BLACK-BILLED PARROT (*AMAZONA AGILIS*) POPULATION VIABILITY ASSESSMENT (PVA): A SCIENCE-BASED PREDICTION FOR POLICY MAKERS

Susan E. Koenig

Windsor Research Centre, Trelawny, Jamaica.
E-mail: windsor@cwjamaica.com

Resumen. – Análisis de variabilidad poblacional (AVP) de la Amazona de Pico Negro (*Amazona agilis*): Una predicción científica para creadores de políticas. – El análisis de viabilidad poblacional (AVP) es una herramienta de conservación importante para el manejo de especies amenazadas. Sus fortalezas son la identificación de estadios críticos en el ciclo de vida de una especie y la evaluación de diferencias relativas entre una variedad de opciones de manejo. Notablemente, permite que los manejadores muestren a los decidores y creadores políticas las consecuencias de prácticas insostenibles. Se realizó un AVP de la Amazona de Pico Negro (*Amazona agilis*), una de dos especies de *Amazona* endémicas de Jamaica, actualmente en estado vulnerable. Se usaron estimados de supervivencia y datos de campo (1996–98) sobre la reproducción, y datos comparitivos de la especies congenérica, la Amazona de Puerto Rico (*A. vittata*). En bosque mínimamente alterado, se estimó que el crecimiento poblacional fue en aumento (λ = 1.12), mientras que en hábitat alterado de borde, el crecimiento poblacional estimado presentó un ligero descenso (λ = 0.99). Recientemente, fueron emitidas dos licencias de exploración de bauxita en más del 60% de 110,000 ha del Área de Conservación Cockpit Country, área que posee más de 42,000 ha de bosque primario contiguo y alberga aprox. 90–95% de la población total de la Amazona de Pico Negro. En adición de crear un extenso mosaico de hábitat de borde alterado de tipo "sumidero" (*sink*) en más del 50% del bosque primario, la actividad minera crearía hábitat propicio para el Gavilán Colirrojo (*Buteo jamaicensis*) y facilitaría la caza de cotorras (tanto de juveniles como adultos) vía un circuito extenso de carreteras. Un declive del 2% en la supervivencia anual de adultos a causa de los factores anteriormente mencionados resultaría en un descenso del 50% de una población hipotética de 5000 en 15 años y a una población menor a 100 en 100 años. Tal predicción no se aleja de la realidad: conteos sistemáticos han estimado la presencia de hasta 20 parejas territoriales/km^2 en Cockpit Country, comparado con < 1 pareja/km^2 en Mount Diablo; un área que ha estado sujeta a tala intensiva y extracción minera de bauxita durante más de 50 años.

Abstract. – Population Viability Assessment (PVA) is an important conservation tool for endangered species management. The strength of PVA is identifying critical stages of a species' life cycle and evaluating relative differences among management options. Notably, it enables managers to demonstrate graphically to decision makers the consequences of unsustainable practices. PVA was applied to Black-billed Parrots (*Amazona agilis*), one of Jamaica's two endemic, vulnerable Amazon parrots, using reproductive data from field studies (1996–98) and survival estimates of the congeneric Puerto Rican Parrot (*A. vittata*). In minimally disturbed forest, population growth was estimated as increasing (λ = 1.12) while, in disturbed edge habitat, population growth was estimated to be in slight decline (λ = 0.99). Recently, two bauxite prospecting licenses were issued for over 60% of the 110,000 ha Cockpit Country Conservation Area, which encompasses more than 42,000 ha of near-contiguous primary forest and which supports between 90 and 95% of the total population of Black-billed Parrots. In addition to creating an extensive mosaic of "sink"

disturbed edge habitat in more than 50% of primary forest, mining would create suitable habitat for Red-tailed Hawks (*Buteo jamaicensis*) and facilitate poaching (both of nestlings and adults) via an extensive road network. A 2% decline in annual adult survival caused by the above factors would lead to a 50% decline in a hypothetical population of 5000 within 15 years, and a population of less than 100 in 100 years. Such a prediction is not far-fetched: systematic surveys have estimated up to 20 territorial pairs per km^2 in Cockpit Country, compared to < 1 pair per km in Mount Diablo, an area that has been subjected to intensive logging and bauxite mining for more than 50 years. *Accepted 21 December 2007.*

INTRODUCTION

Population viability assessment (PVA) has become a common tool in the conservation of endangered species (Crouse *et al.* 1987, Doak *et al.* 1994). With demographic data on age- (or stage-) specific and sex-specific mortality and reproduction, it becomes possible to determine population growth – declining, stable, increasing – and, consequently, estimate the long-term viability of a species. One important strength of PVA lies in its ability to identify the critical stages of a species' life cycle that contribute significantly to population growth (Beissinger 1995, Heppell *et al.* 1995), screen hypotheses for causes of species decline, and evaluate the relative differences among potential management options (Caughley 1994, Beissinger & Westphal 1998, Brook *et al.* 2000). By making explicit the factors that influence population growth and then quantitatively altering demographic parameters on a computer screen, PVA enables conservation biologists and natural resource managers to demonstrate graphically to decision makers the potential consequences of unsustainable practices, hopefully before these practices are implemented and intensive mitigation actions are required.

The Black-billed Parrot (*Amazona agilis*) is one of two endemic *Amazona* species endemic to Jamaica. Listed by the IUCN as Vulnerable (*www.redlist.org*), its range is restricted almost entirely to the central-west karst limestone region known as Cockpit Country, an area of nearly 110,000 ha which includes two of the largest remnant blocks of primary moist/wet evergreen forest on Jamaica (Fig. 1). Within Cockpit Country, the Black-billed Parrot is locally common, with breeding surveys detecting up to 20 territorial pairs per km^2, and an estimated 17,000 ± 3,000 (sd) individuals (Davis 2002). However, with c. 90–95% of the global population restricted to the Cockpit Country Conservation Area, protection of the remnant forest habitats is critical for the survival of this species. In addition to being the stronghold of Black-billed Parrots, Cockpit Country also supports large populations of Jamaica's second endemic, vulnerable Amazon parrot, the Yellow-billed Parrot (*A. collaria*).

