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

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

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

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

1. How sensitive are long-term population trajectories likely to be to small changes/uncertainties in harvest volume which are inevitable under current trade management?

2. Do different trapping methods affect populations differentially for a given harvest volume?

3. What are the effects of variation in annual harvests on harvest sustainability?

4. What are the compound effects of habitat loss and trapping volume and method on long-term population viability?

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

Methods

Study area and population

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

Nonetheless, the species remains relatively common in some parts of its range (Marsden et al. 2015). One such area is the small (136 km^2) island of Príncipe (São Tomé and Príncipe, Gulf of Guinea), which hosts a demographically isolated, relatively healthy, and well-studied population (Fahlman 2002; Juste 1996; Marsden et al. 2015; Melo 1998; Valle et al. 2017). Grey Parrots were harvested at an average rate of 600 birds per year from the wild in the 1990s (Juste 1996; Melo 1998) until a regional ban on all trade was put in place in 2005 (Valle 2015). Príncipe is broadly divided into two geographically and climatically distinct regions: a low-lying basalt platform in the north, with hills below 180 m a.s.l. (around 65% of island), and a mountainous region in the south (Jones and Tye 2006). By the beginning of the twentieth century, the forest in the north had been modified in many places by clear-felling, selective logging and the creation of cocoa, coffee and coconut plantations (Exell 1973). After the country gained independence (1975) most estates were abandoned and today the north is covered by secondary forest interspersed with some commercial species (e.g. Oil Palm *Elaeis guineensis*). The south, owing to its inaccessibility, remains covered in pristine forest with much floral endemism (Figueiredo et al. 2011).

Model implementation

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

$$\lambda = \sqrt[x]{\frac{\mathrm{N}_{t+x}}{\mathrm{N}_t}} \qquad (1)$$

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

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

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

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

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

Modelling population dynamics and the sustainability of harvest

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

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

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

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

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

Modelling interactions between habitat quantity, habitat quality and harvest volume

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

Results

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

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

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

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

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

Discussion

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

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

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

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

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

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References

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Tables

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

Life history trait	*Value used in the model*
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

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).*

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

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 ±~~(~~100~~)~~, dashed line = 900 ±~~(~~100~~)~~, dotted line = 1,200 ±~~(~~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 ± 1,821 nests); Medium = 17% and 83% (i.e. 3,570 ± 1,498 nests); and High = only 17% primary (i.e. 1,674 ± 606 nests)~~low, medium and high (see Methods)~~.

