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Biological Conservation

DOI:

[10.1016/j.biocon.2017.11.001](https://doi.org/10.1016/j.biocon.2017.11.001)

Published: 01/01/2018

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Valle, S., Collar, N., W. Edwin, H., & Marsden, S. (2018). Trapping method and quota observance are pivotal to population stability in a harvested parrot. *Biological Conservation*, 217, 428-436. <https://doi.org/10.1016/j.biocon.2017.11.001>

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1 Trapping method and quota observance are pivotal to 2 population stability in a harvested parrot

3
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11 12 **Abstract**

13 Wildlife trade is currently regulated mainly in terms of ‘volume’, i.e. the number of individuals
14 taken from the wild or numbers appearing on the market in a given year. To explore the possible
15 effects of other factors such as capture methods, variability in annual harvest, and habitat, we
16 built and validated a demographic model for a closed population of Grey Parrots *Psittacus*
17 *erithacus* on Príncipe, and ran 50-year simulations for the population under different harvest
18 scenarios. There was a fine line between capture volumes being robustly sustainable (11%
19 harvested) and dramatically unsustainable (15%). Population trajectories were highly sensitive to
20 changes in adult survivorship, such that the inclusion of even a small number of adults among
21 the harvest had a far greater impact than a similar number of juveniles. High annual variation in
22 capture rate (reflecting poor national management of trade), could make the difference between
23 sustainability and non-sustainability if quotas were set around critical harvest volumes. While
24 these patterns may be common to large traded parrots generally, sufficient habitat and secure
25 nest sites exist on Príncipe to render the effects of habitat loss on the island less important than
26 in most other situations. If trade in parrots is to continue sustainably it will require reliable
27 demographic and harvest data and must eliminate instability in quota observance (exceeded
28 quotas are not compensated by shortfalls in other years) and, especially, the indiscriminate
29 capture of adults.

30 31 **Keywords**

32 Demographic modeling, Grey Parrot, CITES, Population dynamics, wildlife trade, P.V.A.

33 34 35 **Introduction**

36 The international trade in live animals and wildlife products is a constituent threat to around
37 one-third of all bird and mammal species (UNEP-WCMC 2015). Legal trade is estimated to be
38 worth over USD 8 billion a year globally (Zhang et al. 2008), and this figure is likely to double
39 when illegal trade is taken into account (Pires 2012). Parrots, and especially the larger species, are
40 the most traded wild-caught group of birds (UNEP-WCMC 2015), and there are serious
41 concerns about the sustainability of current harvest levels in many species (Beissinger and
42 Bucher 1992a). Such concerns arise not just from the sheer volume of parrots in trade, but also
43 from the birds' poor resilience to overharvesting (Beissinger 2001; Pain et al. 2006; Wright et al.
44 2001), inadequate enforcement of trade regulations (Martin et al. 2014), and the paucity of
45 reliable population and demographic data to support harvest models (Marsden and Royle 2015).

46 The Convention on International Trade in Endangered Species of Wild Fauna and Flora
47 (CITES) allows international trade in a taxon only if the proposed harvest has been scientifically
48 proven to be not detrimental to its survival (Rosser and Haywood 2002). Ideally, 'non-detriment'
49 findings should be underpinned by a robust demographic model that predicts a population's
50 long-term response to harvest (e.g. Beissinger and Westphal 1998). Such models have rarely been
51 built for parrots (Beissinger 2001; Koenig 2008; Strem and Bouzat 2012), and indeed for most
52 other traded species. Of course, the reliability of harvest models depends both on the availability
53 of appropriate data to support them, and on how well the interactions of parameters within the
54 model reflect the reality of population dynamics in the wild (Boyce 1992).

55 Across the tropics, methods of trapping parrots range from the particular 'chick-only'
56 harvest from nest cavities (e.g. Juste 1996), to indiscriminate mass trapping of individuals of any
57 age class from aggregation sites, usually by means of glue-traps or nets (e.g. Ngenyi 2002, 2003).
58 Moreover, annual CITES-reported imports/exports from range countries vary considerably
59 (UNEP-WCMC 2015), reflecting supply, demand, and enforcement/trade management issues.
60 Important questions in relation to demographic modelling of harvested parrot populations
61 therefore are:

- 62 1. How sensitive are long-term population trajectories likely to be to small changes/uncertainties
63 in harvest volume which are inevitable under current trade management?
- 64 2. Do different trapping methods affect populations differentially for a given harvest volume?
- 65 3. What are the effects of variation in annual harvests on harvest sustainability?
- 66 4. What are the compound effects of habitat loss and trapping volume and method on long-term
67 population viability?

68 To explore these issues, we built and validated a stage-classified female-based demographic
69 model (Caswell 1989) for a closed (insular) population of Grey Parrots *Psittacus erithacus* (with
70 demographic rates typical of other large parrots) to examine the influence of important trapping-
71 related and habitat change variables on harvest sustainability and, as a broader case study, to
72 investigate the population dynamics of large parrots (mean body mass ≥ 300 g).

73

74 **Methods**

75 *Study area and population*

76 The heavily traded Grey Parrot has suffered a dramatic global decline (Annorbah et al. 2016;
77 BirdLife International 2017). As a result, its global conservation status has deteriorated from
78 Near Threatened through Vulnerable to Endangered in just five years (IUCN 2016), and calls for
79 a ban on its trade have only recently been accepted, albeit not unanimously (CITES 2017).
80 Nonetheless, the species remains relatively common in some parts of its range (Marsden et al.
81 2015). One such area is the small (136 km²) island of Príncipe (São Tomé and Príncipe, Gulf of
82 Guinea), which hosts a demographically isolated, relatively healthy, and well-studied population
83 (Fahlman 2002; Juste 1996; Marsden et al. 2015; Melo 1998; Valle et al. 2017). Grey Parrots were
84 harvested at an average rate of 600 birds per year from the wild in the 1990s (Juste 1996; Melo
85 1998) until a regional ban on all trade was put in place in 2005 (Valle 2015). Príncipe is broadly
86 divided into two geographically and climatically distinct regions: a low-lying basalt platform in
87 the north, with hills below 180 m a.s.l. (around 65% of island), and a mountainous region in the
88 south (Jones and Tye 2006). By the beginning of the twentieth century, the forest in the north
89 had been modified in many places by clear-felling, selective logging and the creation of cocoa,
90 coffee and coconut plantations (Exell 1973). After the country gained independence (1975) most
91 estates were abandoned and today the north is covered by secondary forest interspersed with
92 some commercial species (e.g. Oil Palm *Elaeis guineensis*). The south, owing to its inaccessibility,
93 remains covered in pristine forest with much floral endemism (Figueiredo et al. 2011).