In 2004, Government of Jamaica issued to Alcoa Minerals of Jamaica LLC and Clarendon Alumina Producers a license to prospect for bauxite (aluminum hydroxides) in over 50% of the Cockpit Country landscape (Figs 2a & 2b). This license was renewed in 2005 and 2006, but was suspended in December 2006 following an intensive public awareness campaign opposing any mining in this globally-unique landscape, which includes 66 site-endemic plants, one bat (Chiroptera: *Phyllonycteris aphylla*) and two frog (Anura: *Eleutherodactylus griphus* and *E. sisyphodemus*) species listed by the Alliance for Zero Extinction and, with 27 of Jamaica's 28 endemic bird species, is the highest-ranked Important Bird
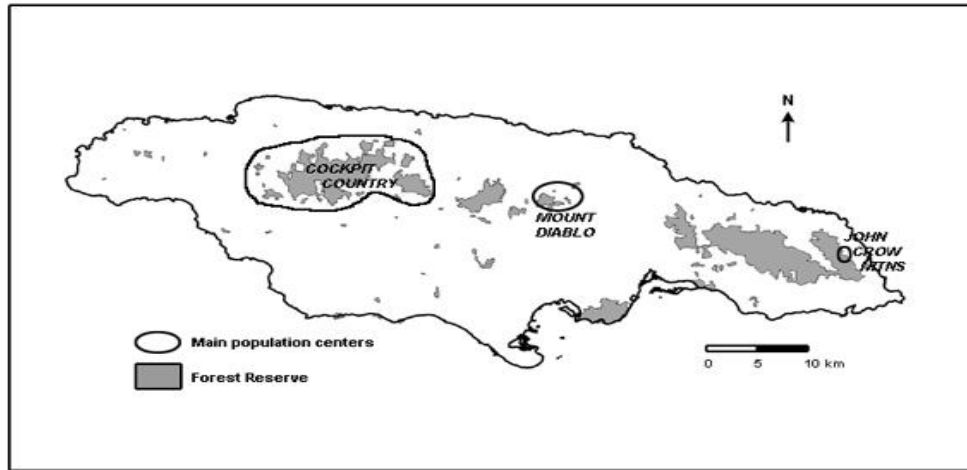
136

FIG. 1. Black-billed Parrot (*Amazona agilis*) distribution in Jamaica.

Area (IBA) on the island. A second prospecting license, also issued to Alcoa Minerals of Jamaica was renewed on 29 November 2006 but was surrendered back to Government of Jamaica on 18 December 2006. The area encompassed by the surrendered license, however, remains "open" to future prospecting. Government currently is reviewing what are multiple boundary definitions of Cockpit Country. Officials insist they will not mine the
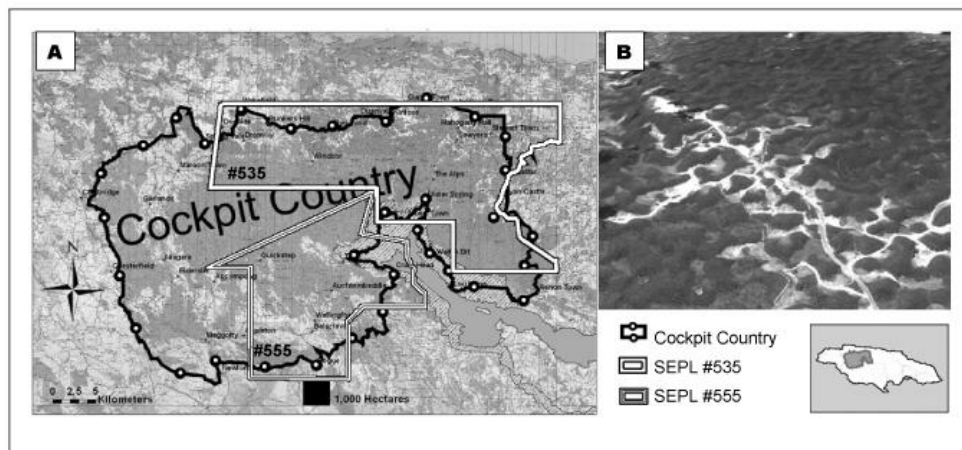

FIG. 2. Areas of Cockpit Country included in the Special Exclusive Prospecting Licenses #SEPL 535 (suspended December 2006) and #SEPL 555 (surrendered December 2006) (A), and typical habitat loss and fragmentation associated with open-pit bauxite mining in Jamaica (B). Government figures for the amount of forest lost annually to mining are only for mined-out ore bodies and do not include deforestation associated with the network of access roads, each of which may be as wide as 30 m. IKONOS image courtesy GeoEye and Forestry Department.

TABLE 1. Stages used in Black-billed Parrot (*Amazona agilis*) female-based population projection and sensitivity-elasticity analysis. Reproductive data F_1 are derived from a three-year field study in northern Cockpit Country. Annual survival, σ_t and longevity data are based on "optimistic" values of the congeneric Puerto Rican Parrot (*A. vittata*) (Snyder *et al.* 1987, Meyers *et al.* 1996). Estimated population growth rate in minimally disturbed forest is (F1) $\lambda = 1.12$; estimated growth in disturbed edge habitat is (F2) $\lambda = 0.99$.

Stage	Stage duration (years)	Annual fecundity minimally disturbed forest	Annual fecundity disturbed edge forest	Annual survival	Maturation probability for survivors	Probability of maturing	Survival probability within stage
	T_i	$F1_i$	$F2_i$	σ_i	γ_i	G_i	P_i
Juvenile	1	0.0	0.00	0.70	1.00	0.00	0.70
Subadult	1	0.0	0.00	0.85	1.00	0.00	0.85
Novice breeder	3	0.3	0.12	0.90	0.30	0.27	0.63
Adult	15	0.6	0.23	0.90	0.03	0.03	0.87

"heart" of Cockpit Country, but seem to fail to appreciate that the patient also needs its "head, arms, and legs" to remain as a functionally-viable ecosystem.

