A Comparative Analysis of Endangered Species Policies in the United States and South America

Andrew Wepner

5/2/2012

Introduce the reader to the Endangered Species Act (ESA), and the Red List. Provide the reader with a case study on a species from both lists (California Condor and Blue-headed Macaw respectively). Explain to the reader why species conservation and biodiversity are good. Compare and contrast the ESA and Red List.

Table of Contents

Introduction

In this paper I will introduce the reader to the United States Endangered Species Act (ESA). After a brief overview of the ESA, I will then discuss the type of decline for the recovery entities as well as taxonomic patterns of decline followed by geographic patterns of decline. I will then provide the reader with the results of the ESA experiment performed by Leidner and Neel (2011). Their results will then be discussed.

An introduction to California Condors will follow. I shall then provide the reader with a pedigree analysis of the California Condor along with the necessary terminology. Heterozygosity, founder genome equivalents, and founder allele survival will then be discussed. Mean kinship and inbreeding are then discussed. I then incorporate clan structure into the pedigree. The status of the population and its subpopulations are then discussed in three subcategories (1) demography, (2) genetic analysis, and (3) genetic structure in the subpopulations.

I then introduce the reader to the Blue-headed Macaw. I then provide the reader with locality and record data. I then discuss flock size and population estimates as well as range size. Habitat and altitudinal range are discussed next as well as clay lick usage. I then provide the reader with encounter rates.

Results and discussion of the Blue-headed Macaw case study follow. These include range size, altitudinal range, association with disturbed habitats, breeding, population size, and population trend. I then discuss Conservation of the Blue-headed Macaw with the reader. This includes: levels of protection and changes in forest cover, captive breeding programs, and applying the Red List criteria. I will then compare the United States Endangered Species Act and the Red List for the reader. The protection of endangered species is important for the purposes of biodiversity as well as benefits that the species may provide for not only the environment, but medicinal and aesthetic purposes for humans as well.

ESA

Species listed as threatened and endangered under the United States Endangered Species Act (ESA) have a high probability of extinction (Wilcove et al., 1993). The type of decline, including declines in geographic range, number of populations, and overall abundance, may vary considerably among species (Leidner and Neel, 2011). While a species can become extinct due to any one of these declines, at some point they all will occur simultaneously (Leidner and Neel, 2011). Species loss, a key indicator of declining biodiversity, is currently estimated to be 1000 times greater than pre-human rates (Pimm et al., 1995).

The greatest threats to biodiversity are thought to be human-mediated shifts in species' ranges (Relva et al., 2010). A species that will become extinct under the current trends, if effective action, such as captive breeding, is not taken in time is considered endangered (Fitter, 1986). Leidner and Neel conducted the first comprehensive analysis of ways in which species listed as threatened or endangered under the U.S. ESA are declining by building on studies done by Neel (2008); Flather et al. (1994, 1998); Dobson et al. (1997); Wilcove et al. (1998); Rutledge et al. (2001).

The types of declines associated with a particular species are usually a function of intrinsic species' traits, extrinsic threats, and their interaction (Leidner and Neel, 2011). For species listed under the ESA, the Secretary of the Interior is required to develop a recovery plan that outlines management actions needed for the conservation and survival of a species, unless the Secretary finds that such a plan will not promote conservation (16 U.S. Code, section 1533[f][1]) (Leidner and Neel, 2011). Recovery plans written for species on the ESA contain specific objective and measurable criteria. This makes it easier to track the progress of the species.

Although growing in popularity, captive breeding is considered the measure of last resort for the conservation of any species (Snyder et al., 1996). Despite the costs involved, many captive breeding programs are established on a subjective basis and projections based on the rate of decline of a species may provide greater objectivity when prioritizing captive breeding programs and habitat restoration when financial resources are limited (Wilson and Roberts, 2010). Information on the rate of decline of a species can identify both the urgency of the need for breeding a species in captivity if its extinction is imminent and an estimate of its potential recovery time if further decline is halted by habitat restoration (Wilson and Roberts, 2010). However, it can be difficult to quantify the rate and spatial patterns of a species decline at regional or local scales (Wilson and Roberts, 2010). Species, whose range occupies a large area, can be difficult to monitor or map, and distributional trends may be complex to extrapolate adequately, particularly when information is scant (Wilson and Roberts, 2010).

