

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

Simon Valle^{1*}, Nigel J. Collar², W. Edwin Harris¹ and Stuart J. Marsden¹

¹ School of Science & the Environment, Manchester Metropolitan University, Chester Street, Manchester M1 5GD, U.K.

² BirdLife International, Cambridge, UK

* Corresponding Author Email: S.Valle@mmu.ac.uk

Abstract

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

Keywords

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

Introduction

The international trade in live animals and wildlife products is a constituent threat to around one-third of all bird and mammal species (UNEP-WCMC 2015). Legal trade is estimated to be worth over USD 8 billion a year globally (Zhang et al. 2008), and this figure is likely to double

37 when illegal trade is taken into account (Pires 2012). Parrots, and especially the larger species, are
38 the most traded wild-caught group of birds (UNEP-WCMC 2015), and there are serious
39 concerns about [the sustainability of current harvest levels](#) in many species (Beissinger and
40 Bucher 1992a). Such concerns arise not just from the sheer volume of [parrots in trade](#), but also
41 from [the birds' poor resilience to overharvesting](#) (Beissinger 2001; Pain et al. 2006; Wright et al.
42 2001), inadequate enforcement of trade regulations (Martin et al. 2014), and the paucity of
43 reliable population and demographic data to support harvest models (Marsden and Royle 2015).

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

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

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

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

71

72 **Methods**

73 *Study area and population*

74 [The heavily traded Grey Parrot has suffered a dramatic global decline \(Annorbah et al. 2016;](#)
75 [BirdLife International 2017\);- As a result, its global conservation status has deteriorated from](#)
76 [Near Threatened through Vulnerable to Endangered in just five years \(IUCN 2016\), and calls for](#)
77 [a ban on its trade have only recently been accepted, albeit not unanimously \(CITES 2017\).](#)

78 [Nonetheless, the species](#) remains relatively common in some parts of its range (Marsden et al.
79 2015). One such area is the small (136 km²) island of Príncipe (São Tomé and Príncipe, Gulf of
80 Guinea), which hosts a demographically isolated, relatively healthy, and well-studied population
81 (Fahlman 2002; Juste 1996; Marsden et al. 2015; Melo 1998; Valle et al. 2017). Grey Parrots were
82 harvested at an average rate of 600 birds per year from the wild in the 1990s (Juste 1996; Melo
83 1998) until a regional ban on all trade was put in place in 2005 (Valle 2015). Príncipe is broadly
84 divided into two geographically and climatically distinct regions: a low-lying basalt platform in
85 the north, with hills below 180 m a.s.l. (around 65% of island), and a mountainous region in the
86 south (Jones and Tye 2006). By the beginning of the twentieth century, the forest in the north
87 had been modified in many places by clear-felling, selective logging and the creation of cocoa,
88 coffee and coconut plantations (Exell 1973). After the country gained independence (1975) most
89 estates were abandoned and today the north is covered by secondary forest interspersed with
90 some commercial species (e.g. Oil Palm *Elaeis guineensis*). The south, owing to its inaccessibility,
91 remains covered in pristine forest with much floral endemism (Figueiredo et al. 2011).

92

93 *Model implementation*

94 The development and the implementation of the model were undertaken in R (R Core Team
95 2014; see Appendix A and B). Quantifying specific life-history traits in parrots is problematic,
96 mainly owing to the difficulties of marking birds individually and determining their lifespan, but
97 also because they range widely in groups and lack individual territories (Beissinger 2001). We
98 parameterized our model with data collected from Príncipe (Valle 2015), from elsewhere in the
99 Grey Parrot's range (i.e. Nigeria: McGowan 2001), from captive Grey Parrots (Taylor and Parkin
100 2008; Young et al. 2012), and from ecologically and morphometrically analogous parrot species
101 (Appendix C). Owing to Príncipe's isolation (>250 km from the nearest source population), its
102 Grey Parrots can be assumed to experience no immigration or emigration (Jones and Tye 2006),
103 and therefore to form a closed biological population. We set the finite rate of population increase
104 (growth rate per year: Rockwood 2006) λ to 1.1, which we calculated using consistently designed
105 pre-breeding population estimates from 2012 (Marsden et al. 2015) and 2014 (Valle et al. 2017),
106 according to the following formula:

$$107 \quad \lambda = \sqrt[x]{\frac{N_{t+x}}{N_t}} \quad (1)$$

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

110 Grey Parrots, like most psittacines, form long-term monogamous pair-bonds (Forshaw
111 1989; Seibert 2006). We assumed all females to breed as long as nest sites were available. In
112 captivity, the age of first successful breeding can vary greatly, depending on husbandry
113 conditions, but the median value (interquartile range) is 7.6 (5.4–9.5) (Young et al. 2012).
114 However, Grey Parrots usually reach sexual maturity between their third and fifth years of age
115 (de Grahl 1987; Lantermann 2000), as in other large parrot species (Young et al. 2012). We
116 assumed that the fourth year of age is the threshold of adulthood and that the subadult stage
117 comprises individuals in their second and third years.

118 Like most large psittacines, Grey Parrots are reported to breed once per year throughout
119 their range (Benson et al. 1988), so in the model we assumed a single annual brood. We collected
120 data on productivity for successful nests (fecundity) from 81 nests on Príncipe, which yielded a

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

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

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

162

163 *Modelling population dynamics and the sustainability of harvest*

164 To understand the effects of Grey Parrot harvest on Príncipe, we ran the model with and
165 without a simulated annual harvest \pm SD of 600 \pm 100 (which is the approximate number of
166 individuals harvested before the [2005](#) trade ban was imposed; Juste 1996; Melo 1998, Valle

167 2015), 900 ± 100 and $1,200 \pm 100$ individuals. Traditionally on the island, Grey Parrots were
168 harvested only as chicks from [the nests, leaving adults unharmed and the nest cavities intact to](#)
169 [be exploited again in the following years](#) (Juste 1996; Melo 1998), [unlike what happens in most](#)
170 [countries where parrot chick harvest results in the destruction of the cavity \(e.g. Beissinger and](#)
171 [Bucher 1992a; Brightsmith 2005\)](#). Although standard deviations were set arbitrarily, these values
172 were based on anecdotal evidence from Príncipe (Valle 2015).