In this paper, I use PVA to explore the potential consequences of bauxite mining on the viability of Black-billed Parrot populations in Cockpit Country. With reproductive data from field surveys (1996–98; Koenig 2001) and survival estimates from congeneric *Amazona* species, I first present a stage-classified population projection matrix. I then use a deterministic version of the model to calculate the growth rate (λ) of the population, conduct elasticity and sensitivity analyses to identify sensitive stages in the life cycle, and next quantitatively alter demographic parameters to evaluate the effects on population growth trajectories for the next 100 years. Finally I relate the hypothetical changes in demographic parameters to potential factors that reasonably will occur or be facilitated by the occurrence of bauxite mining, including habitat loss and fragmentation, alterations in predator-prey dynamics, poaching, and increased vulnerability to tropical storms and hurricanes as the population size becomes reduced in association with decreased available habitat.

METHODS

I developed a model of the four stage classes typically recognized for *Amazona* parrots: (1) juvenile, which has a period of post-fledging parental care, estimated 3–12 months; (2) subadult, sexually immature individuals (1–2 years of age); (3) novice breeders, sexually mature but inexperienced (3–5 years); and (4) adult (5+ years) (Snyder *et al.* 1987, Gnam & Rockwell 1991, Enkerlin-Hoefflich 1995, Enkerlin-Hoefflich & Hogan 1997). Limited availability of annual survival data (see below) and the fact that reproduction of Black-billed Parrots has not been monitored in relation to the species' lifespan (Caswell 1989) precluded development of a more precise age-based model. For a female-based model, I derived inputs for reproductive performance from a 3-year field study (1996–98) conducted on the northern edge of Cockpit Country (Koenig 2001). For the baseline model, I used the mean annual reproductive value (F_i) calculated for females breeding in (a) minimally disturbed, interior habitat and (b) in edge habitat (Table 1). I assumed the former to represent the "normal" rate of reproduction in the absence of human disturbance while the latter represents the poorest quality habi-

tat used by parrots in the study area. Disparity exists among avian taxa as to whether reproductive performance improves with experience (Pietiainen 1988, Gaston *et al.* 1994, Komdeur 1996). Observations of the congeneric Puerto Rican Parrot (*A. vittata*) suggest that, although sexual maturity occurs around three years of age, first breeding in the wild usually occurs from four to five years (Snyder *et al.* 1987). In my models, I reduced the fecundity of experienced adults by 50% and applied this value to novice breeders to account for the possibility of early recruitment into the breeding population. I estimated the lifespan of Black-billed Parrots to be 20 years in the wild, comparable to the similarly-sized Puerto Rican Parrot (Snyder *et al.* 1987).

Survival rates are poorly known for Neotropical parrots and the Black-billed Parrot is no exception. One species, however, has been the subject of intensive research and management. The Puerto Rican Parrot (IUCN critically endangered), whose population plummeted to 13 individuals in the 1970s and whose population continues to fluctuate between 20 and 50 individuals (U. S. Fish and Wildlife Service 1999), has been monitored for over 40 years (Snyder *et al.* 1987, Wiley *et al.* 2004). The identification of individual Puerto Rican Parrots and long-term monitoring of cohorts has provided the most reliable survival data of any of the 29 species in the genus *Amazona* and has long served as a benchmark for comparison (Gnam 1991, Enkerlin 1995). Caution, however, is warranted in applying survival rates from a population that has been intensively managed for decades and which is small and, consequently, vulnerable to stochastic (e.g., predation, environmental variance) and catastrophic (. hurricanes) events (Gilpin & Soulé 1986). When "best guess" survival estimates of Puerto Rican Parrots (Snyder *et al.* 1987, Meyers *et al.* 1996; Appendix 1) are modelled with Black-

billed Parrot reproductive performance in minimally-disturbed forest and edge habitat, within-habitat growth rates (λ are 1.09 and 0.98, respectively; these results suggest potential "source/sink" dynamics (Koenig 1999). Similarly, when "optimistic" survival rates are modelled, Black-billed Parrot population growth is positive for forest ($\lambda = 1.12$) and slightly negative for edge ($\lambda = 0.99$). Because the Black-billed Parrot population in Cockpit Country is large and not currently subjected to the high levels of Red-tailed Hawk (*Buteo jamaicensis*) predation experienced by Puerto Rican Parrots (White *et al.* 2005), I used "optimistic" survival estimates to parameterize the model.

The resulting Lefkovitch stage-classified model took the general form of:

$$\begin{bmatrix} 0 & 0 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & G_3 & 0 \\ 0 & 0 & P_3 & P_4 \end{bmatrix} \qquad (1)$$

F_i is stage-specific annual fecundity, the number of nestlings fledged successfully. $G_{i,j}$ is the probability of surviving and maturing to the next stage, and P_i is the probability of surviving and remaining within a stage. The estimates of the probabilities $G_{i,j}$ and P_i depend upon the growth probability γ_i for surviving individuals, and their survival probability σ_i such that:

$$G_{i,j} = \sigma_t \gamma_t \qquad (2)$$
$$P_i = \sigma_t (1 - \gamma_t) \qquad (3)$$

By assuming the age distribution within a stage has stabilized and the probability of maturing out of stage *i* is constant, maturation probability required for the above equations can be calculated:

$$\gamma_i = \frac{(\sigma_i / \lambda)^T - (\sigma_i / \lambda)^{T-1}}{(\sigma_i / \lambda)^T - 1} \qquad (4)$$