Leidner and Neel (2011) believe understanding the nature of declines for specific species can help ensure that these recovery objectives are appropriate. Detailed quantitative data on the distribution and population size trends of species are the preferred basis for defining scientifically defensible recovery objectives because such data can be used to assess the probability of extinction (Leidner and Neel, 2011). It is understandable that quantitative data would be preferred because you can graph it and look at trends. Evaluations of recovery plans indicate the status of a threatened or endangered species may be more likely to improve if recovery criteria are clearly linked to species biology (Gerber and Hatch, 2002). If there is any shift away from quantitative data, it could have very easily resulted from not having enough information on species statuses because that information can be difficult, time consuming, and costly to collect (Leidner and Neel, 2011).

Leidner and Neel (2011) evaluated the qualitative type of decline for species listed under the ESA and examined the proportion of species that declined in range, number of populations, and overall abundance and through a combination of these types of decline. They then examined how the prevalence of these types of decline varied among three broad taxonomic groups (invertebrates, vertebrates, and plants) and eleven more finely resolved taxonomic groups. They also examined the association between patterns of decline and geography.

Type of Decline for Recovery Entities

Leidner and Neel (2011) next talk about determination of species and analyze recovery plans. For this, their primary interest was in domestically listed species for which recovery plans have been approved. In the United States, species and subspecies of all plants and animals and distinct populations segments of vertebrates can be listed under the ESA (Leidner and Neel 2011). These are referred to by Leidner and Neel (2011) as recovery entities. The recovery entities used by Leidner and Neel (2011) largely correspond to those provided by the National Marine Fisheries Service (NMFS) and the U.S. Fish and Wildlife Service's (FWS) Threatened and Endangered Species Database System (TESS). In certain instances, Leidner and Neel (2011) treated a species as more than one recovery entity. They did this only if it was treated as such during the recovery planning process, despite how it was treated in TESS or by NMFS (Leidner and Neel 2011).

Leidner and Neel (2011) examined recovery entities that occurred in the 50 states, District of Columbia, U.S. Virgin Islands, Commonwealth of Puerto Rico, Territory of Guam, Commonwealth of the Northern Mariana Islands, and Territory of American Samoa. For each recovery entity, Leidner and Neel (2011) collected data from the latest recovery plans approved as of 31 December 2009. Leidner and Neel (2011) excluded recovery entities that were delisted due to taxonomic error or because new information had been discovered or had a recovery plan before being federally listed.

The type of Decline for Recovery Entities was next discussed by Leidner and Neel (2011). For each recovery entity, Leidner and Neel (2011) determined from the final approved recovery plan whether the domestic range, number of populations, or abundance was the same or smaller at the time the recovery plan was written relative to historic levels. Recovery plans are the only documents that provide a synoptic assessment of status that is relatively standard across all threatened or endangered species (Leidner and Neel, 2011). Leidner and Neel (2011) did not collect any data from sources such as peer-reviewed literature, gray literature, or assessments by conservation organizations because collecting such information was beyond the scope of their study.

Leidner and Neel (2011) considered qualitative data on range size, number of populations, and abundance of a recovery entity only if a recovery plan explicitly stated that these values were equal or less than historic values. The definition of historic as given by Leidner and Neel (2011) is not associated with a given time because the date when human activities or other environmental changes became threats varies across species and is often unknown. If a plan did not include clear information on range size, number of populations, or abundance, Leidner and Neel (2011) recorded the data as “not specified”. Leidner and Neel (2011) considered only the way in which a recovery entity declined, not improvements in status due to recovery actions. Leidner and Neel (2011) calculated the percentage of recovery entities associated with a type of decline and made no inferences about the magnitude of such declines for individual recovery entities.

Leidner and Neel (2011) defined a population of a recovery entity as it was defined in the recovery plan. However, if the definition of a population was unclear, they used criteria from the recovery objectives to guide their definition. Although the definition of a population as given by Leidner and Neel (2011) is loose, they believe it is sufficient for their purposes. Abundance was defined by Leidner and Neel (2011) as the overall number of individuals of a species. Whether a recovery plan contained quantitative or qualitative dada was recorded for each type of decline. Leidner and Neel (2011) considered quantitative data available only if both historic and current (at or around the time the plan was written) values were provided.

