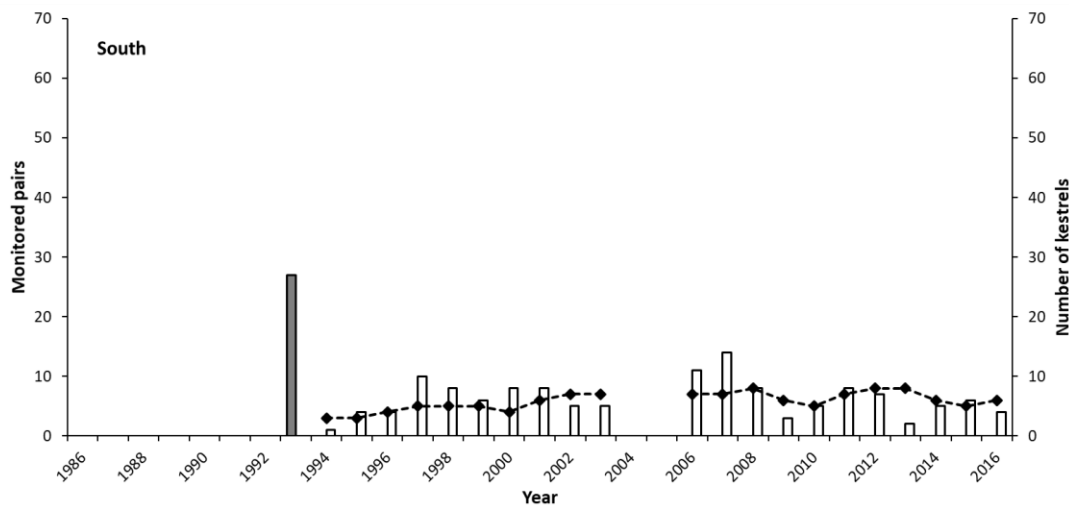
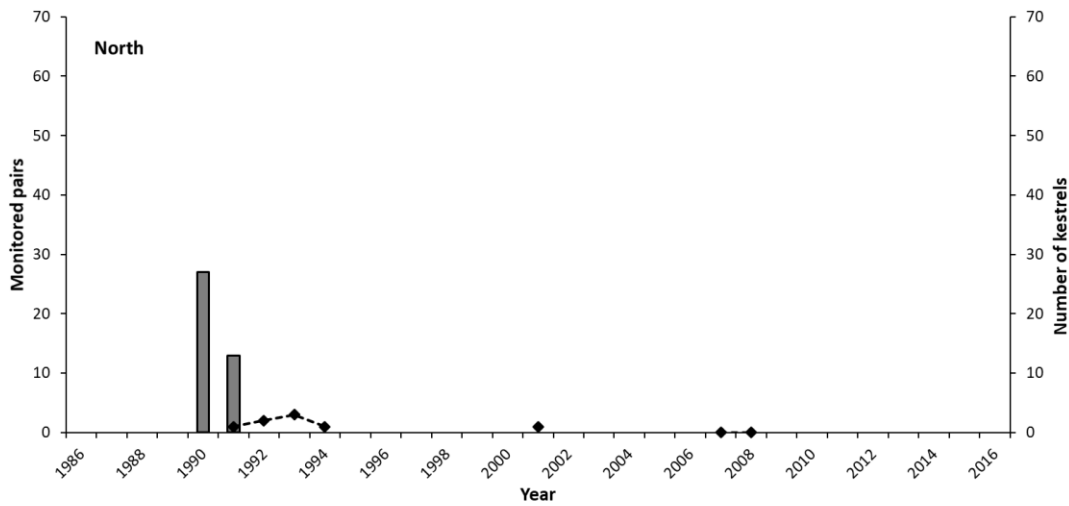
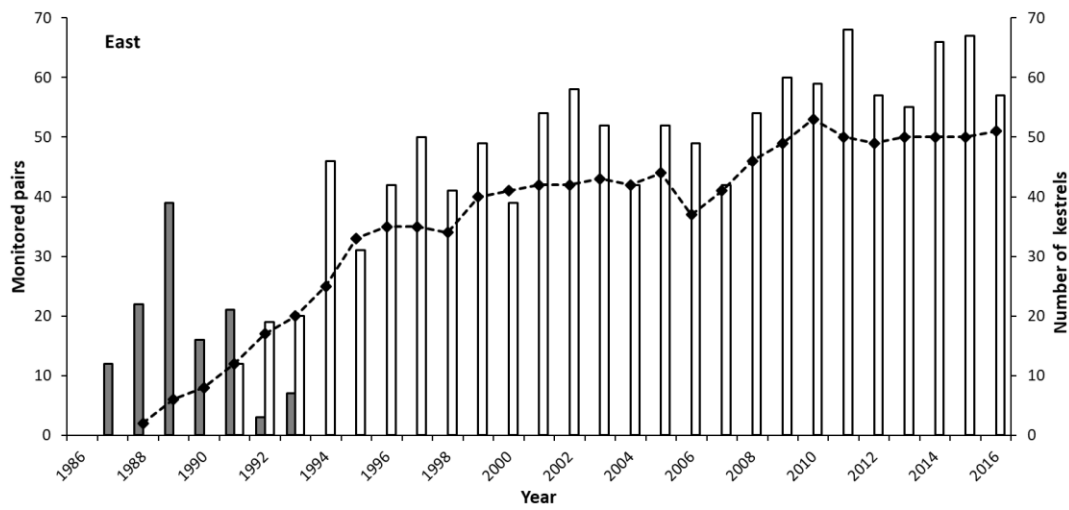
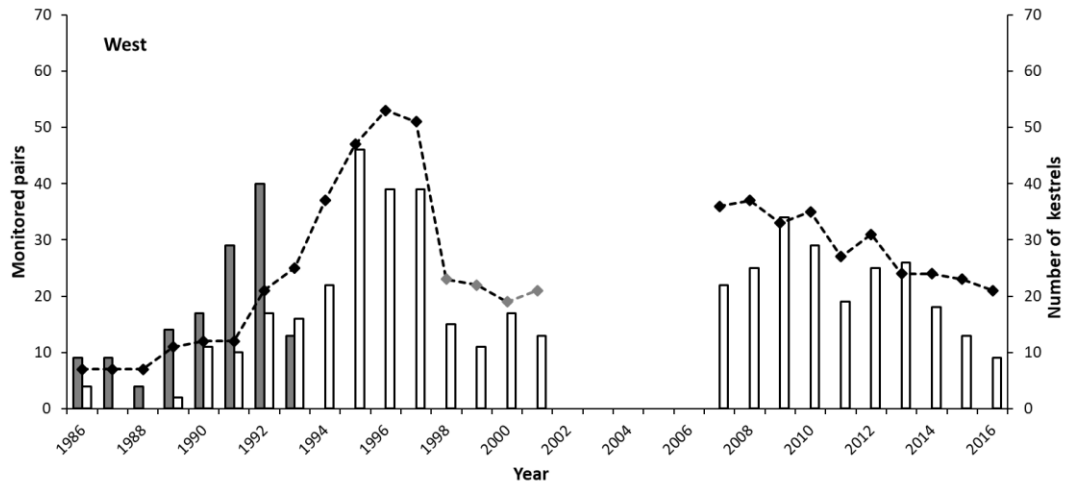