Figures

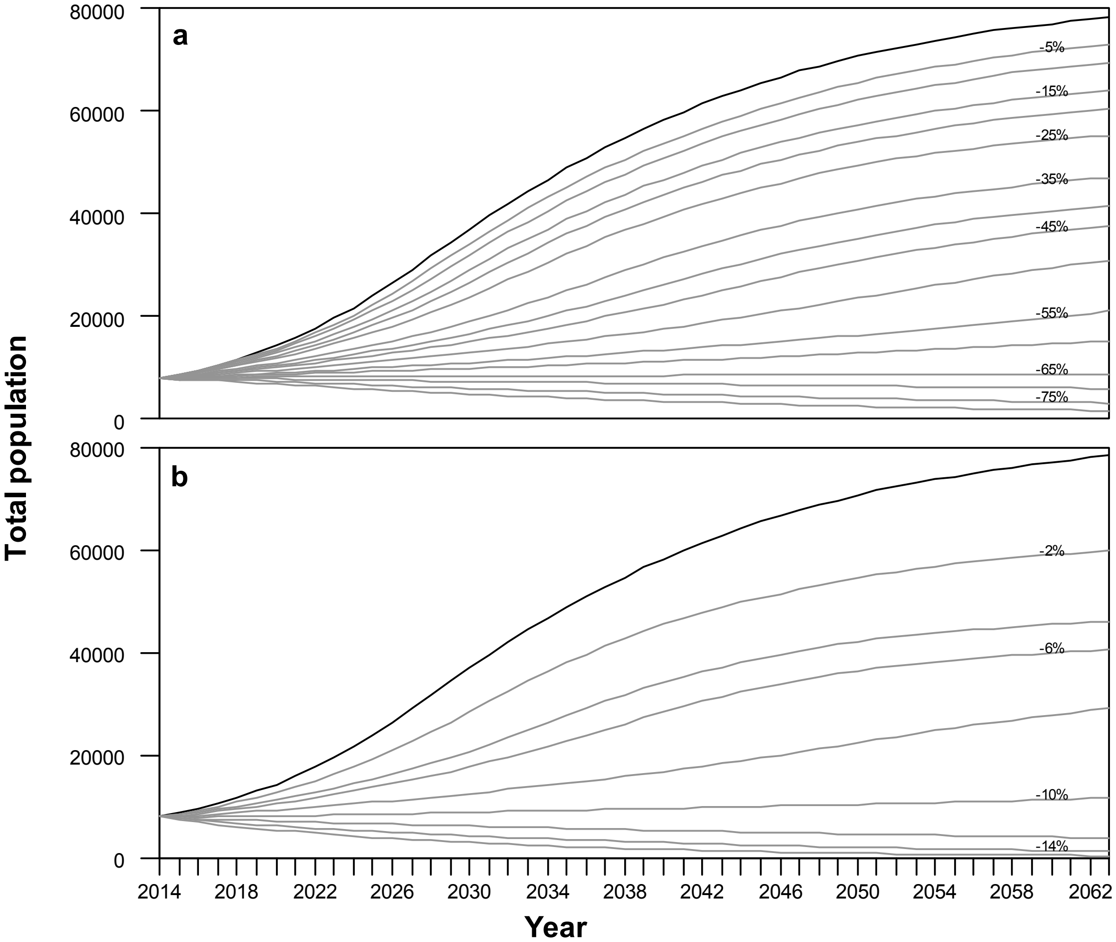


Figure 1

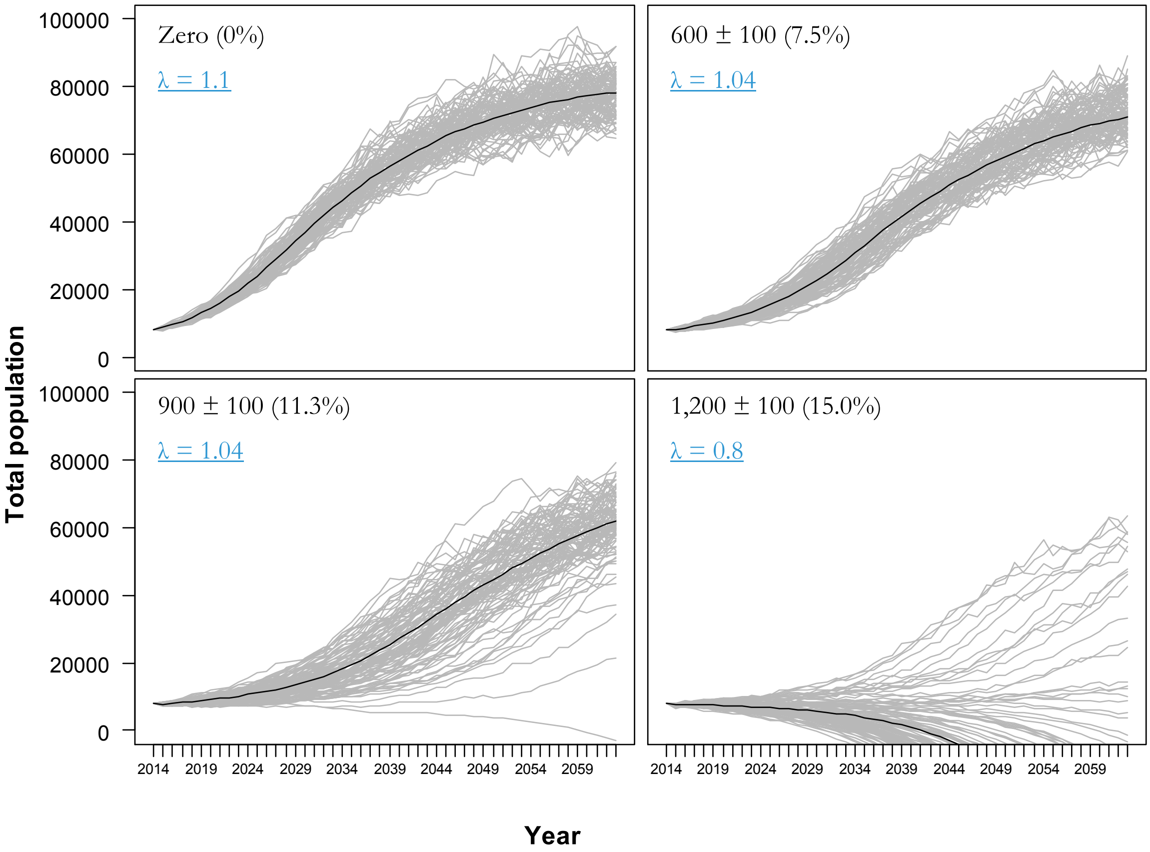

Zero (0%)
λ = 1.1
600 ± 100 (7.5%)
λ = 1.04
900 ± 100 (11.3%)
λ = 1.04
1,200 ± 100 (15.0%)
λ = 0.8
Total population
100000
80000
60000
40000
20000
0
2014
2019
2024
2029
2034
2039
2044
2049
2054
2059
Year