94

95 *Model implementation*

96 The development and the implementation of the model were undertaken in R (R Core Team
97 2014; see Appendix A and B). Quantifying specific life-history traits in parrots is problematic,
98 mainly owing to the difficulties of marking birds individually and determining their lifespan, but
99 also because they range widely in groups and lack individual territories (Beissinger 2001). We
100 parameterized our model with data collected from Príncipe (Valle 2015), from elsewhere in the
101 Grey Parrot's range (i.e. Nigeria: McGowan 2001), from captive Grey Parrots (Taylor and Parkin
102 2008; Young et al. 2012), and from ecologically and morphometrically analogous parrot species
103 (Appendix C). Owing to Príncipe's isolation (>250 km from the nearest source population), its
104 Grey Parrots can be assumed to experience no immigration or emigration (Jones and Tye 2006),
105 and therefore to form a closed biological population. We set the finite rate of population increase
106 (growth rate per year: Rockwood 2006) λ to 1.1, which we calculated using consistently designed
107 pre-breeding population estimates from 2012 (Marsden et al. 2015) and 2014 (Valle et al. 2017),
108 according to the following formula:

$$109 \quad \lambda = \sqrt[x]{\frac{N_{t+x}}{N_t}} \quad (1)$$

110 where N_{t+x} and N_t are the number of individuals in the population at two different times
111 separated by x number of years.

112 Grey Parrots, like most psittacines, form long-term monogamous pair-bonds (Forshaw
113 1989; Seibert 2006). We assumed all females to breed as long as nest sites were available. In
114 captivity, the age of first successful breeding can vary greatly, depending on husbandry
115 conditions, but the median value (interquartile range) is 7.6 (5.4–9.5) (Young et al. 2012).
116 However, Grey Parrots usually reach sexual maturity between their third and fifth years of age
117 (de Grahl 1987; Lantermann 2000), as in other large parrot species (Young et al. 2012). We

118 assumed that the fourth year of age is the threshold of adulthood and that the subadult stage
119 comprises individuals in their second and third years.

120 Like most large psittacines, Grey Parrots are reported to breed once per year throughout
121 their range (Benson et al. 1988), so in the model we assumed a single annual brood. We collected
122 data on productivity for successful nests (fecundity) from 81 nests on Príncipe, which yielded a
123 mean \pm SD = 1.94 ± 0.72 chicks per brood (Valle 2015); since clutch-size is negatively correlated
124 with longevity (Ricklefs 2000), this is likely to be similar in other equally long-lived large parrot
125 species. Inter-annual variability in productivity on Príncipe was low (Valle 2015), so we assumed
126 an arbitrary low variance (SD) of 0.1 here. At birth, Grey Parrots have a ratio of 1 female to 1.17
127 males i.e. 46% ($n=3,892$, $\chi^2=25.01$, $p < 0.001$: Taylor and Parkin 2008). This is also the same as
128 that in other large parrots (mean \pm SD = $46\% \pm 5\%$, $n=22$; Taylor and Parkin 2008). Longevity
129 and age-specific survivorship of Grey Parrots in the wild are unknown, and such data are lacking
130 for most parrot species. Since longevity is positively correlated with body mass (Brouwer et al.
131 2000; Young et al. 2012) and adult survivorship (Lindstedt and Calder 1976), we used the mean
132 survivorship from three surrogate species whose mean body mass is closest to that of Grey
133 Parrots (≤ 60 g difference: Western Corella *Cacatua pastinator*, Major Mitchell's Cockatoo *C.*
134 *leadbeateri* and Glossy Black-cockatoo *Calyptorhynchus lathami*) involving only comparable data (e.g.
135 del Hoyo et al. 2017) and for which data on both first year and adult survivorship were available.
136 Thus, we assumed that (a) survivorship (\pm SD) is $52\% \pm 0.8\%$ for the first year of life, and 91%
137 $\pm 0.3\%$ for birds older than one year; (b) subadults, as fully formed and independent individuals,
138 exhibit the same survivorship as adults (Appendix C); (c) nest success (i.e. at least one chick
139 fledged) rate is 77%, based on all relevant and available literature on parrots (i.e. the mean
140 percentage nest success rate weighted by the number of nest years: see Appendix C); and (d) nest
141 site availability limits the annual number of reproductive pairs (Beissinger and Bucher 1992b).
142 We inferred the maximum number of available nest sites, i.e. $5,502 \pm 2,132$, from the mean
143 minimum density of nests (SD) for primary and secondary forest estimated on Príncipe, i.e. $72 \pm$
144 26 , and 17 ± 8 nests km^{-2} respectively (Valle 2015), and used a theta-logistic model to simulate
145 nest site availability (see Appendix A).

146 A factor likely to influence population growth and carrying capacity is food availability.
147 This parameter is difficult to quantify and predict because it is heavily dependent on fine habitat
148 characteristics (e.g. floristic composition and plantation quality), intra- and inter-annual climate
149 variability, and the ability of Grey Parrots to adapt to them. However, since the focus of the
150 analysis is to inform management of small and declining populations where intraspecific
151 competition for food is not a limiting factor, we set no further carrying capacity to the model
152 other than nest site availability.