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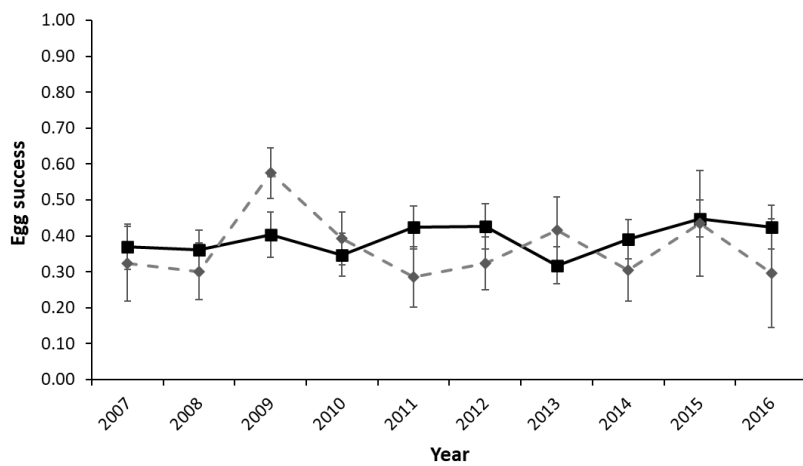
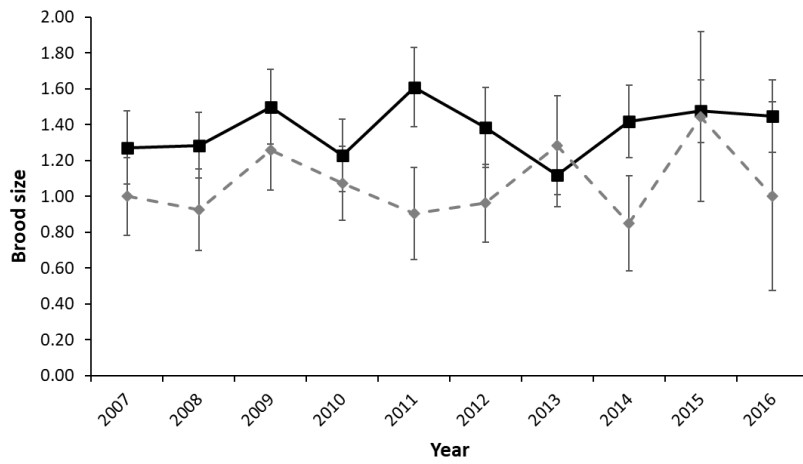
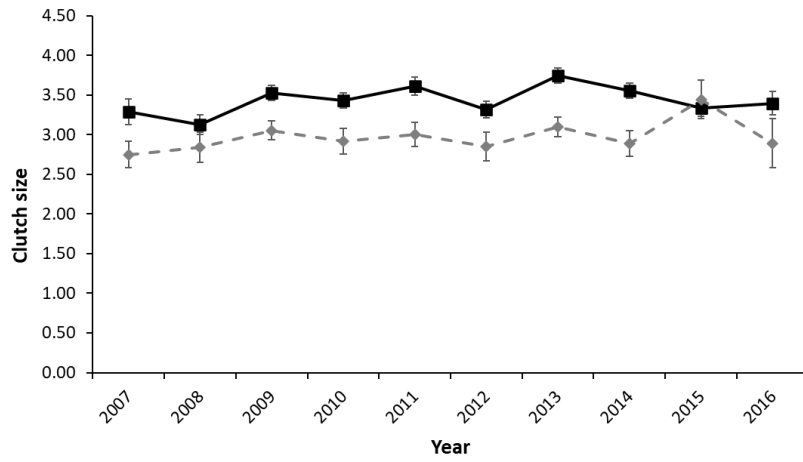