Figure 2

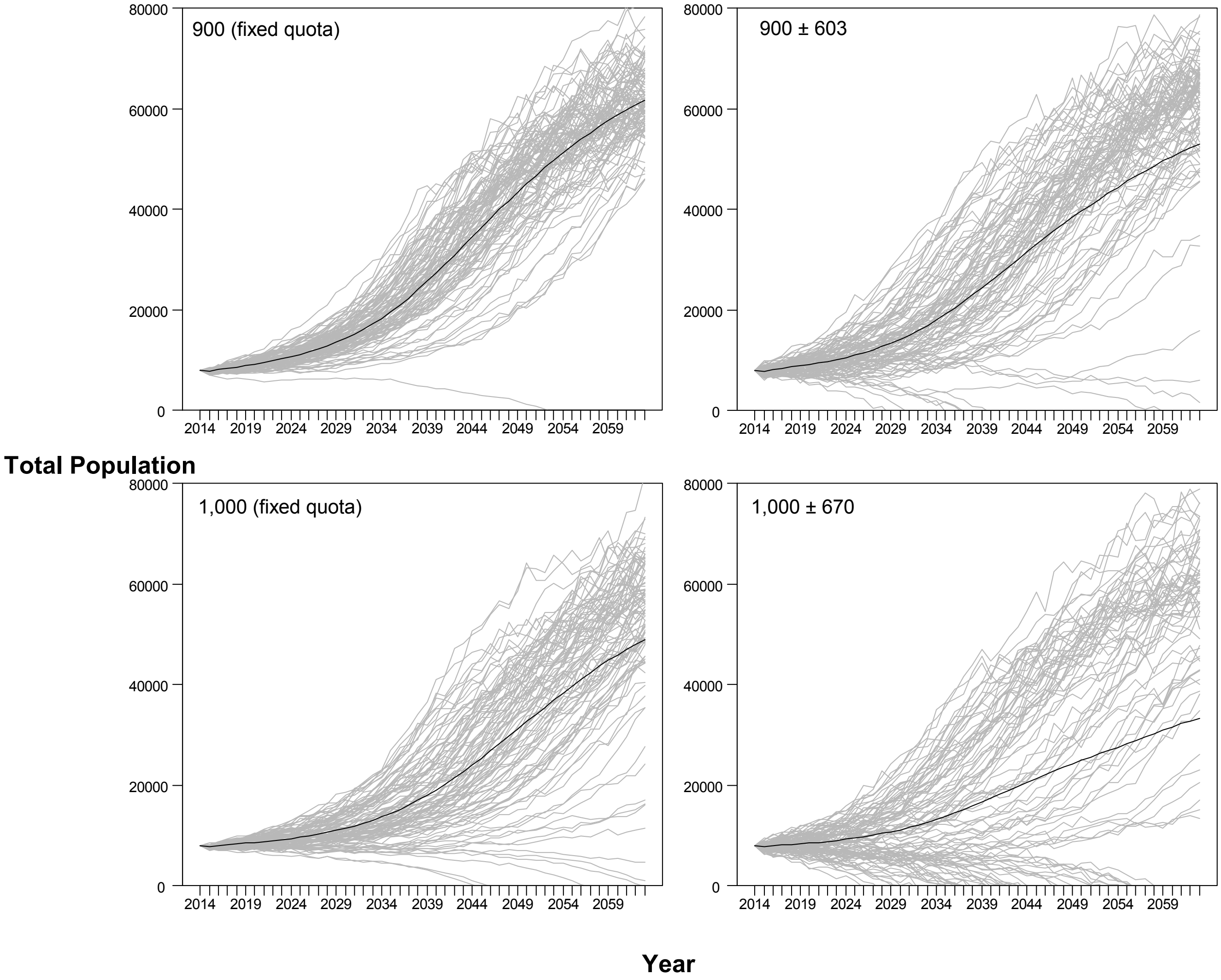

900 (fixed quota)
900 ± 603
1,000 (fixed quota)
1,000 ± 670
Total Population
Year
0
20000
40000
60000
80000
2014
2019
2024
2029
2034
2039
2044
2049
2054
2059