153 In captivity, parrot lifespans vary greatly with the conditions in which the birds are kept
154 (in Grey Parrot: median = 8.2 years, IQR = 5.8–12.2, maximum = 48, $n = 1,979$: Young et al.
155 2012). There are virtually no data on wild parrot mortality, so we assumed an arbitrary maximum
156 lifespan of 45 years in the model, as adults are probably somewhat shorter-lived in the wild than
157 in captivity (Brouwer et al. 2000). Because no data are available on the effects of senescence on
158 reproductive output, we assumed parrots to be active breeders until they are old, as suggested by
159 studies in captivity (Young et al. 2012); i.e. in our model, lifespan and age of last breeding
160 coincide. Owing to annual mortality rates, adults are very unlikely to reach such old age in the
161 wild anyway. The life-history traits used in the baseline model are summarized in Table 1. The
162 model was validated using the known population trajectory of Grey Parrots on Príncipe in the
163 1995–2014 period (Valle 2015; Appendix A).

164

165 *Modelling population dynamics and the sustainability of harvest*

166 To understand the effects of Grey Parrot harvest on Príncipe, we ran the model with and
167 without a simulated annual harvest \pm SD of 600 ± 100 (which is the approximate number of
168 individuals harvested before the 2005 trade ban was imposed; Juste 1996; Melo 1998, Valle
169 2015), 900 ± 100 and $1,200 \pm 100$ individuals, representing up to a doubling of the recorded
170 harvest levels. Traditionally on the island, Grey Parrots were harvested only as chicks from the
171 nests, leaving adults unharmed and the nest cavities intact to be exploited again in the following
172 years (Juste 1996; Melo 1998), unlike what happens in most countries where parrot chick harvest
173 results in the destruction of the cavity (e.g. Beissinger and Bucher 1992a; Brightsmith 2005) .
174 Although standard deviations were set arbitrarily, these values were based on anecdotal evidence
175 from Príncipe (Valle 2015).

176 Unless otherwise stated we initialized all simulations with a population size of 7,996
177 individuals, as estimated from the 2014 post-breeding Distance Sampling survey (Valle et al.
178 2017), i.e. 3,678 females based on the sex ratio of 46% given above. We performed sensitivity
179 analysis to explore how predicted population trajectories responded to sequential 5% decreases
180 in juvenile survivorship, and 2% decreases in subadult and adult survivorship.

181 In some countries, harvest pressure on Grey Parrot populations has been highly variable
182 over time, owing to supply/demand dynamics, changes in legislation, and inconsistent levels of
183 enforcement (UNEP-WCMC 2015). We explored the effects of this variability by first running
184 simulations for a fixed annual quota of exactly 900 and a 1,000 chicks. These figures represent
185 the region around the tipping point (critical harvest volume) between sustainability and non-
186 sustainability (see results), and hence a useful ‘total harvest value’ to explore the issue of
187 variability in harvest volume. We then repeated the analysis for the same average annual quota
188 but with a variability of 67% (i.e. 900 ± 603 and $1,000 \pm 670$ chicks, respectively) which mirrors
189 that reported by CITES for Cameroon, the world’s major exporter of Grey Parrots between
190 1981 and 2013 (UNEP-WCMC 2015). While this estimate of variation is based on the most
191 relevant available data, it does not account for pre-export mortality, which is almost impossible
192 to quantify with any degree of precision i.e. 30–66% for Grey Parrots (Fotso 1998; McGowan
193 2001).

194 To explore the impact of different trapping methods, we simulated a critical yield of 900
195 ± 100 individuals under three different trapping scenarios: (1) *chick harvesting*, where only chicks
196 are taken from nests, as was the tradition in Príncipe (Juste 1996; Melo 1998); (2) *nest raiding*,
197 where one adult is taken with every two chicks, as a simulation of the removal of a parent at the
198 moment of chick harvest (e.g. as in Ghana: Dändliker 1992); and (3) *indiscriminate trapping*, where
199 individuals are taken randomly from the population (e.g. by trapping at aggregations in
200 Cameroon or Democratic Republic of the Congo [DRC]: Marsden et al. 2013, Ngenyi 2003).

201

202 *Modelling interactions between habitat quantity, habitat quality and harvest volume*

203 We investigated the responses of the population to habitat loss or degradation simulating a
204 decrease in available nest sites (the most immediate limiting factor in parrots: Beissinger and
205 Bucher 1992b; Munn 1992). Thus, we modelled three possible scenarios of habitat loss using
206 nest density data given under ‘Model implementation’: (1) ‘low’, where (as at present) 30% of

207 Príncipe is covered by primary and 70% by secondary forest, i.e. 4,553 nest sites \pm 1,821; (2)
208 'medium', where secondary forest has extended to 83% of the island and 17% is left protected,
209 to comply with the target set by the Convention on Biological Diversity (CBD), which
210 established protection goals for terrestrial and inland water areas by 2020, i.e. 3,570 \pm 1,498 nest
211 sites (Millennium Ecosystem Assessment 2005); and (3) 'high', where all suitable habitat has been
212 cleared apart from a protected (primary forest) area equivalent to 17% of the island, i.e. 1,674 \pm
213 606 sites. For each of these scenarios we ran the model for four different regimes: (1) chick
214 harvesting; (2) nest raiding; (3) indiscriminate trapping; and (4) no harvest. For each scenario
215 involving some harvest, we modelled different harvest quotas, i.e. 600 \pm 100, 900 \pm 100 and
216 1,200 \pm 100. All simulations were run for 50 years.

217

218 **Results**

219 The modelled population showed much greater sensitivity to variations in adult than in juvenile
220 survivorship (Fig. 1). Juvenile survival could be halved (from 52% to 26%) without inverting the
221 long-term population trajectory, whereas reductions of only around 12% in adult survival (from
222 91%) were predicted to do so.

223 When subject to annual harvest of chicks, population growth was unaffected to around a
224 harvest equivalent to 11.3% (900 \pm 100 chicks per year; Fig. 2) of the initial population.
225 However, increasing the harvest by 300 individuals (to 15% of the initial population; Fig. 2)
226 would most probably drive the population to extinction within decades.