Indeed, because transition probabilities and fecundities in a deterministic matrix model are constant through time, after several iterations the model population converges on a constant growth rate, λ, and an equilibrium stage distribution (ln [λ] = r, the intrinsic rate of increase). After calculating the matrix values (Table 2), I used linear algebra eigenanalysis software (MATHEMATICA, Wolfram Research, Inc.) to obtain the dominant eigenvalue (i.e., λ) and eigenvectors of the matrix. The right eigenvector "ω" presents the stable age distribution (i.e., the proportion of individuals at equilibrium within each stage class). The left eigenvector (ν) presents the reproductive value of an individual in each stage, scaled to the youngest class and accounts for individual's future reproductive potential as it matures to the next stage class. By knowing the stable age distribution, reproductive values and population growth rate, it is then possible to calculate the proportional change in the growth rate caused by proportional changes in one of the life history parameters (i.e., the elasticity or proportional sensitivity of λ):

$$E_{i,j} = \frac{a_{i,j}}{\lambda} * \frac{\delta\lambda}{\delta a_{i,j}} = \frac{a_{i,j}}{\lambda} * \frac{(\nu_t \omega_\nu)}{\sum(\nu_t \omega_\nu)} \qquad (5)$$

where a_{ij} is any matrix element and $\Sigma (\nu_t \omega_t)$ represents the inner product of the two eigenvectors. Because elasticity values sum to 1.0, it is possible to avoid problems of metric differences among fecundity, maturation, and survival. Further, biologically implausible values (e.g., in the case of Black-billed Parrots, increasing fecundity of first- and second-year immature birds) are removed from the matrix. By these means, it is possible to identify critical life history stages.

I then used the model to explore the potential population growth trajectories in response to a diverse range of effects associated with bauxite mining. While it is clear that mining will result in an overall reduction of habitat (i.e., reduced carrying capacity/total population of Black-billed Parrot), I was interested in exploring the possible consequences of (a) increasing edge habitat, with the resultant decline in reproductive performance, as already observed during field surveys (Koenig 2001, Koenig *et al.* 2007); and (b) increases in mortality of each stage class. The latter could arise as the contiguous forest becomes fragmented by the network of roads used to access each mining pit: fragmentation not only increases the area of habitat suitable for Red-tailed Hawks but also improves access for poachers (pers. obs. in areas currently being mined in Jamaica) and could leave individuals more vulnerable to high winds and rain during hurricanes (see Wunderle & Wiley 1996, Meyers *et al.* 1996). Using an Excel spreadsheet, I ran deterministic population projections for 100 years to examine overall trends in growth trajectories. I set initial population size for each simulation at 2500 females to represent a "no mining" starting point. The portion of the Cockpit Country Conservation Area included in the temporally suspended prospecting license encompasses approximately 23,000 ha of closed-canopy forest. With densities of territorial pairs reported up to 20 pairs (10 females) per km^2 (Davis 2002), the prospecting area might support a population of 4600 pairs (2300 females). The underlying question of the scenarios was what percentage change in population parameters would be tolerated before we find Black-billed Parrots sliding into a conservation crisis from bauxite mining?

RESULTS

Population health under "normal" conditions. Assuming Jamaica's Black-billed Parrots enjoy the "optimistic" annual adult survival and have

TABLE 2. Stage-classified population matrix for Black-billed Parrot based on fecundity (F) observed in Cockpit Country, Jamaica, 1996–98, and survival (P) and maturation (G) data of Puerto Rican Parrots (see Appendix 1). The baseline matrix presented here and subsequently used for elasticity analysis uses reproductive data for females breeding in minimally disturbed forest.

	Juvenile	Subadult	Novice	Adult
F	0	0	0.30	0.60
P	0.70	0	0	0
G/P	0	0.85	0.27	0
P	0	0	0.63	0.87

the long lifespans of the congeneric Puerto Rican Parrot, their population growth rate is increasing 12% per year ($\lambda = 1.12$) in the minimally disturbed interior forest of Cockpit Country. As expected for a species with high annual adult survival and low annual fecundity, the highest proportion of individuals in the stable-age distribution is the adult class (Table 3). Further, and because of a long lifespan, adults also have the greatest reproductive value for the population (Table 3).

The elasticity analysis revealed that adult survival is overwhelmingly the matrix element most sensitive to change (Table 4). This factor is three to four times more important than any other element.

The model prediction of a population increasing by more than 12% per annum represents what may be the best, as close to natural conditions as possible in the interior forest of Cockpit Country, but it is clear that the population is not experiencing unlimited growth. Indeed, the population is limited by the surrounding landscape matrix of rural settlements and extensive agriculture of sugarcane and yam. At the interface of forest and edge habitat, field data revealed Black-billed Parrot fecundity is much lower (0.23/pair; n = 30 nest trees) compared to interior nest sites (n = 5 nest trees; Koenig 1991). With this

TABLE 3. Stable age distribution and reproductive value for the Black-billed Parrot demographic matrix presented in Table 2.

Stage class	Stable age distribution (ω)	Reproductive values (v)
1 (juvenile)	0.27	1.00
2 (subadult)	0.16	1.60
3 (novice breeder)	0.16	2.11
4 (adult)	0.41	2.38

lower reproductive performance, population growth rate becomes slightly negative ($\lambda = 0.99$). Across the Cockpit Country landscape, approximately 42,000 ha might be considered as core forest, with an additional buffer zone contributing perhaps 25% edge habitat (core : edge = 3:1). With such a spatial configuration, overall population growth remains positive ($\lambda = 1.06$), with the interior serving as "source" habitat for the "sink" edge.

Simulated scenarios of bauxite mining. According to the model, activities that affect adult survival will have a large effect on population growth. As annual adult mortality approached 20%, population growth became negative (Fig. 3). Similarly, if all stages classes exceeded 10% annual mortality, trajectories became negative. Changes in fecundity values, on the other hand, had comparatively small effects on population growth (Fig. 4). Indeed, it required more than a 50% reduction in annual fecundity to cause negative growth of the population. As noted previously, such poor reproductive performance has been documented in edge habitat in Cockpit Country, and serves as a first scenario for the effects of mining (Table 5). Notably, as a road network is established to access every cockpit "bottom" for mining, the forested hillsides become isolated in the mosaic such that each hill is encircled by edge (Fig. 2b). Post-mining reclamation and rehabilitation currently see the planting of a non-native grass, *Pennisetum*

141

TABLE 4. Sensitivity of Black-billed Parrot populations to changes in demographic parameters. Numbers represent the he proportional effects that changes in fecundity (F), maturation (G), and survival (P) would have on population growth (λ). The proportional sensitivities (elasticity) were calculated from the stable age distribution and reproductive values for pairs breeding in minimally disturbed interior forest, where $\lambda = 1.12$.