Taxonomic Patterns of Decline

Leidner and Neel (2011; Table 1) aggregated recovery entities into 11 taxonomic groups used by the FWS. Leidner and Neel (2011) then calculated the proportion of recovery entities in each group (with available data) associated with each type of decline. The data were then consolidated into 3 categories: vertebrates, invertebrates, and plants. Leidner and Neel (2011) then calculated the proportion of recovery entities in each of these groups associated with each type of decline. After eliminating arachnids from the analysis because of their small sample size, Leidner and Neel (2011) used a 10 x 2 contingency table to test for differences in type of decline among taxonomic groups. Nearly all of the recovery entities analyzed by Leidner and Neel (2011) declined in abundance, so they did not analyze the declines further.

Leidner and Neel (2011) had no way to determine whether declines in range, number of populations and abundance occurred simultaneously or sequentially. They did use a 2 x 2 contingency table in cases when both the qualitative range and number of populations were known for recovery entities to examine their joint distribution among taxonomic groups and among vertebrates, invertebrates, and plants.

Geographic Patterns of Decline

Leidner and Neel (2011) collected data from TESS on the historic distribution of recovery entities at the state or equivalent (e.g., territory, commonwealth) level. When these data were not available Leidner and Neel (2011) used the FWS or NMFS website and the recovery plan for the entity to delineate its geographic extent. Although finer-resolution data on historic distribution were available for some species, Leidner and Neel (2011) used state-level data because they were the data most consistently available for many recovery entities.

Leidner and Neel (2011) calculated the proportion of recovery entities within a state or equivalent for which ranges had contracted or populations were extirpated. Leidner and Neel (2011) considered a recovery entity had declined in a state or equivalent if it had declined anywhere within its range (even if it had not declined in that state or equivalent). Because taxonomic group was associated with the proportion of recovery entities for which both range size and number of populations had declined and because there was a geographical difference in the taxonomic distribution of recovery entities (e.g., more invertebrates in the southeast, more plants in Hawaii and California), Leidner and Neel (2011) calculated range and population reductions separately for vertebrates, invertebrates, and plants.

Results of the ESA experiment performed by Leidner and Neel (2011).

Leidner and Neel (2011) reviewed 599 recovery plans that included 1164 recovery entities that can be found in Table 1 of their article. Quantitative data on change in abundance, range size, and number of populations were available for 64% (n = 742), 75% (n =871), and 80% (n = 933), respectively, of recovery entities. Qualitative data on all three types of declines were available for 45% (n = 526) of recovery entities and no data on any type of decline were available for 7% (n = 85) of recovery entities. Four percent of recovery plans (n = 42) had quantitative data on both the historic and current range size of recovery entities and 2% of recovery plans (n = 28) had data on abundances. For approximately half the recovery entities (49%, n = 566), the number of historic and current populations was available. Of the recovery entities with qualitative data available, a considerable majority had declined in abundance (99%), range size (77%), and number of populations (79%). (All of this information can be found in Table 1 of Leidner and Neel's article).

The Taxonomic Patterns of Decline portion of their results was given next. The 10 taxonomic groups and the 3 taxonomic categories differed significantly in the proportion of recovery entities with declines in range and extirpations (Leidner and Neel 2011; Table 2; Figs. 1 & 2). Generally, fewer plants (72%, n = 497) declined than vertebrates (79%, n = 231) declined in range, but extirpations were more prevalent among plants (83%, n = 547) than vertebrates (64%, n = 231). Invertebrates had the greatest percentage of range contractions and extirpations (88% in each category, n = 153 for range,, n = 155 for populations).

Declines in range and number of populations were not independent (Leidner and Neel 2011; Table 3). Many (74%) recovery entities had a reduction in both range and number of populations, whereas nearly 17% had neither. About 8% of plants had extirpations without decreases in range size, whereas <3.5% of other taxa exhibited this pattern (i.e., populations were extirpated from the central portions of their ranges). About 14% of vertebrates had range contractions without extirpations. For several taxa (e.g., crustaceans, amphibians, and reptiles), the expected values for an individual cell were <5; thus, significant values should be interpreted with caution (Leidner and Neel, 2011).