227 The impact of harvest was also sensitive to large inter-annual variation in capture rate
228 (i.e. as shown by Cameroon between 1981 and 2013), which around a hypothetical quota of 900
229 chicks increased the extinction risk to the population over a fixed quota of the same volume (Fig.
230 3). If applied to the already critical harvest of 1,000 chicks per year (see above), variability in
231 annual harvests both increased the chances of decline and accelerated the decline process (i.e.
232 steeper negative trajectory; Fig. 3).

233 Sustainability of harvests of a given volume varied greatly with capture technique. While
234 an annual harvest of 900 chicks did not affect the natural population trajectory, trajectories were
235 very different under the alternative trapping regimes (Fig. 4). If an adult was harvested with every
236 two chicks, then trajectories were highly variable across runs, but most showed inexorable long-
237 term declines to extinction. Trapping the same number of individuals indiscriminately across age
238 classes was certain to cause extinction within a few years.

239 The addition of incremental habitat loss to the models reduced carrying capacity and,
240 consequently, accelerated the negative effects of harvest. Once again capture method and harvest
241 quota were, in that order, the variables which most affected the long-term survival of the
242 population (Table 2, Fig. 5).

243

244 **Discussion**

245 Our demographic models point to the crucial effect that capture method and, by extension, the
246 age of traded birds have on population stability in Grey Parrots. The implications of sex- or age-
247 selective harvest have been documented in herbivores (Giles and Findlay 2004), large carnivores
248 (Packer et al. 2009), birds (Hunter and Caswell 2005) and fish (Birkeland and Dayton 2005), and

249 indeed a consideration of age structure is recognized as being critical in sustainable harvest
250 management (Getz and Haight 1989). However, whilst CITES does not provide clear guidelines
251 on the matter, too often scientific authorities set quotas without consideration of population
252 dynamics (Smith et al. 2011). Certainly, as with most CITES-listed taxa (Smith et al. 2011), none
253 of the substantial export quotas for Grey Parrots has ever been based on population modelling
254 (CITES 2006, 2014). A change in this approach has been urged by the scientific community for
255 several taxa, where alternative age-based harvest regulations have been proposed (e.g. Balme et
256 al. 2012). Our study indicates that such a change is likely to be crucial in all medium and large
257 psittacines which have low annual reproductive rates and long lifespans, and in which trade is
258 permitted.

259 Differences in capture method may at least partly explain why Grey Parrot populations
260 have collapsed dramatically in Ghana and elsewhere on the African mainland (Annorbah et al.
261 2016; Martin et al. 2014) while at the same time remaining relatively healthy on Príncipe. When
262 many mainland populations became depleted but demand remained strong, it is plausible that a
263 shift occurred from taking only nestlings to taking any bird possible. On Príncipe, by contrast,
264 owing to local tradition and the higher market value of chicks, adult parrots have been trapped
265 only very occasionally, during times of high demand and low supply, e.g. outside the breeding
266 season (Valle 2015). This raises serious concern for the species in countries like DRC, Cameroon
267 and Congo where birds, legally or not, are indiscriminately caught with nets and glue traps at
268 natural aggregations such as saltlicks and roosts, inevitably involving considerable numbers of
269 adults (Hart et al. 2016; Marsden et al. 2013). DRC is also the only range state to have entered a
270 reservation on the recent uplisting of Grey Parrot to Appendix I, thus effectively exempting itself
271 from the trade ban (CITES 2017).

272 Variation in parrot harvest volume across years also compromised the sustainability of a
273 given harvest level. Irregular spikes in numbers captured, as often reported by many exporting
274 countries (Martin et al. 2014; UNEP-WCMC 2015), are more likely to be detrimental to the
275 survival of a population than are 'steady' annual harvests. In effect, if quotas are set around a
276 critical harvest volume, individual years or clusters of years with particularly heavy yields can
277 send populations on negative trajectories which subsequent years of lighter harvests do not
278 reverse. Thus, if quotas are to be set for a population, they are more likely to be sustainable if the
279 harvest is uniform across years, and this can only come from effective trade management.
280 However, even if precise monitoring of bird numbers within trade is possible, it is still likely to
281 fall short of ensuring a uniform harvest, since post-capture mortality can be extremely high in
282 parrots and it is also highly variable across 'shipments' (UNEP-WCMC 2015).

283 Our model indicates that the negative impact of habitat loss on Príncipe was likely to be
284 far less immediately important than trapping volume or method, and acted mainly to dampen
285 population growth and reduce carrying capacity. This is consistent with what has been found for
286 other parrot species (Beissinger and Bucher 1992b; Munn 1992), and is more likely to be due to
287 the reduced availability of nest cavities than to a shortage of food (Newton 1994; Newton 1998).
288 Moreover, our results support the theory that, if food resources are not limiting, any
289 management intervention aimed at increasing the number of available nest cavities (i.e. artificial
290 alternatives that are readily used by the species) has the potential to increase the carrying capacity
291 of the habitat and, therefore, the maximum size of the population (Cockle et al. 2010). In well-
292 preserved forests such as those in Príncipe or parts of Cameroon, habitat loss may not be as
293 important as capture issues, but this may not be the case where availability of nest sites is limited
294 (e.g. Cornelius et al. 2008; Saunders et al. 2014). Indeed, in Ghana, loss of forest cover generally,
295 and felling of huge trees in particular, have probably greatly compounded the effects of trade on

296 Grey Parrots (Annorbah et al. 2016). Moreover, extreme habitat loss is likely to exacerbate inter-
297 and intraspecific competition for food resources, introducing a further limiting factor (Newton
298 1998), particularly in small and isolated populations (e.g. Echo Parakeet; Jones 2004). Although
299 parrots are known for their dietary plasticity, the extent to which such adaptability can withstand
300 the pressure of global changes is understudied (Renton et al. 2015). Interestingly, the Grey Parrot
301 population on Príncipe spent a great proportion of their time feeding on the fruits of Oil Palms
302 *Elaeis guineensis*, an abundant source of food on the island (Valle 2015).