	Juvenile	Subadult	Novice	Adult
F	0	0	0.02	0.04
P	0.08	0	0	0
G/P	0	0.13	0.04	0
P	0	0	0.29	0.41

purpureum, which stubbornly prevents regeneration of native vegetation, with a consequence that forest hillsides remain isolated. Thus, the entire mined-out area becomes "edge" habitat and the population growth trajectory becomes negative ($\lambda = 0.99$), launching the Black-billed Parrot population into a gradual decline, which, unlike in the model output graphs, may be difficult to detect for several decades because of long adult lifespan. Under the scenario that the habitat is degraded for breeding, all other changes in fecundity or survival serve to hasten population decline (Figure 5). When all scenarios are imposed upon the population, population growth rate (λ) decreases to 0.95 and only 9 females persist at the end of 100 years. This number approaches what was the lowest population point for the Critically Endangered Puerto Rican Parrot in the 1970s.

DISCUSSION

One of the most important uses of PVA lies not in its application as an "absolute" predictor of the probability of population (or species) extinction but in its use for evaluating "relative" effects that changes in demographic parameters, such as may result from management interventions, may have on pop-
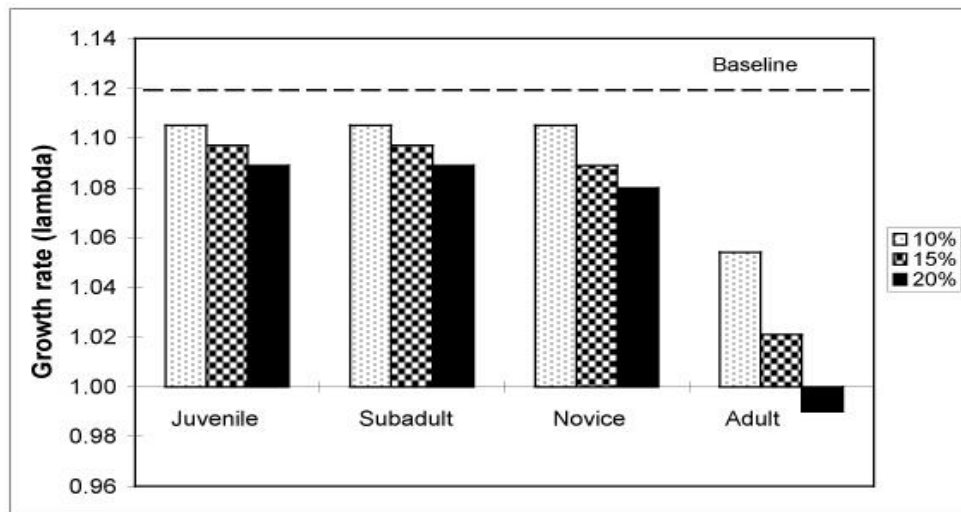

FIG. 3. Changes in population growth (λ) resulting from 10%, 15%, and 20% decreases in survival of individual life history stages of the Black-billed Parrot. The results represent single-stage reduction, other components held constant. The baseline represents growth rate from the initial "no mining" run of the model.
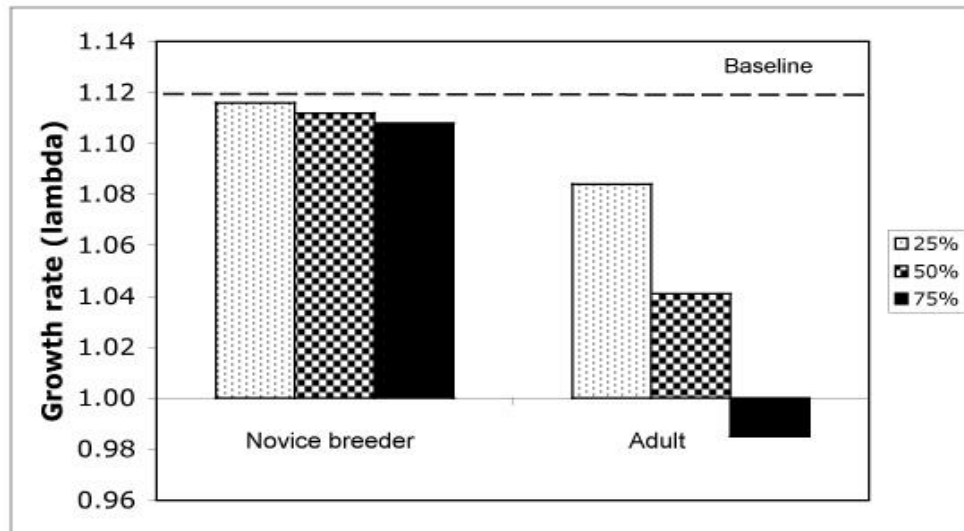
FIG. 4. Changes in population growth (λ) resulting from 25%, 50%, and 75% decreases in novice and experienced (adult) female fecundity. The baseline represents predicted population growth for birds breeding in minimally disturbed interior forest.

ulation growth rate (Beissinger & Westphal 1998). Conversely, PVA can be used to explore the possible consequences of habitat mismanagement before decisions are made that will result in the irreversible physical alteration of a landscape. My objective with the modelling was not to predict whether, or how quickly, Black-billed Parrots might go extinct, but to develop ecologically plausible scenarios about how mining-associated habitat loss and fragmentation could affect population health. To my knowledge, PVA has not been used in any environmental impact assessments (EIA) and certainly for no pre-mining feasibility assessments to evaluate the potential localised and landscape level consequences of open-pit mining on Jamaica's biodiversity.