The Geographic Patterns of Decline were discussed next by Leidner and Neel (2011). For the 3 taxonomic categories of recovery entities, geographic patterns of range contractions and extirpations were somewhat correlated (Leidner and Neel, 2011; Fig. 3). Overall, recovery entities in the southwest had a lower proportion of range and population declines relative to those in the eastern United States and California (Leidner and Neel, 2011). Generally, plants followed this trend, but vertebrates had a higher proportion of range and population declines in the southwest (Leidner and Neel, 2011). Invertebrates had a high prevalence of range contractions and extirpations regardless of their location (Leidner and Neel, 2011).

Discussion of results from the experiment by Leidner and Neel (2011).

They first discussed Taxonomic Patterns of Decline. Range contractions and extirpations were common to the majority of listed species, but exceptions highlight the effects of the interaction of geography and range sizes (Leidner and Neel, 2011). They then discussed the Geographic Patterns of Decline. The general geographic patterns of declines in range and number of populations reflect in part the geographic clustering of taxonomic groups (Leidner and

Neel, 2011; Fig. 3). The last thing discussed by Leidner and Neel (2011) was Inference for Recovery Planning. The high percentage of recovery entities for which extirpations and reductions in overall abundance have been documented suggests that the common use of downlisting and delisting criteria expressed in terms of the number and size of populations (Wilcove et al., 1993; Tear et al., 1995; Gerber and Hatch, 2002; M.C.N., unpublished data).

Introduction to California Condors

California Condors (Gymnogyps californianus) once ranged over much of southern North America (Ralls and Ballou, 2004). After the end of the Pleistocene, the range of the species contracted toward the West Coast (Emslie, 1987). After Europeans arrived, the population began a precipitous decline due to a variety of human impacts (Snyder and Snyder, 2000). A small wild population persisted in California until the 1980s (Ralls and Ballou, 2004). However, high mortality continued and the last wild California Condor was brought into captivity in 1987 to avoid extinction of the species (Ralls and Ballou, 2004). The total population then consisted of 27 captive birds (Wallace and Toone, 1992). Reproduction in captivity was highly successful and by August 2002 the population consisted of 206 individuals divided into four subpopulations: the captive population and reintroduced populations in California, Arizona, and Mexico (Ralls and Ballou, 2004).

Because of this population’s history, pedigrees are available for every individual, regardless of its location (Ralls and Ballou, 2004). Thus, California Condors are one of the few species where management recommendations for both captive and wild populations can be based on pedigree analyses (Haig and Ballou, 2002). Pedigree analyses provide powerful methods for describing current population structure, determining the genetic importance of specific individuals to current and future populations, and monitoring loss of genetic diversity over time (Haig and Ballou, 2002). While pedigree analyses are routinely used for management of captive populations, they are unfortunately often unavailable for wild populations (Ralls and Ballou, 2004).

The specific objectives of Ralls and Ballou (2004) were to (1) determine the growth rate and age structure of the population; (2) determine the current genetic structure of the total population; (3) compare the genetic structure of the various subpopulations; and (4) conduct analyses to assist with 2002 management needs. These management needs included a genetic evaluation of existing pairs, recommendations for new pairings, identification of genetically less valuable birds that could be used for purposes other than breeding (e.g., as exhibit birds), selection of pairs to begin a new captive subpopulation at the Oregon Zoo, and recommendations for appropriate placement of the chicks hatched in 2002 in the various subpopulations (Ralls and Ballou, 2004).

Pedigree Analysis and Terminology

Pedigree analyses measure genetic parameters relative to a base population, which is assumed to be a wild source population from which randomly captured individuals (founders) would be unrelated (i.e., the kinship coefficients among founders are 0.0 (Falconer and Mackay, 1996). Thus measures of genetic diversity determined by pedigree analyses estimate losses or changes relative to this hypothetical wild base or source population (Pollak et al., 2002). Here Ralls and Ballou (2004) use the pedigree analysis software PM2000 (Pollak et al. 2002) to calculate changes in heterozygosity, levels of inbreeding, mean kinship among individuals, and survival and loss of founder alleles in the condor population.