173 Unless otherwise stated we initialized all simulations with a population size of 7,996
174 individuals, as estimated from the 2014 post-breeding Distance Sampling survey (Valle et al.
175 2017), i.e. 3,678 females based on the sex ratio of 46% given above. We performed sensitivity
176 analysis to explore how predicted population trajectories responded to sequential 5% decreases
177 in juvenile survivorship, and 2% decreases in subadult and adult survivorship.

178 In some countries, harvest pressure on Grey Parrot populations has been highly variable
179 over time, owing to supply/demand dynamics, changes in legislation, and inconsistent levels of
180 enforcement (UNEP-WCMC 2015). We explored the effects of this variability by running
181 simulations for a fixed annual quota of exactly 1,000 chicks, and for the same average annual
182 quota but with a variability of 67% (i.e. $1,000 \pm 670$ chicks), which mirrors that reported by
183 CITES for Cameroon, the world's major exporter of Grey Parrots between 1981 and 2013
184 (UNEP-WCMC 2015). [After running a number of trial simulations, a quota of 1,000 individuals](#)
185 [was arbitrarily chosen, as it best illustrated the difference between the presence and the absence](#)
186 [of variability](#). While this estimate of variation is based on the most relevant available data, it does
187 not account for pre-export mortality, which is almost impossible to quantify with any degree of
188 precision i.e. 30–66% for Grey Parrots (Fotso 1998; McGowan 2001).

189 To explore the impact of different trapping methods, we simulated a critical yield of 900
190 ± 100 individuals under three different trapping scenarios: (1) *chick harvesting*, where only chicks
191 are taken from nests, as was the tradition in Príncipe (Juste 1996; Melo 1998); (2) *nest raiding*,
192 where one adult is taken with every two chicks, as a simulation of the removal of a parent at the
193 moment of chick harvest (e.g. as in Ghana: Dändliker 1992); and (3) *indiscriminate trapping*, where
194 individuals are taken randomly from the population (e.g. by trapping at aggregations in
195 Cameroon or Democratic Republic of the Congo [DRC]: Marsden et al. 2013, Ngenyi 2003).

196

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

198 We investigated the responses of the population to [habitat loss or degradation simulating](#) a
199 decrease in available nest sites (the most immediate limiting factor in parrots: Beissinger and
200 Bucher 1992b; Munn 1992). [Thus, we modelled](#) three possible scenarios of [habitat loss](#) using
201 nest density data given under 'Model implementation': (1) 'low', where (as at present) 30% of
202 Príncipe is covered by primary and 70% by secondary forest, i.e. $4,553$ nest sites $\pm 1,821$; (2)
203 'medium', where secondary forest has extended to 83% of the island and 17% is left protected,
204 to comply with the target set by the Convention on Biological Diversity (CBD), which
205 established protection goals for terrestrial and inland water areas by 2020, i.e. $3,570 \pm 1,498$ nest
206 sites (Millennium Ecosystem Assessment 2005); and (3) 'high', where all suitable habitat has been
207 cleared apart from a protected (primary forest) area equivalent to 17% of the island, i.e. $1,674 \pm$
208 606 sites. For each of these scenarios we ran the model for four different regimes: (1) chick
209 harvesting; (2) nest raiding; (3) indiscriminate trapping; and (4) no harvest. For each scenario
210 involving some harvest, we modelled different harvest quotas, i.e. 600 ± 100 , 900 ± 100 and
211 $1,200 \pm 100$. All simulations were run for 50 years.

212

213 **Results**

214 The modelled population showed much greater sensitivity to variations in adult than in juvenile
215 survivorship (Fig. 1). Juvenile survival could be halved (from 52% to 26%) without inverting the
216 long-term population trajectory, whereas reductions of only around 12% in adult survival (from
217 91%) were predicted to do so.

218 When subject to annual harvest of chicks, population growth was unaffected to around a
219 harvest equivalent to 11.3% (900 ± 100 chicks per year; Fig. 2) of the initial population.
220 However, increasing the harvest by 300 individuals (to 15% of the initial population; Fig. 2)
221 would most probably drive the population to extinction within decades.

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

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

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

238

239 **Discussion**

240 Our demographic models point to the crucial effect that capture method and, by extension, the
241 age of traded birds have on population stability in Grey Parrots. The implications of sex- or age-
242 selective harvest have been documented in herbivores (Giles and Findlay 2004), large carnivores
243 (Packer et al. 2009), birds (Hunter and Caswell 2005) and fish (Birkeland and Dayton 2005), and
244 indeed a consideration of age structure is recognized as being critical in sustainable harvest
245 management (Getz and Haight 1989). However, whilst CITES does not provide clear guidelines
246 on the matter, too often scientific authorities set quotas without consideration of population
247 dynamics (Smith et al. 2011). Certainly, as with most CITES-listed taxa (Smith et al. 2011), none
248 of the substantial export quotas for Grey Parrots has ever been based on population modelling
249 (CITES 2006, 2014). A change in this approach has been urged by the scientific community for
250 several taxa, where alternative age-based harvest regulations have been proposed (e.g. Balme et
251 al. 2012). Our study indicates that such a change is likely to be crucial in [all medium and large
252 psittacines which have low annual reproductive rates and long lifespans, and in which trade is
253 permitted](#).