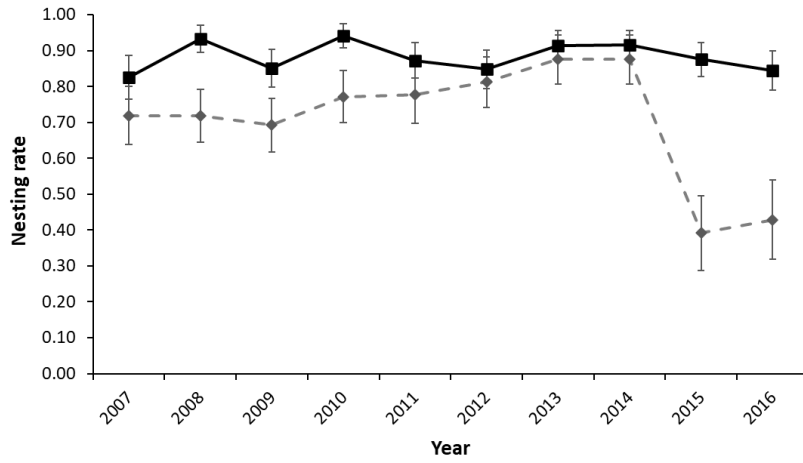


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717 Figure 1.



719 Figure 2.



721 Figure 3.

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