303 The sustainability of parrot trade is managed by CITES through a system of quotas, i.e.
304 through regulating harvest volume (Martin et al. 2014). These quotas are rarely based on those
305 ‘non-detriment findings’ which are much sought after by CITES itself (Rosser and Haywood
306 2002). Our study reveals that the line between safe and ruinous harvest volumes is fine, and that
307 trapping method and quota observance are pivotal to the stability of harvested populations of
308 large parrots. Reliable data on such factors are hardly ever available for traded parrots (Poole and
309 Shepherd 2016). Thus, for a population model to yield a reliable ‘non-detriment finding’ for a
310 given harvest quota (Smith et al. 2011), in-country population monitoring and trade enforcement
311 systems would need to improve significantly. Indeed, if capture method, post-capture mortality,
312 occasional but high exceeding of quotas, and reliability of reported figures were all factored into
313 models of the sustainability of parrot harvesting, it is unlikely that recent trade in Grey Parrots
314 and many other psittacines of similar size could be judged ‘non-detrimental’ with any reasonable
315 degree of confidence.

316

317 **Aknowledgements**

318

319 Parrots International generously funded the research reported here. Eng. Arlindo Carvalho
320 (National General Director of the Environment), Eng. Nestor Umbelina (Regional Secretary to
321 the Infrastructures and the Environment), and Daniel Ramos (Director of the Parque Natural
322 d’Óbo do Príncipe) fully endorsed the project and facilitated our work. Here Be Dragons (HBD)
323 investment group kindly provided invaluable logistical support during fieldwork. Satiro and Lynsey
324 Crellin provided crucial assistance in the collection of the data. Finally, four referees made helpful
325 suggestions which we gratefully followed.

326

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502 **Tables**

503 **Table 1.** *Parameters of the model used to validate the population model for Grey Parrots on Príncipe.*

<i>Life history trait</i>	<i>Value used in the model</i>
Number of iterations	1,000
Number of year modelled	20 (1995–2014)
Number of population modelled	1
Inbreeding depression	No inbreeding depression assumed
Immigration rate	N/A
Emigration rate	N/A
Reproductive system	Long-term monogamy
Age of first reproduction	4 years
Maximum age of reproduction	45 years
Maximum lifespan	45 years
Maximum number of broods/year	1
Maximum number of progeny/brood	3
Mean number of chicks per brood (SD)	1.94 (0.7)
Nest success	77%
Female : male ratio at birth	46%
Density dependence in reproduction	Availability of nest sites (SD)=5,502 (2,132)
Proportion of adult females breeding	All
λ - finite rate of increase	1.1
Juvenile survivorship (SD)	52 % (0.8)
Subadult survivorship (SD)	91 % (0.3)
Adult survivorship (SD)	91 % (0.3)
Initial population size	Various depending from simulation
Age distribution (%) of initial population	1:2:2.5
Carrying capacity	None
Number of juveniles harvested (SD)	600 (100)
Number of subadults harvested	0
Number of adults harvested	0

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513 **Table 2.** *Predicted probability of the population going extinct within 50 years (percentage of model iterations that resulted*
 514 *in extinction, n = 1,000) when the population is subject to different magnitudes of harvest within three hypothetical scenarios*
 515 *of habitat loss (see also Figure 5).*

		Low	Medium	High
No harvest		0	0	0
	<i>600 ± 100</i>	0	0	0
Chicks harvest	<i>900 ± 100</i>	0.4 %	0.3 %	0.4 %
	<i>1,200 ± 100</i>	81.3 %	80.1 %	84.0 %
	<i>600 ± 100</i>	0	0	0
Nest raiding	<i>900 ± 100</i>	53.5 %	54.8 %	59.0 %
	<i>1,200 ± 100</i>	100 %	100 %	100 %
	<i>600 ± 100</i>	0	0	0
Indiscriminate trapping	<i>900 ± 100</i>	34.3 %	35.2 %	38.2 %
	<i>1,200 ± 100</i>	100 %	100 %	100 %

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532 **Figure Legends**

533 **Figure 1.** Sensitivity of the population trend to (a) an incremental 5% decrease in juvenile
534 survivorship (grey lines) from the current (SD) 52% (8) (black line); and (b) an incremental 2%
535 decrease in subadult and adult survivorship (grey lines) from the original (SD) 91% (3) (black
536 line).

537 **Figure 2.** Predicted population trend and individual simulations in response to no harvest (0%
538 of the initial population); and an annual harvest (SD) of 600 (100), i.e. 7.5% of the initial
539 population, 900 (100), i.e. 11.3% of the initial population, and 1,200 (100) chicks, i.e. 15% of the
540 initial population, with associated finite rate of population increase (λ). Light grey lines =
541 population trajectories resulting from each simulation; black solid lines = mean trajectory.

542 **Figure 3.** Predicted population trend and individual simulations in response to harvesting a fixed
543 (left) or variable (right) quota of 900 (top) and of 1,000 (bottom) chicks each year.

544 **Figure 4.** Difference in predicted 50-year trends when the population is subject to a harvest of
545 900 ± 100 harvesting chicks only, nest raiding (i.e. one adult is collected with every two chicks)
546 and indiscriminate trapping.

547 **Figure 5.** Predicted 50-year trends (y axis expressed in thousands) when the population is
548 subject to different magnitudes of harvest (SD), i.e. solid line = 600 ± 100 , dashed line = 900
549 ± 100 , dotted line = $1,200 \pm 100$, yielded with a variety of techniques (chick harvesting, nest
550 raiding and indiscriminate trapping), in three hypothetical scenarios of habitat loss, i.e. Low =
551 30% primary and 70% secondary forest (i.e. $4,553 \pm 1,821$ nests); Medium = 17% and 83% (i.e.
552 $3,570 \pm 1,498$ nests); and High = only 17% primary (i.e. $1,674 \pm 606$ nests).