254 Differences in capture method may at least partly explain why Grey Parrot populations
255 have collapsed dramatically in Ghana and elsewhere on the African mainland (Annorbah et al.
256 2016; Martin et al. 2014) while at the same time remaining relatively healthy on Príncipe. When
257 many mainland populations became depleted but demand remained strong, it is plausible that a
258 shift occurred from taking only nestlings to taking any bird possible. On Príncipe, by contrast,
259 owing to local tradition and the higher market value of chicks, adult parrots have been trapped
260 only very occasionally, during times of high demand and low supply, e.g. outside the breeding
261 season (Valle 2015). This raises serious concern for the species in countries like DRC, [Cameroon](#)
262 [and Congo](#) where birds, [legally or not](#), are indiscriminately caught with nets [and glue traps](#) at
263 natural aggregations such as saltlicks and roosts, inevitably involving considerable numbers of
264 adults (Hart et al. 2016; Marsden et al. 2013). [DRC is also the only range state to have entered a](#)
265 [reservation on the recent uplisting of Grey Parrot to Appendix I, thus effectively exempting itself](#)
266 [from the trade ban \(CITES 2017\).](#)

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

278 Our model indicates that the negative impact of habitat loss on Príncipe was likely to be
279 far less immediately important than trapping volume or method, and acted mainly to dampen
280 population growth and reduce carrying capacity. This is consistent with what has been found for
281 other parrot species (Beissinger and Bucher 1992b; Munn 1992), and is more likely to be due to
282 the reduced availability of nest cavities than to a shortage of food (Newton 1994; Newton 1998).
283 [Moreover, our results support the theory that, if food resources are not limiting, any](#)
284 [management intervention aimed at increasing the number of available nest cavities \(i.e. artificial](#)
285 [alternatives that are readily used by the species\) has the potential of increasing the carrying](#)
286 [capacity of the habitat and, therefore, the maximum size of the population](#) (Cockle et al. 2010).
287 In well-preserved forests such as those in Príncipe or parts of Cameroon, habitat loss may not be
288 as important as capture issues, but this may not be the case where availability of nest sites is
289 limited (e.g. Cornelius et al. 2008; Saunders et al. 2014). Indeed, in Ghana, loss of forest cover
290 generally, and felling of huge trees in particular, have probably greatly compounded the effects of
291 trade on Grey Parrots (Annorbah et al. 2016). [Moreover, extreme habitat loss is likely to](#)
292 [exacerbate inter- and intraspecific competition for food resources, introducing a further limiting](#)
293 [factor](#) (Newton 1998), [particularly in small and isolated populations \(e.g. Echo Parakeet; Jones](#)
294 [2004\). Although parrots are known for their dietary plasticity, the extent to which such](#)
295 [adaptability can withstand the pressure of global changes is understudied](#) (Renton et al. 2015).
296 [Interestingly, the Grey Parrot population on Príncipe spent a great proportion of their time](#)
297 [feeding on the fruits of Oil Palms *Elaeis guineensis*, an abundant source of food on the island](#)
298 [\(Valle 2015\).](#)

299 The sustainability of parrot trade is managed by CITES through a system of quotas, i.e.
300 through regulating harvest volume (Martin et al. 2014). These quotas are rarely based on those

301 ‘non-detriment findings’ which are much sought after by CITES itself (Rosser and Haywood
302 2002). Our study reveals that the line between safe and ruinous harvest volumes is fine, and that
303 trapping method and quota observance are pivotal to the stability of harvested populations of
304 large parrots. Reliable data on such factors are hardly ever available for traded parrots (Poole and
305 Shepherd 2016). Thus, for a population model to yield a reliable ‘non-detriment finding’ for a
306 given harvest quota (Smith et al. 2011), in-country population monitoring and trade enforcement
307 systems would need to improve significantly. Indeed, if capture method, post-capture mortality,
308 occasional but high exceeding of quotas, and reliability of reported figures were all factored into
309 models of the sustainability of parrot harvesting, it is unlikely that recent trade in Grey Parrots
310 and many other psittacines of similar size could be judged ‘non-detrimental’ with any reasonable
311 degree of confidence.

312

313 **Aknowledgements**

314

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

322

323 **References**

324 Annorbah, N.N.D., Collar, N.J., Marsden, S.J., 2016. Trade and habitat change virtually eliminate
325 the Grey Parrot *Psittacus erithacus* from Ghana. *Ibis* 158, 82-91

326 Balme, G.A., Hunter, L., Braczkowski, A.R., 2012. Applicability of age-based hunting regulations
327 for African leopards. *PLoS ONE* 7, e35209

328 Beissinger, S.R., 2001. Trade of live wild birds: potentials, principles, and practices of sustainable
329 use, In *Conservation of exploited species*. eds J.D. Reynolds, G.M. Mace, K.H. Redford, J.G.
330 Robinson, pp. 182-202. Cambridge University Press, Cambridge.

331 Beissinger, S.R., Bucher, E.H., 1992a. Can parrots be conserved through sustainable harvesting?
332 *Bioscience* 42, 164-173

333 Beissinger, S.R., Bucher, E.H., 1992b. Sustainable harvesting of parrots for conservation., In New
334 world parrots in crisis: solutions from conservation biology. eds S.R. Beissinger, N.F.R. Snyder,
335 pp. 73-115. Smithsonian Institution Press, Washington, DC.

336 Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability
337 in endangered species management. *The Journal of Wildlife Management* 62, 821-841

338 Benson, C., Benson, F., Stuart, S., Fry, C., 1988. Parrots, parakeets and lovebirds, In *The Birds of*
339 *Africa*. eds C. Fry, S. Keith, E. Urban, pp. 1-25. Academic Press, London, UK.

340 BirdLife International, 2017. Species factsheet: *Psittacus erithacus*.
341 <http://datazone.birdlife.org/species/factsheet/22724813> (Accessed 10 October 2017)

342 Birkeland, C., Dayton, P.K., 2005. The importance in fishery management of leaving the big ones.
343 *Trends in Ecology & Evolution* 20, 356-358

344 Bouzat, J.L., Strem, R.I., 2012. Population viability analysis of the blue-throated macaw (*Ara*
345 *glaucogularis*) using individual-based and cohort-based PVA programs. *Open Conservation Biology*
346 *Journal* 6, 12

347 Boyce, M.S., 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23,
348 481-506

349 Brightsmith, D.J., 2005. Parrot nesting in southeastern Peru: seasonal patterns and keystone trees.
350 *The wilson bulletin* 117, 296-305

351 Brouwer, K., Jones, M., King, C., Schifter, H., 2000. Longevity records for Psittaciformes in
352 captivity. *International Zoo Yearbook* 37, 299-316

353 Caswell, H., 1989. *Matrix Population Models*. Sinauer Sunderland, MA.

354 CITES, 2006. Twenty-second meeting of the Animals Committee, Lima, Peru. 7-13 July 2006 AC
355 22 Doc.10.2 Annex 1.

356 CITES, 2014. Review of Significant Trade in specimens of Appendix-II species. 27th meeting of
357 the Animals Committee. AC27 Doc. 12.4.