The model made salient two important characteristics of the Black-billed Parrot population in Cockpit Country: (1) population growth was most sensitive to changes in adult survival; and (2) interior forest fecundity

appears adequate for population persistence ($\lambda = 1.12$) whereas edge habitat fecundity, over 60% lower than in the interior, is not sufficient to maintain populations ($\lambda = 0.99$). The first characteristic matches expectations for a species with high annual adult survival and long lifespan, such as is found commonly throughout the order Psittaciformes (Snyder et al. 1987, Stearns 1992, Smith & Rowley 1995). From the standpoint of species management, a simplistic statement is that the most effective management strategies will be those that prevent or minimize adult mortality. To this end, we need a much clearer understanding of what are the causes of mortality in adult Black-billed Parrots (and other stage classes) and an understanding of how the environment mediates mortality factors. The sensitivity analysis further highlighted the critical need for reliable, long-term data with a marked population to ensure that Black-billed Parrot survival is, indeed, comparable to the Puerto Rican Parrot. In all likelihood, Black-
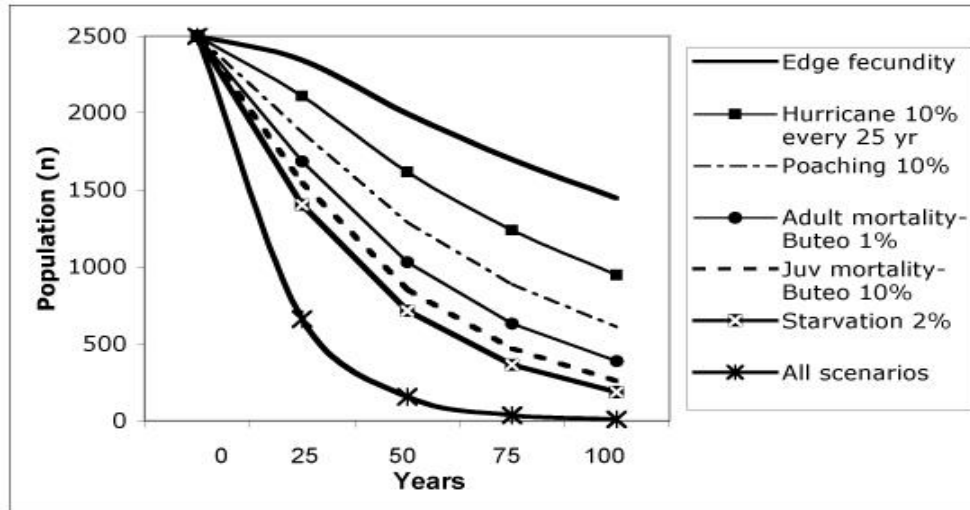
143

FIG. 5. One-hundred-year population projections of the potential effects of bauxite mining on different stage classes of Black-billed Parrots. Initial population was 2500 females for all simulations. The baseline simulation was of fecundity associated with breeding in edge habitat (F = 0.23; λ = 0.99), which would be the resultant habitat after mining. Each change in demographic parameter was first modelled independently i.e., no curve is cumulative of > 1 scenario, except for the final curve, "All Scenarios," which is of all scenarios enacted concurrently. With the population subjected to all scenarios, λ = 0.95.

billed Parrot survival is similar or higher owing to different ecological pressures on the two islands. First-year survival, particularly, is expected to be higher. The Puerto Rican Parrot population located in the Caribbean National Forest in eastern Puerto Rico falls within an area of the world's highest densities of Red-tailed Hawks (Waide 1996), an important predator of fledgling and juvenal parrots (Meyers 1996, White *et al.* 2005). This raptor occurs in low densities across the closed-canopy forest of Cockpit Country but is more commonly observed in fragmented peripheral habitat (unpubl. data; C. Kennedy pers. com.). There are no other large resident raptors to pose a significant risk: Jamaica has no resident forest-dwelling broad-winged hawk, such as in Puerto Rico, Hispaniola, and Cuba. The nocturnal Jamaican boa (*Epicrates subflavus*) is perhaps the only native predator to be of potential consequence for roosting parrots.

While the model revealed that fecundity was not as sensitive as survival to changes in value, it did show that the reproductive performance of pairs in edge habitat, which was over 60% poorer compared to interior sites, may represent a "sink" component of the forest gradient (Van Horne 1983, Howe *et al.* 1991). Overall, and because of the large, near-contiguous interior "source" habitat, the Black-billed Parrot population in Cockpit Country appears locally viable. However, the model output highlights potential consequences should the core forest become fragmented, with an associated increase in the pervasiveness of edge habitat as, indeed, would occur if bauxite mining took place. In this situation, it is critical that we understand why Black-billed Parrot reproductive performance was significantly lower in edge habitat in Cockpit Country. For this species, vegetation structure in edge habitat is an important

mediating factor in nesting success. Of the suite of nest stand, tree, and cavity characteristics, the presence of vines on the tree and an interlocking canopy with neighboring trees were the only significant factors; these appeared to facilitate predation of nestlings by Jamaican boas (Koenig *et al.* 2007). Whether boas, themselves, occur at higher densities in edge habitat remains to be determined.

Simulated scenarios. The scenario of greatest concern for the effects of bauxite mining is that fecundity will decline to "edge" rates in over 50% of the current range of Black-billed Parrot in Cockpit Country. The resultant long-term, gradual decline may be extremely difficult to detect as the mining slowly and permanently degrades the habitat. Further, the life history characteristics of high annual adult survival and long lifespan may mask poor reproductive performance and decreased recruitment of young birds into the breeding population. It may be a decade or more before the mature adults in the population succumbed to factors of old age. By the time population decreases are detected, it is likely that considerable areas of closed-canopy forest will have been destroyed and fragmented.