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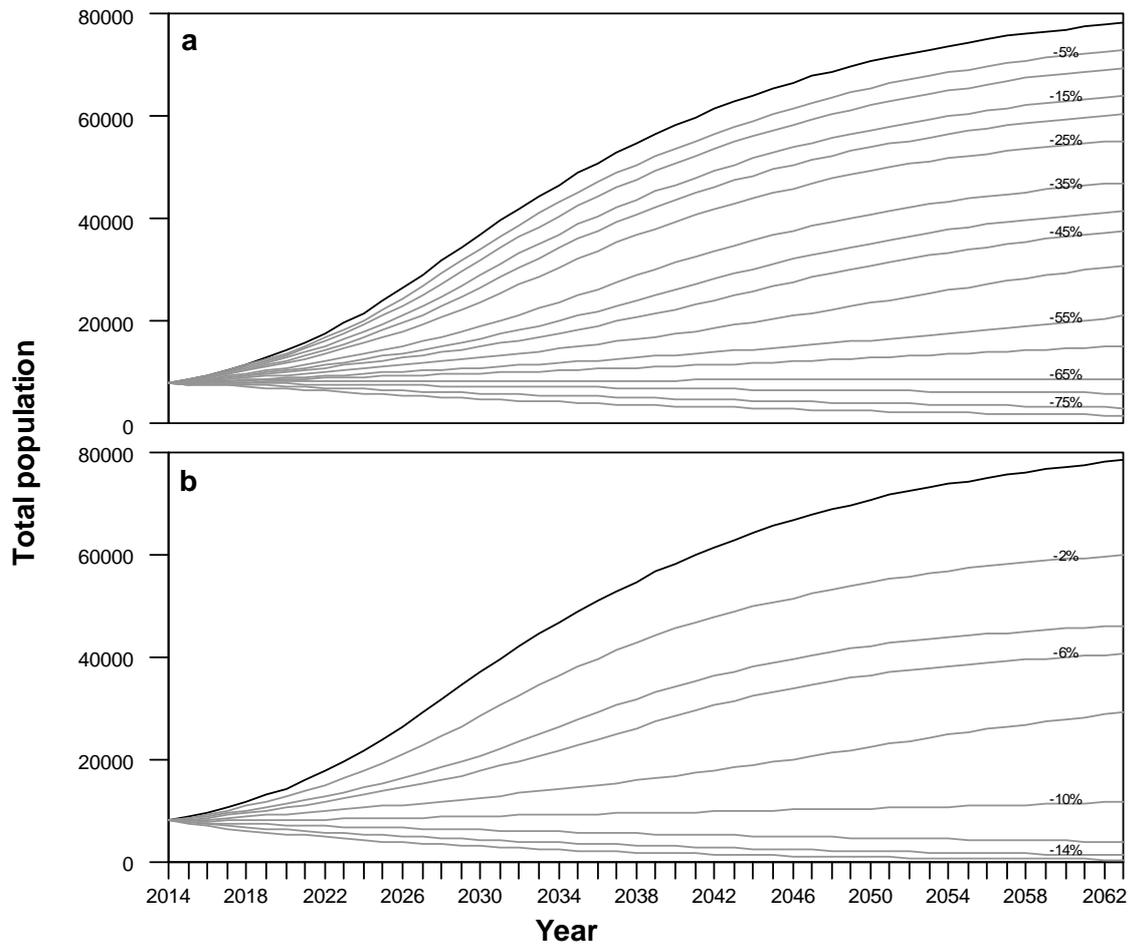
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561 **Figures**

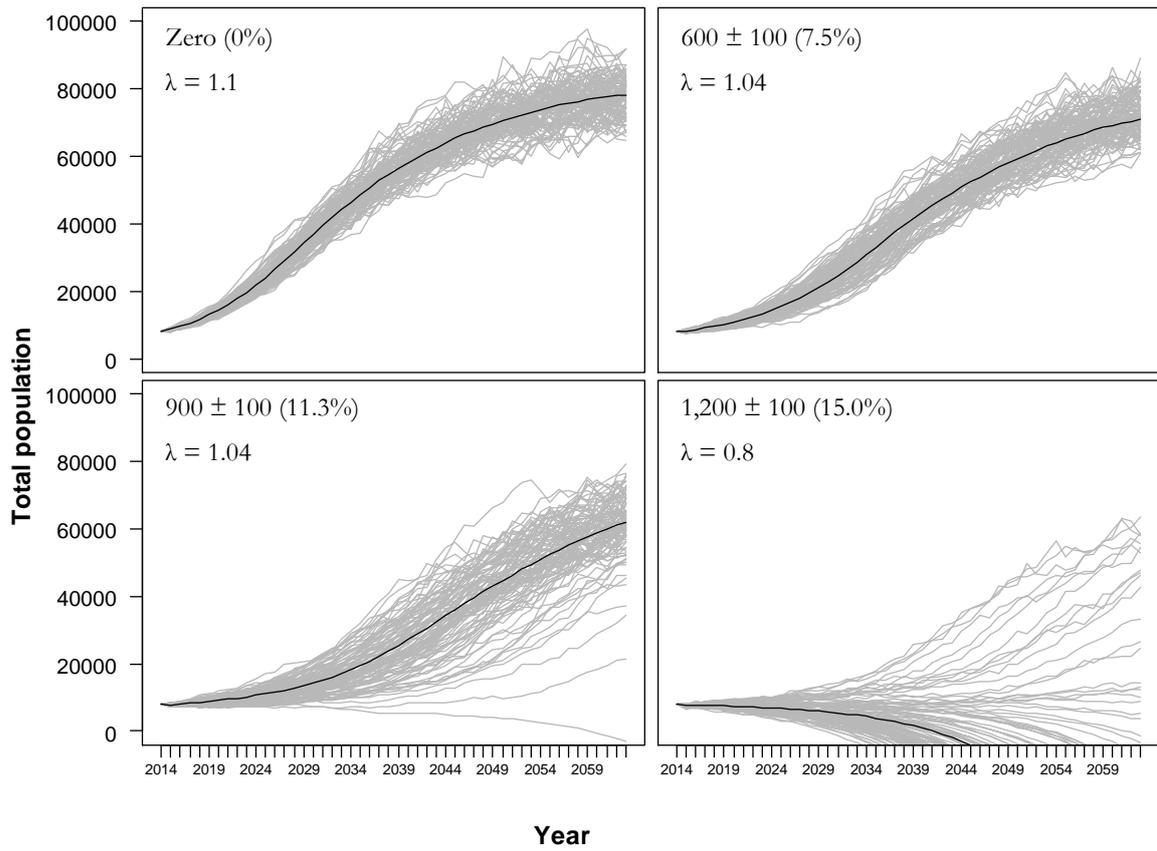
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564 **Figure 1**