358 CITES, 2017. Notification to the parties No. 2017/010 - Reservations on Appendices I and II.

359 Cockle, K.L., Martin, K., Drever, M.C., 2010. Supply of tree-holes limits nest density of cavity-
360 nesting birds in primary and logged subtropical Atlantic forest. *Biological Conservation* 143, 2851-
361 2857

362 Cornelius, C., Cockle, K., Politi, N., Berkunsky, I., Sandoval, L., Ojeda, V., Rivera, L., Hunter Jr,
363 M., Martin, K., 2008. Cavity-nesting birds in neotropical forests: cavities as a potentially limiting
364 resource. *Ornitologia Neotropical* 19, 253-268

365 Dändliker, G., 1992. The Grey Parrot in Ghana: A population survey, a contribution to the biology
366 of the species, a study of its commercial exploitation and management recommendations. A report
367 on CITES Project S-30. CITES Secretariat, Geneva.

368 de Grahl, W., 1987. The grey parrot. TFH Publications, Neptune City, NJ.

369 del Hoyo, J., Elliott, A., Sargatal, J., Christie, D., de Juana, E., 2017. Handbook of the Birds of the
370 World Alive (Accessed 10 October 2017)

371 Exell, A.W., 1973. Angiosperms of the islands of the gulf of Guinea (Fernando Po, Príncipe, S.
372 Tomé, and Annobón). *Bulletin of the British Museum (Natural History). Botany* 4, 325-411

373 Fahlman, Å., 2002. African Grey Parrot conservation: a feasibility evaluation of developing a local
374 conservation program in Principe, In Arbetsgruppen för Tropisk Ekologi. Uppsala University,
375 Uppsala.

376 Figueiredo, E., Paiva, J., Stevart, T., Oliveira, F., Smith, G., 2011. Annotated catalogue of the
377 flowering plants of São Tomé and Príncipe. *Bothalia* 41, 41-82.doi: 10.4102/abc.v41i1.34

378 Forshaw, J.M., 1989. Parrots of the world, 3rd Revised edn. Blandford Press Ltd, London.

379 Fotso, R., 1998. Survey status of the distribution and utilization of the grey parrot (*Psittacus erithacus*)
380 in Cameroon. CITES Secretariat, Geneva.

381 Getz, W.M., Haight, R.G., 1989. Population harvesting: demographic models of fish, forest, and
382 animal resources. Princeton University Press, Princeton.

383 Giles, B.G., Findlay, C.S., 2004. Effectiveness of a selective harvest system in regulating deer
384 populations in Ontario. *Journal of Wildlife Management* 68, 266-277

385 Hart, J., Hart, T., Salumu, L., Bernard, A., Abani, R., Martin, R., 2016. Increasing exploitation of
386 grey parrots in eastern DRC drives population declines. *Oryx* 50, 16-16

387 Hunter, C.M., Caswell, H., 2005. Selective harvest of sooty shearwater chicks: effects on
388 population dynamics and sustainability. *Journal of Animal Ecology* 74, 589-600

389 IUCN, 2016. IUCN Red List of Threatened Species. Version 2016.3. www.iucnredlist.org
390 (Accessed 10 October 2017)

391 Jones, C.G., 2004. Conservation management of endangered birds, In *Bird ecology and*
392 *conservation: a handbook of techniques.* eds W.J. Sutherland, I. Newton, R.E. Green, pp. 269-
393 293. Oxford University Press, New York.

394 Jones, P., Tye, A., 2006. The birds of São Tomé & Príncipe, with Annobón, islands of the Gulf of
395 Guinea: an annotated checklist. British Ornithologists' Union (BOU Checklist Series no.22),
396 Oxford, U.K.

397 Juste, J., 1996. Trade in the gray parrot *Psittacus erithacus* on the Island of Principe (São Tomé and
398 Príncipe, Central Africa): initial assessment of the activity and its impact. Biological Conservation
399 76, 101-104

400 Koenig, S.E., 2008. Black-billed parrot (*Amazona agilis*) population viability assessment (PVA): a
401 science-based prediction for policy makers. Ornithologia Neotropical 19, 135-149

402 Lantermann, W., 2000. Graupapageien: Artgerechte Haltung, Pflege und Zucht. Oerter und
403 Spörer, Reutlingen.

404 Lindstedt, S.L., Calder, W.A., 1976. Body size and longevity in birds. Condor 78, 91-94

405 Marsden, S.J., Loqueh, E., Takuo, J.M., Hart, J.A., Abani, R., Ahon, D.B., Annorbah, N., Johnson,
406 R., Valle, S., 2015. Using encounter rates as surrogates for density estimates makes monitoring of
407 heavily-traded grey parrots achievable across Africa. Oryx 50, 617-625.doi:
408 10.1017/S0030605315000484

409 Marsden, S.J., Loqueh, E., Takuo, J.M., Hart, J.A., Abani, R., Ahon, D.B., Showers, C., Annorbah,
410 N., Johnson, R., Valle, S., 2013. A protocol to allow density estimation and monitoring of the
411 heavily traded grey parrots across their huge African ranges, In Strengthening Capacity for
412 Monitoring and Regulation of International Trade of African Grey Parrot. ed. CITES, pp. 1-18.
413 CITES Secretariat, Geneva.