Figure 3

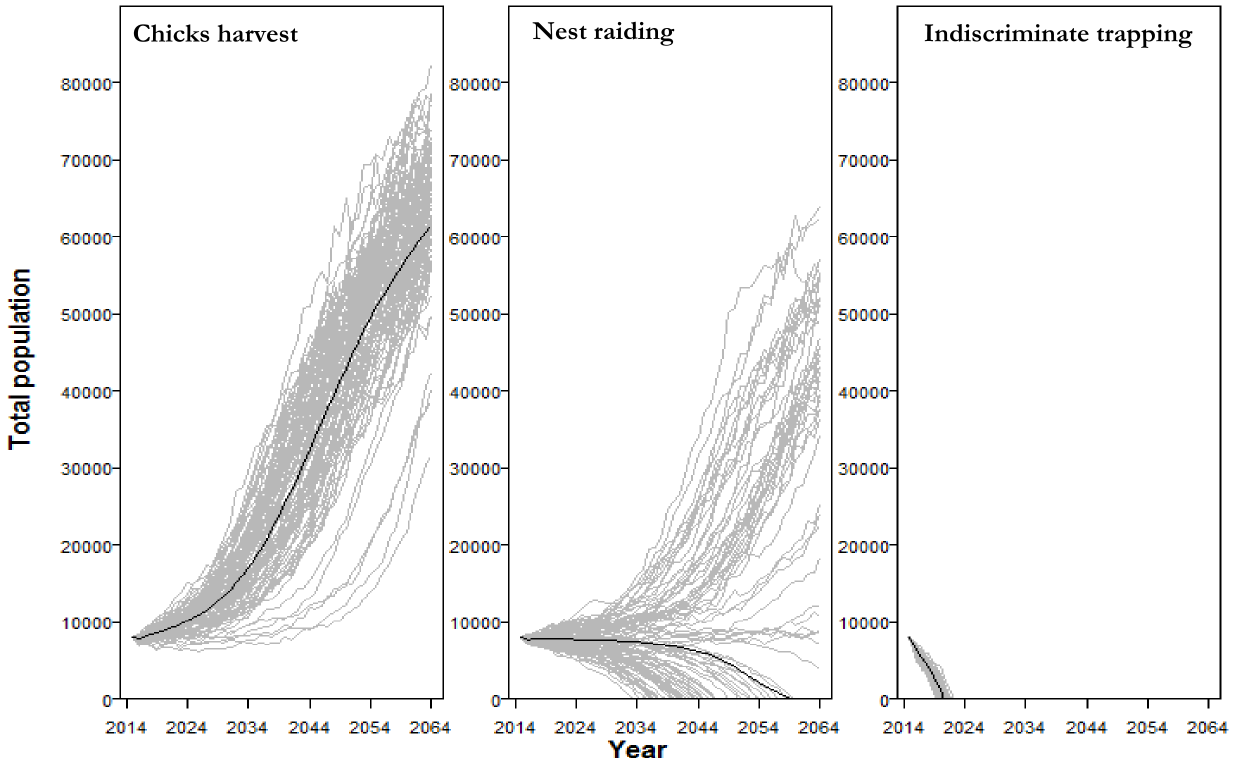
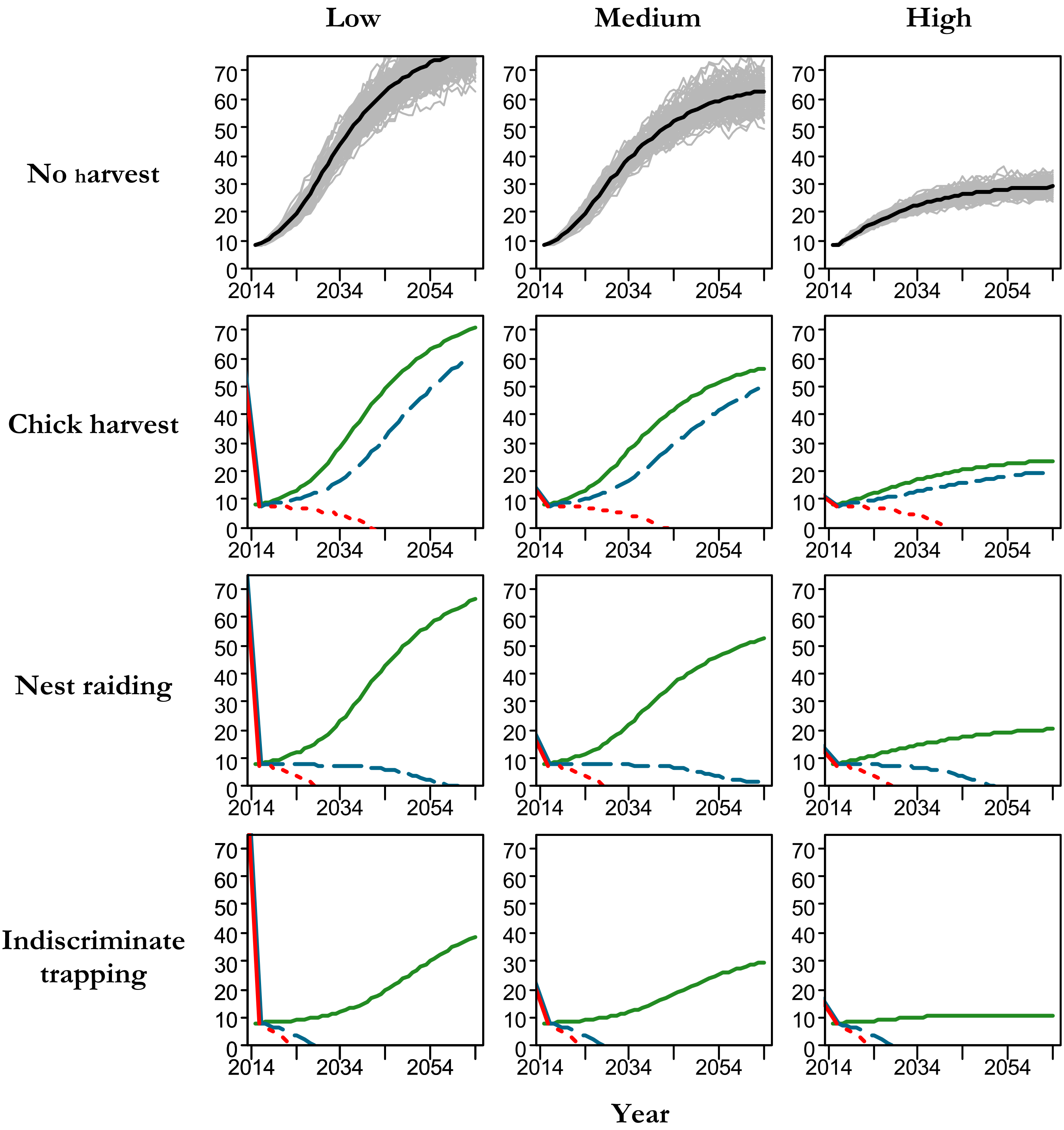

Chicks harvest
Nest raiding
Indiscriminate trapping
Total population
80000
70000
60000
50000
40000
30000
20000
10000
0
2014
2024
2034
2044
2054
2064
Year

Figure 4



571 **Figure 5**

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