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567 **Figure 2**

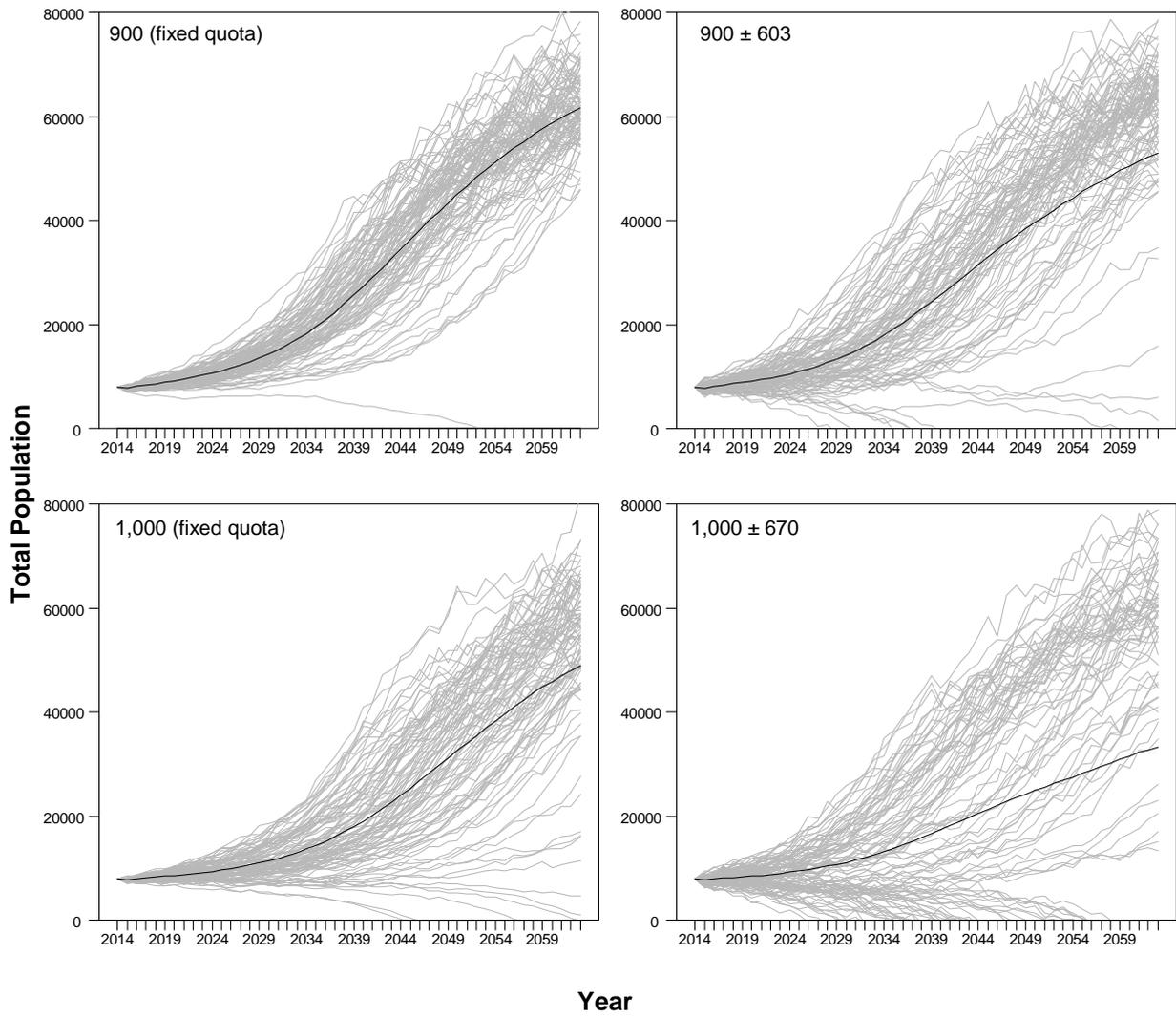
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573 **Figure 3**