414 Marsden, S.J., Royle, K., 2015. Abundance and abundance change in the world's parrots. Ibis 157,
415 219-229.doi: 10.1111/ibi.12236

416 Martin, R.O., Perrin, M.R., Boyes, R.S., Abebe, Y.D., Annorbah, N.D., Asamoah, A., Bizimana,
417 D., Bobo, K.S., Bunbury, N., Brouwer, J., Diop, M.S., Ewnetu, M., Fotso, R.C., Garteh, J., Hall,
418 P., Holbech, L.H., Madindou, I.R., Maisels, F., Mokoko, J., Mulwa, R., Reuleaux, A., Symes, C.,
419 Tamungang, S., Taylor, S., Valle, S., Waltert, M., Wondafrash, M., 2014. Research and conservation
420 of the larger parrots of Africa and Madagascar: a review of knowledge gaps and opportunities.
421 Ostrich 85, 205-233

422 McGowan, P., 2001. Status, management and conservation of the African Grey Parrot, *Psittacus*
423 *erithacus* in Nigeria. CITES, Geneva.

424 Melo, M., 1998. Differentiation between Principe Island and mainland populations of the African
425 Grey Parrot *Psittacus erithacus*: Genetic and behavioural evidence and implications for conservation.
426 Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Cape Town.

427 Millennium Ecosystem Assessment, 2005. Ecosystems and human well-being. Island Press,
428 Washington, DC.

429 Munn, C., 1992. Macaw biology and ecotourism, or when a bird in the bush is worth two in the
430 hand, In New world parrots in crisis: solutions from conservation biology. eds S.R. Beissinger,
431 N.F.R. Snyder, N. Collar, pp. 47-72. Smithsonian Institution Press, Washington, DC.

432 Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review.
433 Biological Conservation 70, 265-276

434 Newton, I., 1998. Population limitation in birds. Academic press, San Diego, CA.

435 Ngenyi, A., 2002. African Grey Parrot Trade in Cameroon. PsittaScene 50, 2-3

436 Ngenyi, A., 2003. The African Grey Parrot status and commercial exploitation in Cameroon.
437 WWF, Jengi SE project.

438 Packer, C., Kosmala, M., Cooley, H.S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss,
439 M., Swanson, A., Balme, G., 2009. Sport hunting, predator control and conservation of large
440 carnivores. PLoS ONE 4, e5941

441 Pain, D., Martins, T., Boussekey, M., Diaz, S., Downs, C., Ekstrom, J., Garnett, S., Gilardi, J.,
442 McNiven, D., Primot, P., 2006. Impact of protection on nest take and nesting success of parrots
443 in Africa, Asia and Australasia. *Animal Conservation* 9, 322-330

444 Pires, S.F., 2012. The illegal parrot trade: a literature review. *Global Crime* 13, 176-190

445 Poole, C.M., Shepherd, C.R., 2016. Shades of grey: the legal trade in CITES-listed birds in
446 Singapore, notably the globally threatened African grey parrot *Psittacus erithacus*. *Oryx FirstView*,
447 1-7.doi:10.1017/S0030605314000234

448 R Core Team, 2014. R: A language and environment for statistical computing, ed. R.F.f.S.
449 Computing, Vienna, Austria.

450 Renton, K., Salinas-Melgoza, A., De Labra-Hernández, M.Á., de la Parra-Martínez, S.M., 2015.
451 Resource requirements of parrots: nest site selectivity and dietary plasticity of Psittaciformes.
452 *Journal of Ornithology* 156, 73-90

453 Ricklefs, R.E., 2000. Density dependence, evolutionary optimization, and the diversification of
454 avian life histories. *The Condor* 102, 9-22

455 Rockwood, L.L., 2006. Introduction to population ecology. Blackwell Publishing, Malden, MA.

456 Rosser, A., Haywood, M., 2002. Guidance For CITES Scientific Authorities: Checklist to assist in
457 making non-detriment findings for Appendix II exports. IUCN.

458 Saunders, D.A., Mawson, P.R., Dawson, R., 2014. Use of tree hollows by Carnaby's cockatoo and
459 the fate of large hollow-bearing trees at Coomallo Creek, Western Australia 1969–2013. *Biological*
460 *Conservation* 177, 185-193

461 Seibert, L.M., 2006. Social behavior of psittacine birds, In *Manual of parrot behavior*. ed. A.U.
462 Luescher, pp. 43-48. Blackwell Publishing, Oxford.

463 Smith, M.J., Benítez-Díaz, H., Clemente-Muñoz, M.Á., Donaldson, J., Hutton, J.M., McGough,
464 H.N., Medellín, R.A., Morgan, D.H., O'Críodain, C., Oldfield, T.E., 2011. Assessing the impacts
465 of international trade on CITES-listed species: current practices and opportunities for scientific
466 research. *Biological Conservation* 144, 82-91

467 Taylor, T., Parkin, D., 2008. Sex ratios observed in 80 species of parrots. *Journal of Zoology* 276,
468 89-94

469 UNEP-WCMC, 2015. CITES trade database. <http://trade.cites.org/> (Accessed 10 October 2017)

470 Valle, S., 2015. Population viability and conservation of Grey Parrots *Psittacus erithacus* on the
471 island of Príncipe, Gulf of Guinea., In *School of Science and the Environment*. Manchester
472 Metropolitan University, Manchester.

473 Valle, S., Collar, N.J., Harris, W.E., Marsden, S.J., 2017. Spatial and seasonal variation in abundance
474 within an insular grey parrot population. *African Journal of*
475 *Ecology*. <http://dx.doi.org/10.1111/aje.12367>

476 Wright, T.F., Toft, C.A., Enkerlin-Hoeflich, E., Gonzalez-Elizondo, J., Albornoz, M., Rodríguez-
477 Ferraro, A., Rojas-Suárez, F., Sanz, V., Trujillo, A., Beissinger, S.R., 2001. Nest poaching in
478 Neotropical parrots. *Conservation Biology* 15, 710-720

479 Young, A., Hobson, E., Lackey, L.B., Wright, T., 2012. Survival on the ark: life- history trends in
480 captive parrots. *Animal Conservation* 15, 28-43

481 Zhang, L., Hua, N., Sun, S., 2008. Wildlife trade, consumption and conservation awareness in
482 southwest China. *Biodiversity and Conservation* 17, 1493-1516

483
484
485
486
487

488 **Tables**

489 **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

490

491

492

493

494

495

496

497

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

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

498

499

500

501

502

503

504

505
506
507
508
509
510
511
512
513
514
515
516
517
518
519
520
521
522
523
524
525
526
527
528
529
530
531
532
533
534
535
536