Heterozygosity

Heterozygosity (H) is calculated from gene drop models by counting the allele frequencies of the founder alleles in the living extant population each simulation, averaging frequencies over simulations to obtain average allele frequencies (p_i) and estimating H using the formula for expected heterozygosity: $H = 1\text{-}\sum p_i^2$ (Ralls and Ballou, 2004). Thus, heterozygosity is interpreted as the proportion of the base population's heterozygosity retained in the extant captive population (Ralls and Ballou, 2004). This relative or proportional heterozygosity is often referred to as gene diversity in the captive-breeding literature (Lacy, 1989). H as calculated in pedigree analysis is not directly relatable to molecular estimates of heterozygosity because it is proportional to expected heterozygosity in the base population (i.e., $h = 0.90$, then the population has 90% of the base population's heterozygosity, whatever that might have been) (Ralls and Ballou, 2004).

Founder Genome Equivalents

A useful concept related to retained heterozygosity is founder genome equivalents (f_g) (Ralls and Ballou, 2004). This is the number of unrelated founders needed to establish a new population with the same levels of heterozygosity as that in the present population and is calculated as $1/[2(1\text{-}H)]$ (Ralls and Ballou, 2004). Thus, for example, a population with $H = 0.9$ has 5 founder genome equivalents; only five unrelated founders would be needed to establish a population with an initial $H = 0.9$ (Lacy, 1989, 1995).

Founder Allele Survival

The proportion of a founder's genome that survives to the extant population ("allele retention," or $\boldsymbol{r}$) is also calculated using gene drop models (Thompson, 1986; Lacy, 1989). A founder that produces only one offspring in the extant population has 50% allele retention because only one-half of its genes have been passed on to the single offspring (Ralls and Ballou, 2004). Founders with more complex descendant pedigrees will show more or less retention depending on the exact structure of their descendant's pedigrees (Ralls and Ballou, 2004). Founder allele survival is calculated as the proportion of a founder's two alleles that are present in the extant population (Ralls and Ballou, 2004). There are only three possibilities for a founder in any given simulation: neither allele present = 0%, or one present = 50%, both present = 100%; these are averaged over all simulations (Lacy, 1989; Thompson, 1986).

Mean Kinship and Inbreeding

Mean kinship is used to identify genetically important individuals (Ralls and Ballou, 2004). Mean kinship (mk_i) is calculated for every living animal in the population as the average kinship between that individual and all individuals in the population, including itself (Ballou and Lacy, 1995). Individuals with low mean kinship have fewer or less closely related relatives than those with high mean kinships (Ralls and Ballou, 2004). Ballou and Lacy (1995) showed that breeding strategies that preferentially select animals with low mean kinships are the best at retaining expected heterozygosity in the population, since average mean kinship is directly related to expected heterozygosity ($H = 1 - mk$). Thus, minimizing average mean kinship in the population maximizes heterozygosity (Ralls and Ballou, 2004). Most, if not all, captive-breeding programs now use mean kinship when selecting animals to breed (Ballou and Foose, 1996).

Inbreeding coefficients (F) measure the degree of kinship between the parents of an individual and are calculated as the probability that an individual will receive two alleles that are identical by decent from the base population (i.e., two copies of the same founder allele;

Falconer and Mackay, 1996). Unrelated parents produce offspring with *F*=0, while brother-sister, mother-son, or father-daughter pairs produce offspring with *F*=0.25 (Ralls and Ballou, 2004). Both mean kinships and inbreeding coefficients are calculated directly from the pedigree using an additive relatedness matrix (Ballou, 1983) rather than gene drop.

Incorporating Clan Structure Into the Pedigree

The relationships among some of the first 27 California Condors in the captive-breeding program were known from observations in the wild (Ralls and Ballou, 2004; Fig. 1). Birds identified as studbook numbers 2,3,4,8,9, and 10 were never brought into captivity but were known to be the parents of some that were (e.g., as eggs) and are therefore included in the studbook (Ralls and Ballou, 2004). The known pedigree relationships suggested that the population descended from 14 individuals (Ralls and Ballou, 2004; Fig. 1). Ralls and Ballou (2004) call these 14 individuals the "apparent founders" (marked by asterisks in Fig. 1). However, DNA fingerprinting indicated that the captive condors fell into three basic groups or clans (Geyer et al., 1993). Birds within clans were more closely related to each other than birds belonging to different clans (Ralls and Ballou, 2004). Although Greyer et al. (1993) could not determine the absolute level of relatedness among clan members with high accuracy, it was clear from their analysis that any captive-breeding strategy designed to maintain genetic diversity would need to incorporate the information on clan structure.