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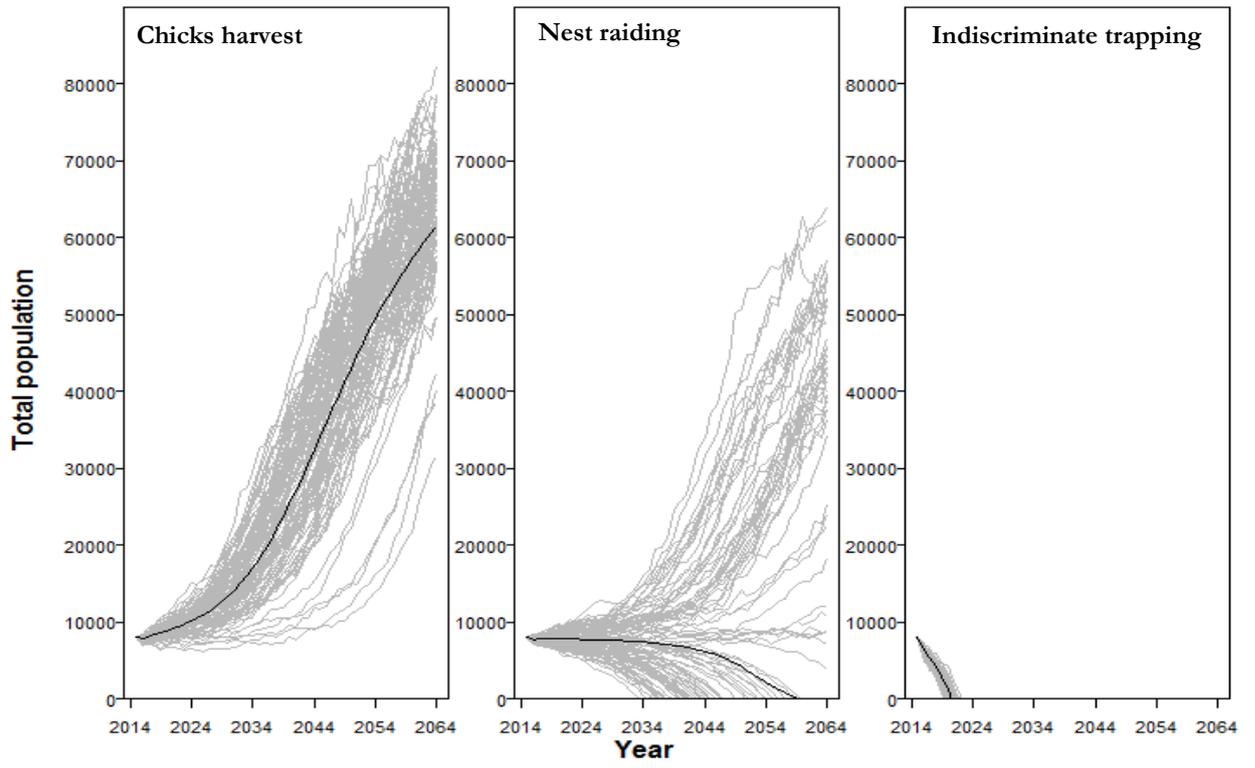
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582 **Figure 4**

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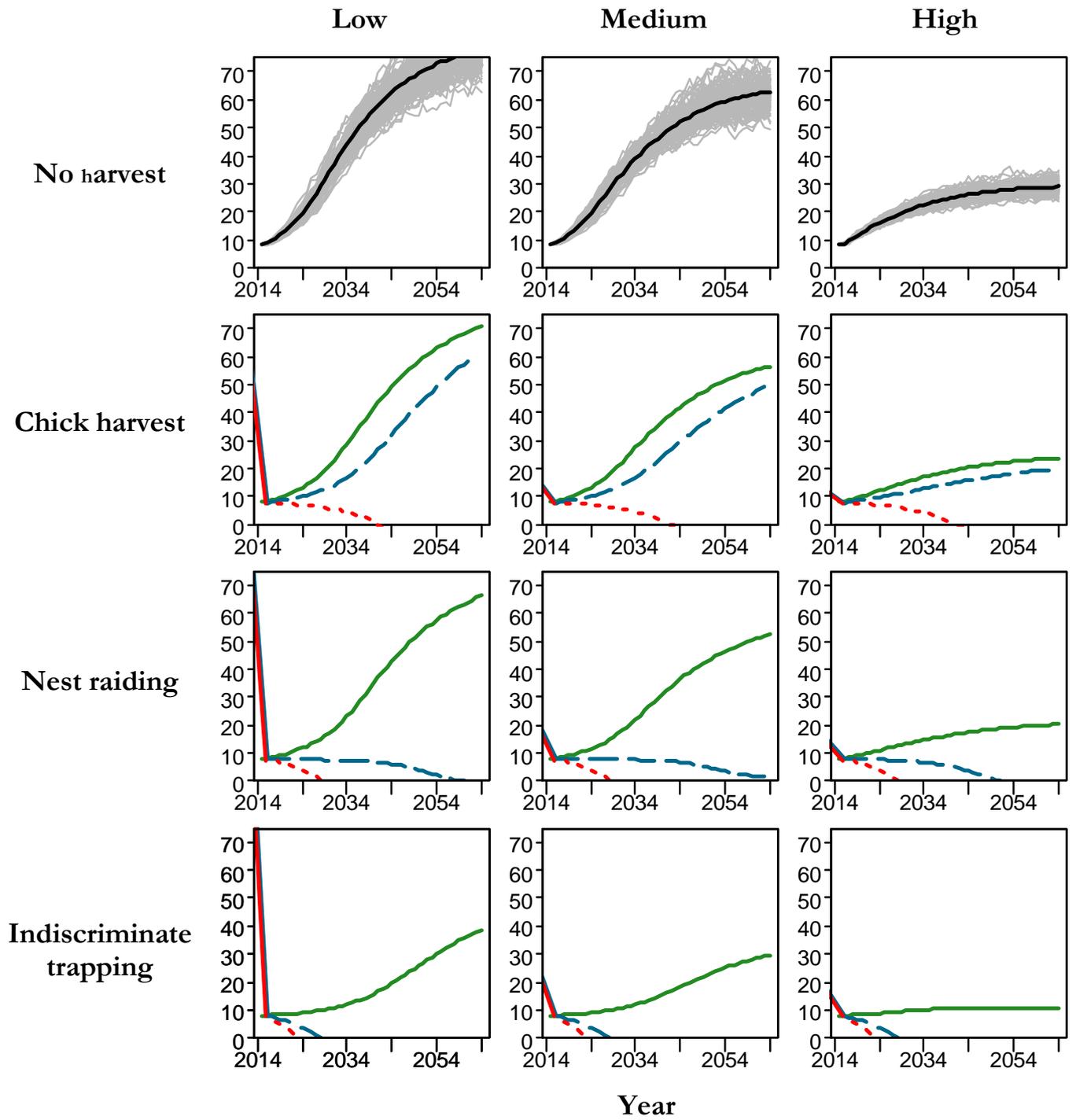
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591 Figure 5

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