Figure Legends

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

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

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

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

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

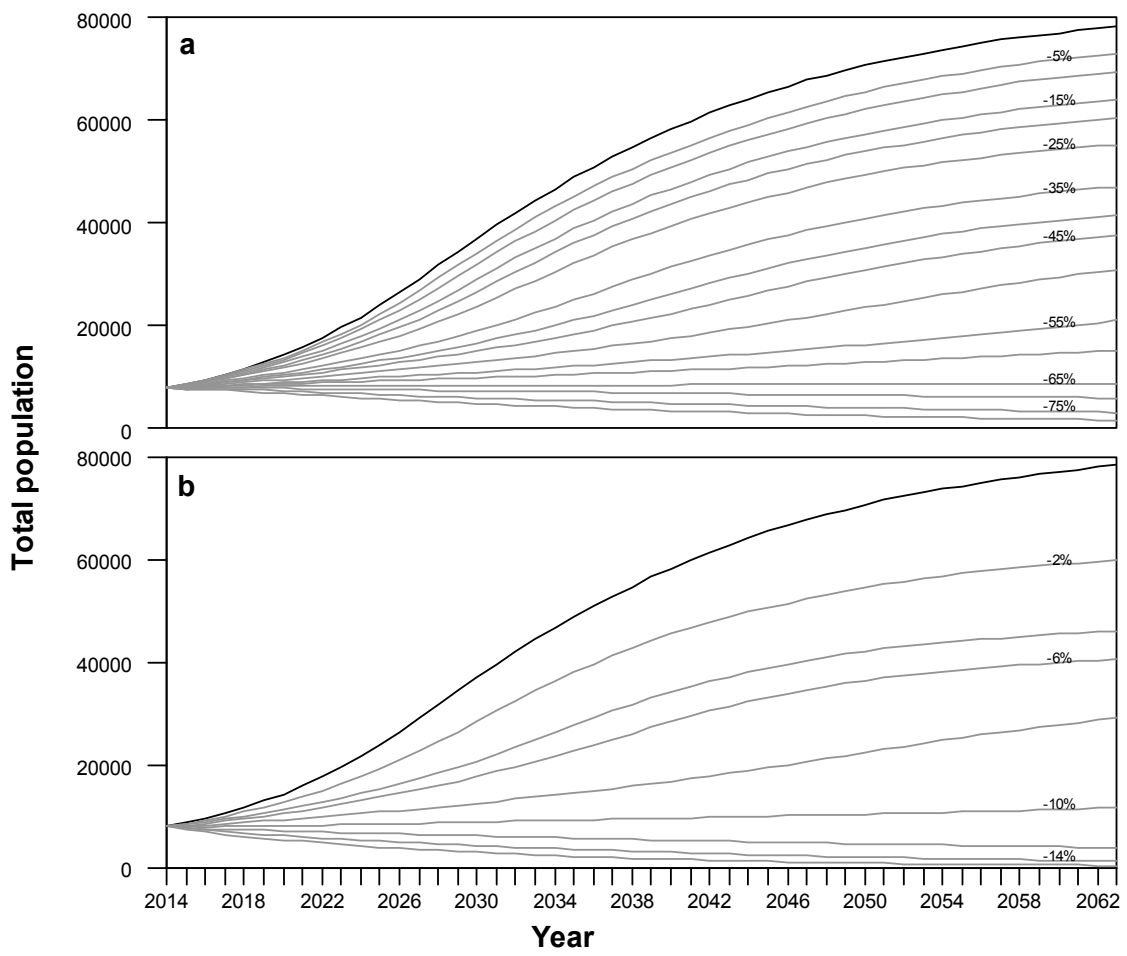
537

538

539

540 **Figures**

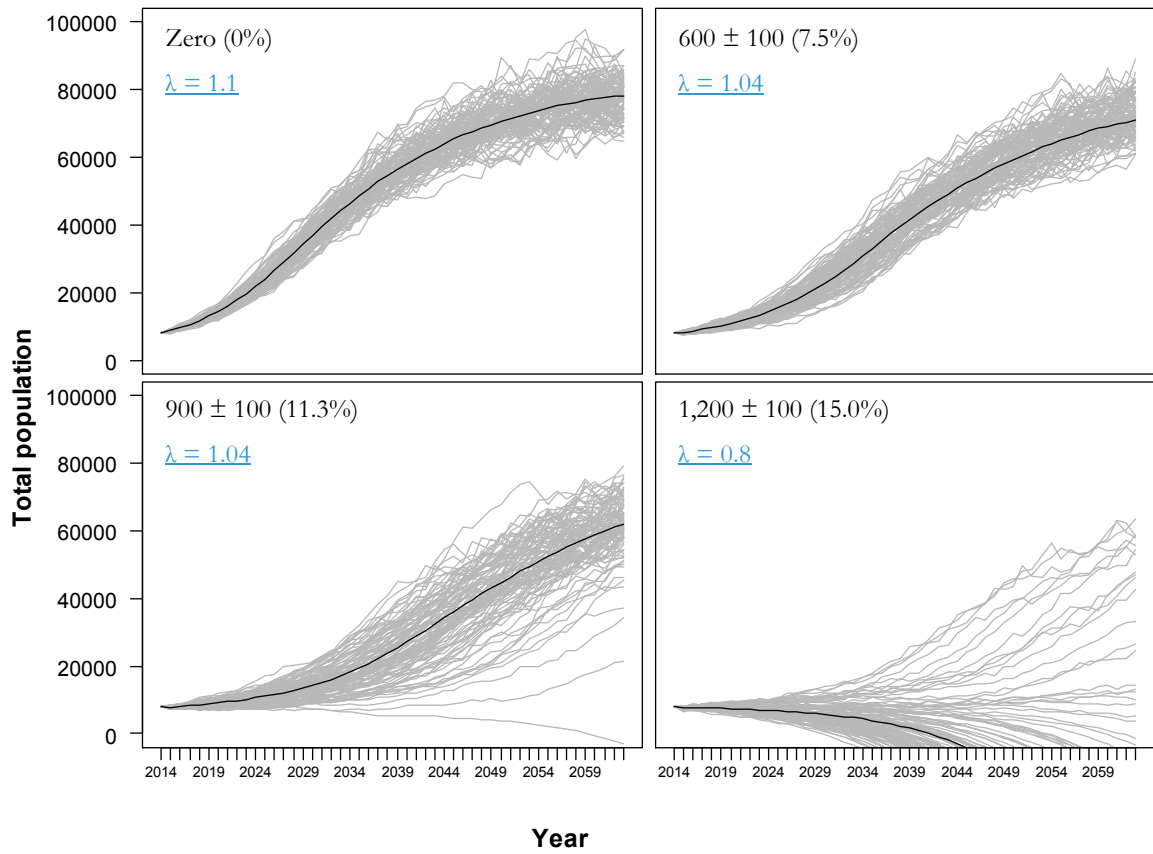
541



542

543 **Figure 1**

544



545

546 **Figure 2**

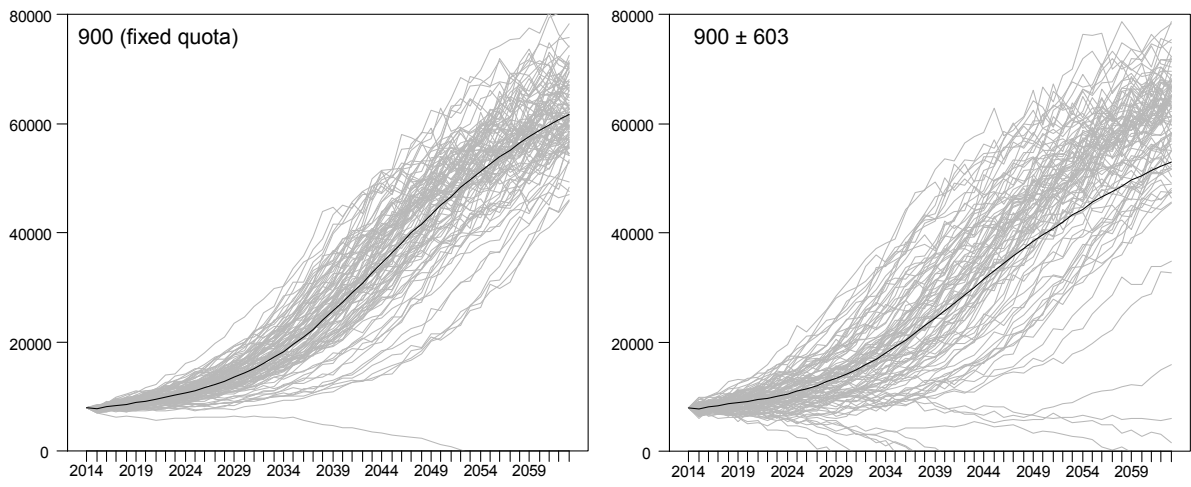
547

548

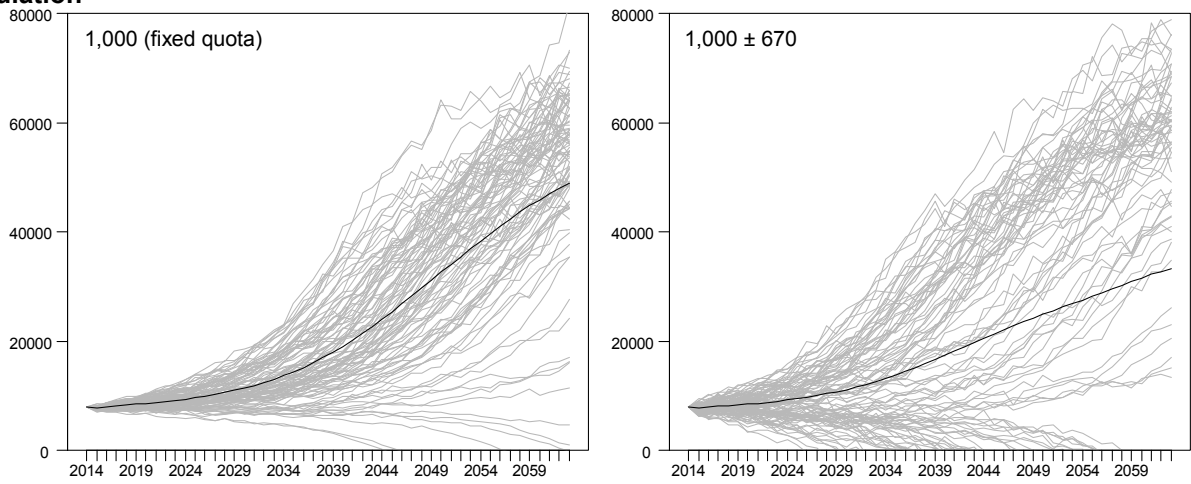