The other model scenarios serve to identify factors that could occur in association with bauxite mining in Cockpit County and underscore how vulnerable Black-billed Parrot populations are to human-induced disturbances of the environment. Indeed, several of these threats are occurring in mining areas east of Cockpit Country, including the central region of Mount Diablo (Fig. 1). Before the arrival of Europeans more than 500 years ago, the central limestone plateau of Jamaica was blanketed in mid-elevation wet limestone forest. The forests of Mount Diablo were part of a continuum across the karst landscape, contiguous with the remnant Cockpit Country Conservation Area. Unfortunately, we lack historic census data on Black-billed Parrots, but based on current abundance in Cockpit Country (c. 20 territorial pairs per km^2, Davis 2002), one could speculate equal densities were found across the Mount Diablo plateau. Over the past 100 years, Mount Diablo has been subjected to forest conversion, logging, and in the past 40 years, to bauxite mining. Surveys of Black-billed Parrots over the past five years find fewer than one pair per km^2 (unpubl.; BirdLife Jamaica's IBA database). Evidence of illegal timber extraction is found throughout the Mount Diablo Forest Reserve and on private lands. Trees with diameter-at-breast-height (dbh) exceeding 50 cm, the average size of nest tree adopted for use by Black-billed Parrots (Koenig 1999) are restricted to hilltops (unpubl. data). And in 2006, I encountered a poacher walking down a paved mining road, with three Yellow-billed Parrot chicks, less than two weeks of age, in a plastic bag. We were unable to return the chicks to their nest as the poacher had cut down the tree. One week prior to this encounter, a palm tree near our field house, which had an active Yellow-billed Parrot nest, was cut down by poachers.

While decision makers may be able to visualize how a reduction in habitat size will cause an absolute reduction in a species' population size, they may have difficulties appreciating how the changes in quality of the remaining habitat can exert influence on population demographics far beyond the initial "habitat loss" event. PVA modelling, and its associated population trajectory figures, enhance the process of visualization and, consequently, understanding. A population of 1000 Black-billed Parrots, with a growth rate of 0.99, likely does not sound to be a pressing conservation concern for some decision makers; a line of negative slope approaching zero may be more effective for communicating concern for a threatened species. With regards to habitat quality, Jamaica's decision

145

TABLE 5. Scenarios of ecologically plausible events associated with bauxite mining and consequences for Black-billed Parrot population growth (λ). Although mining would occur over several decades, any rehabilitation and regeneration of native habitat that might occur would likely require more than 100 years for its return to suitable habitat, particularly for the regeneration of large trees with nesting cavities. Consequently, then entire mined-out "interior forest" area assumes the properties of "edge habitat", shifting the population's "interior forest" $\lambda = 1.12$ to a new baseline $\lambda = 0.99$ (Scenario 1.1). As all subsequent scenarios would be in association with mining and edge dynamics, and not occur in an undisturbed interior forest, their effects on λ are against the new population growth baseline of scenario 1.1. All changes in demographic parameters are negative.

Demographic parameter	Scenario	% change in demographic parameter	λ
1. Fecundity	1.1. Annual adult fecundity decreased from "interior" = 0.6 to "edge" = 0.23 as the forest becomes fragmented and each cockpit hillside is surrounded by edge-pasture; because of increased sunlight, the edge forest will experience increased growth and abundance of vines and lianas, which will facilitate access to nestling parrots by predators (Koenig et al. 2007); illegal logging will be facilitated by the network of mining road, resulting in decreased availability of nesting cavities.		0.99
	1.2 Poaching of nestlings will reduce the annual fecundity of both novice and experienced breeding pairs. Poaching is facilitated by the mining road network. The current deterministic model only explores the harvesting of chicks; it does not account for a cumulative effect that would occur if poachers cut down the nest tree to access chicks, thereby precluding all future reproduction.	10%	0.98
2. Survival	2.1. Starvation: all stage classes affected by the loss of food resources associated with deforestation; even without fragmentation, frugivorous parrots must range over large areas to obtain seasonally available fruit; fragmentation will cause longer foraging trips, with associated increased energy expenditure and increased predation risk (see below) (Saunders 1989).	2%	0.97
	2.2. Increased predation by Red-tailed Hawks as habitat becomes more open: stage class 1-juvenile survival decreases. Fledglings will be most vulnerable because of weak flight and difficulties maintaining a tight flight formation with parents.	10%	0.97
	2.3. Increased predation by Red-tailed Hawks as habitat becomes more open: stage classes 2, 3, 4 - subadult, novice breeder, adult survival decreases. Birds will be vulnerable because under normal closed-canopy conditions this species does not demonstrate vigilant behaviour against aerial predators; during breeding season, males foraging alone will be vulnerable.	1%	0.98
	2.4. Increased vulnerability to tropical storms and hurricanes (small, fragmented populations vulnerable to catastrophic events; increased direct mortality associated with exposure to wind in "edge" habitat, increased indirect mortality associated with loss and slow recovery of food resources (see Wunderle et al. 1992). Survival of all stage classes will be affected both during and in the immediate aftermath of a storm. From 1951-2000, Jamaica experienced 2 hurricanes (0.04/annum). Over the past 300 years, 43 hurricanes have struck (0.14/annum).	10% reduction in population every 25 years	

makers recognize, at least for humans, that there is an important difference between "barely surviving" and "thriving to see one's grandchildren." For Black-billed Parrots, there is a visible risk that bauxite mining will put this forest-dependent species on a negative population trajectory of "barely surviving" solely because of degradation of its nesting environment. Improved access of humans via a mining road network and the alteration of natural predator-prey dynamics associated with modifications to habitat structure are predicted to hasten the decline of the Black-billed Parrot and, equally likely, the co-occurring Yellow-billed Parrot. Critical management objectives include, therefore, the conservation of the existing closed-canopy forests to maximize the ratio of interior : edge habitat and the prohibition of new access roads. Bauxite mining, as it is currently undertaken on Jamaica, is incompatible with these objectives. The scenarios I presented (which is by no means an exhaustive list), serve to draw the attention of decision makers and natural resource managers to a number of factors not normally associated directly with bauxite mining on Jamaica. These factors, their mitigation costs, and our uncertainties, must be evaluated against the benefits of bauxite mining.