549

550

551



Total Population



Year

553 **Figure 3**

554

555

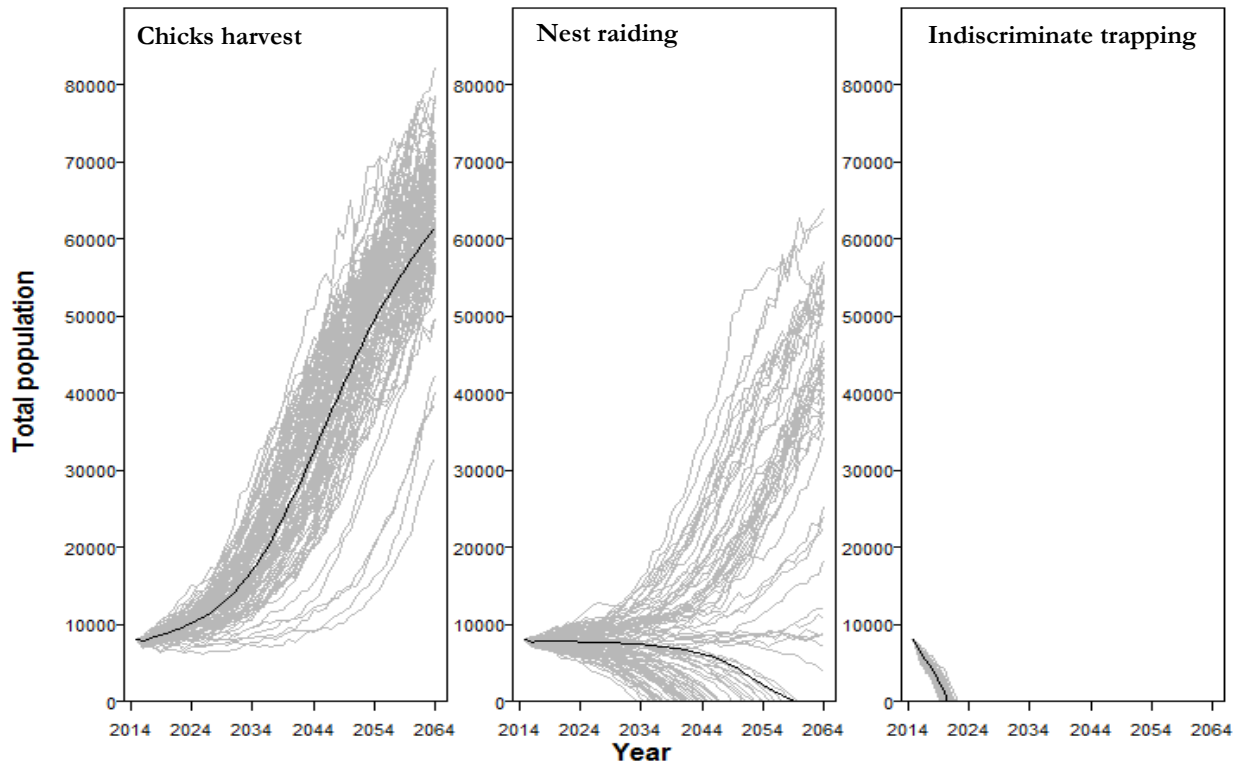
556

557

558

559

560



561

562 **Figure 4**

563

564

565

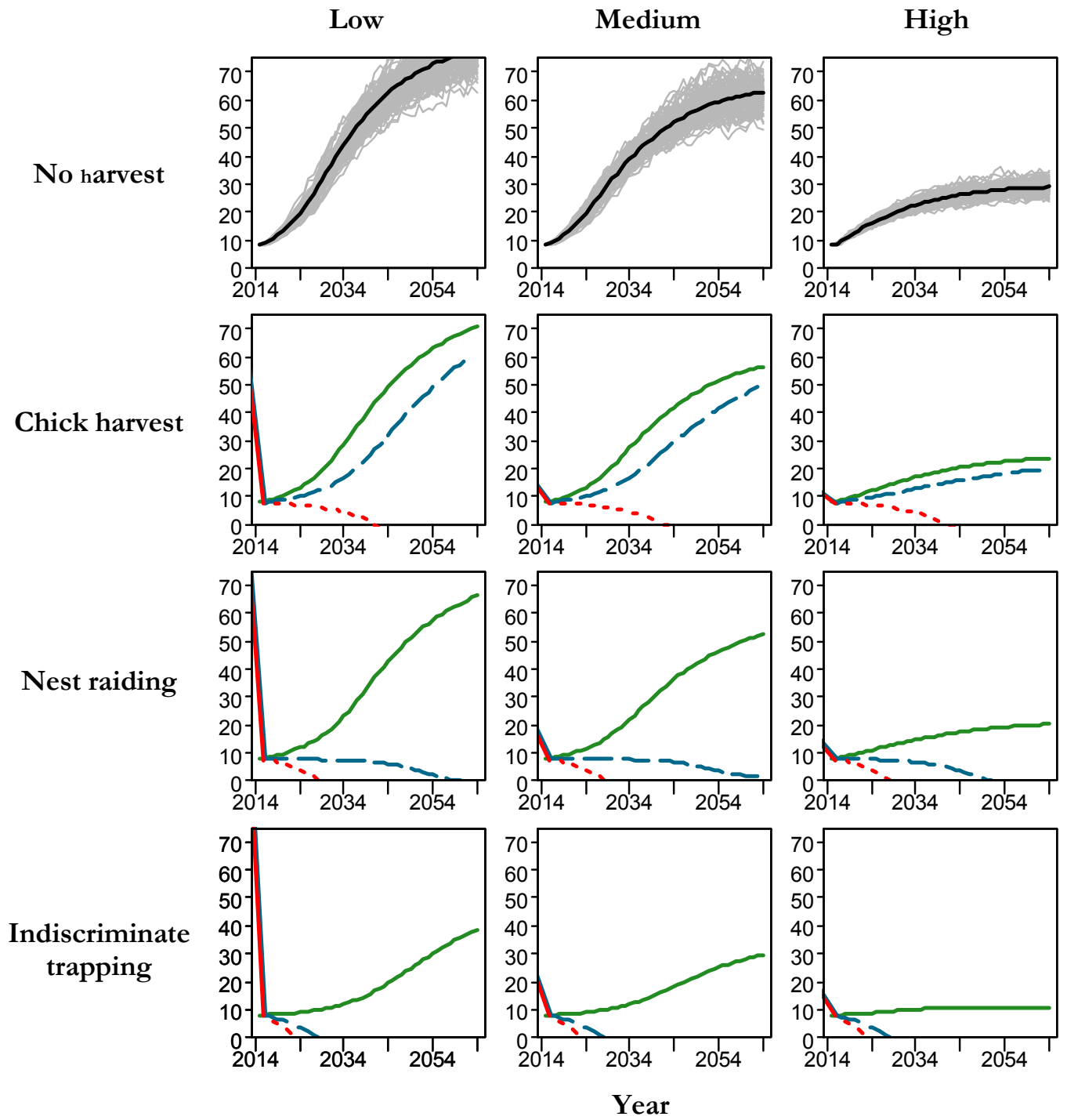
566

567

568

569

570



571 Figure 5

572