ACKNOWLEDGMENTS

REFERENCES

Beissinger, S. R. 1995. Modeling extinction in periodic environments: Everglades water levels and Snail Kite population viability. Ecol. Appl.5: 618–631.

Beissinger, S. R., & M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. J. Wildl. Manage. 62: 821–841.

Brook, B. W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akçakaya, & R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature 404: 385–387.

Caswell, H. 1989. Matrix population models: Construction, analysis, and interpretation. Sinauer & Associates, Sunderland, Massachusetts.

Caughley, G. 1994. Directions in conservation biology. J. Anim. Ecol. 63: 215–244.

Crouse, D. T., L. B. Crowder, & H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68: 1412–1423.

Davis, H. A. 2002. Distribution and population size of *Amazona* parrots in Cockpit Country, a limestone karst region of Jamaica. M.Sc. thesis, Univ. of the West Indies, Mona, Jamaica.

Doak, D., P. Kareiva, & B. Klepetka. 1994. Modeling population viability for the desert tortoise in the Western Mojave Desert. Ecol. Appl. 4: 446–460.

Enkerlin-Hoeflich, E. C. 1995. Comparative ecology and reproductive biology of three species of *Amazona* parrots in northeastern Mexico. PhD thesis, Texas A&M Univ., Collage Station, Texas.

Enkerlin-Hoefflich, E. C., & K. M. Hogan. 1997.

Red-crowned Parrot. Pp. 1–20 *in* Poole, A., & F.Gill (eds.). The birds of North America, No 62. Academy of Natural Sciences, Philadelphia, Pennsylvania.

Gaston, A. J., L. N. DeForest, G. Donaldson G. & D. G. Noble. 1994. Population parameters of Thick-billed Murres at Coats-Island, Northwest Territories, Canada. Condor 96: 935–948.

Gilpin, M. E., & M. E. Soulé. 1986. Minimum viable populations: processes of species extinctions. Pp 19–34 *in* Soulé, M. E. (ed.). Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts.

Gnam, R. 1991. Breeding biology of the Bahama Parrot (*Amazona leucocephala bahamensis*). Ph.D. Thesis, The City Univ. of New York, New York.

Gnam, R., & R. F. Rockwell. 1991. Reproductive potential and output of the Bahama Parrot *Amazona leucocephala bahamensis*. Ibis 133: 400–405.

Heppell, S. S., L. B. Crowder, & D. T. Crouse. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. Ecol. Appl. 6: 556–565.

Howe, R. W., G. J. Davies, & V. Mosca. 1991. The demographic significance of 'sink' populations. Biol. Conserv. 57: 239–255.

Koenig, S. E. 1999. The reproductive biology of Jamaica's Black-billed Parrot (*Amazona agilis*) and conservation implications. DFES thesis, Yale Univ., New Haven, Connecticut.

Koenig, S. E. 2001. The breeding biology of Black-billed Parrot *Amazona agilis* and Yellow-billed Parrot *A. collaria* in Cockpit Country, Jamaica. Bird Conserv. Int. 11: 205–225.

Koenig, S. E. , J. M. Wunderle, Jr., & E. C. Enkerlin-Hoeflich. 2007. Vines and canopy contact: a route for snake predation on parrot nests. Bird Conserv. Int. 17: 1–15.

Komdeur, J. 1996. Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: A translocation experiment. Behav. Ecol. 7: 326–333.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21: 1–18.

Meyers, J. M., W. Arendt, & G. D. Lindsey. 1996.

Survival of radio-collared nestling Puerto Rican Parrots. Wilson Bull. 108: 159–163.

Pietiainen H. 1988. Breeding season quality, age, and the effect of experience on the reproductive success of the Ural Owl *Strix uralensis*. Auk 105: 316–324.

Saunders D. A. 1989. Changes in the avifauna of a region, district and remnant as a result of fragmentation of native vegetation: the wheatbelt of Western Australia. Biol. Conserv. 50: 99–135.

Smith, G. T., & I. C. R. Rowley. 1995. Survival of adult and nestling Western Long-billed Corellas, *Cacatua pastinator*, and Major Mitchell Cockatoos, *C. leadbeateri*, in the wheatbelt of western Australia. Wildl. Res. 22: 155–162.

Snyder, N. F. R., J. W. Wiley, & C. B. Kepler. 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles, California.

Stearns, S. C. 1992. The Evolution of life histories. Oxford Univ. Press, Oxford.

U. S. Fish and Wildlife Service. 1999. Technical/Agency Draft Revised Recovery Plan for the Puerto Rican Parrot (*Amazona vittata*). US Fish Wildlife Service Reg. 4, Atlanta, Georgia.

White, T. H., Jr., J. A. Collazo, & F. J. Vilella. 2005. Survival of captive-reared Puerto Rican Parrots released in the Caribbean National Forest. Condor 107: 424–432.

Wiley, J. W., R. Gnam, S. E. Koenig, A. Dornelly, X. Gálvez, P. Bradley, T. E. White, Jr., M. Zamore, P. R. Reillo, & D. Anthony. 2004. Status and conservation of the family Psittacidae in the West Indies. J. Carib. Ornithol. 17: 94–154.

Wunderle, J. M., Jr. & J.W. Wiley. 1996. Effects of hurricanes on wildlife: implications and strategies for management. Pp. 253–264 *in* DeGraaf, R. M., & R. I. Miller (eds.). Conservation of faunal diversity in forested landscapes. Conservation Biology Series 6, Chapman & Hall, London, UK.

Wunderle, J. M., Jr., D. J. Lodge, & R. B. Waide. 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaic. Auk 109: 148–166.

APPENDIX 1. Survival estimates for Puerto Rican Parrot (*Amazona vittata*) (Snyder *et al.* 1987, Meyers *et al.* 1996.

Age (years)	Percent surviving		
	Optimistic	Best-guess	Pessimistic
1	70	65	60
2	85	78	67
3	91	85	75
4	91	90	82
5+	91	90	90