To incorporate the clan structure into the pedigree prior to analysis, we modified some studbook data to create an analytical studbook that we used for all analyses (Greyer et al., 1993; Fig. 1). For analytical purposes, Ralls and Ballou (2004) therefore assumed that the birds within a clan had a coefficient of kinship of 0.125 (half-sibs), unless known otherwise from recorded pedigree information, and that kinship coefficients were 0 for individuals belonging to different clans. Assuming half-sib relationships among clan members is not unrealistic, given the California Condor's known history of small population size before the last birds were brought into captivity (Ralls and Ballou, 2004).

To establish these levels of relationships among the apparent founder birds in the studbook, we created hypothetical parents for them (Ralls and Ballou, 2004; Fig. 1). Each wild-caught bird within a clan was given a common hypothetical sire (i.e., HA, HB, or HC) and a unique hypothetical dam (e.g., H1, H2, etc, where the number was the same as the studbook number of the wild-caught individual) (Ralls and Ballou, 2004). This structure achieved the desired result of members within a clan having kinships of 0.125, but kinships between clans being 0 (Ralls and Ballou, 2004). By adding these hypothetical parentages, we increased the number of founders that contributed to the captive population (Ralls and Ballou, 2004). The population now had 17 founders (a unique dam for each apparent founder plus three added sires; Ralls and Ballou, 2004; Fig. 1). Ralls and Ballou (2004) call these 17 individuals the "analytical" founders.

Status of the Population and its Subpopulations

Demography

There were 206 birds in the population on 21 August 2002, with 113 in captivity and 93 in the wild (Ralls and Ballou, 2004). The captive birds were distributed among three facilities: 32 at the Los Angeles Zoo, 35 at the San Diego Wild Animal Park, and 46 at the World Center for Birds of Prey in Boise, Idaho (Ralls and Ballou, 2004). The wild birds were divided into three subpopulations: 50 in California, 37 in Arizona, and 6 in Baja California, Mexico (Ralls and Ballou, 2004). Growth of the total population has been between 10% and 15% per year since 1987 (Ralls and Ballou, 2004; Fig. 2), when the last wild birds were brought into captivity. Since 1992, the growth of the captive population has been only about 5% per year due to the removal of chicks for reintroduction each year (Ralls and Ballou, 2004).

The age structure of the current population is relatively young because the captive population has been in existence only since the late 1980s (Ralls and Ballou, 2004). Most birds older than about 14 years are wild-caught birds and their ages are estimates (Ralls and Ballou, 2004). Overall, there is a balance between males and females, and the age structure is typical of a rapidly growing population (Ralls and Ballou, 2004; Fig. 3a). The wild population consists mostly of young birds and a few adults that have recently attained sexual maturity (at 5-6 years of age; Ralls and Ballou, 2004; Fig. 3b). The age structure of the captive population (Ralls and Ballou, 2004; Fig. 3c) shows a deficit of animals in age classes 1-4 years because almost all chicks for the last 5 years have been reintroduced.

Given management goals and the current demography of the population, it is still appropriate to breed all adult females in captivity to increase the size of the population as rapidly as possible and provide chicks for reintroduction (Ralls and Ballou, 2004). There is also a need to begin retaining some chicks in captivity to rectify the deficit of younger individuals in the captive population (Ralls and Ballou, 2004).

Genetic Analyses

Any assumption that the 14 apparent founders are related in some way will result in an immediate loss of heterozygosity in the captive population compared to the amount that would have been present if the founders had been unrelated (Ralls and Ballou, 2004). The assumption of Ralls and Ballou (2004; Table 1) that the birds within clans were half-sibs resulted in an average kinship of 8% among the 14 apparent founders, meaning that on average they were slightly more related to each other than cousins. Under this assumption, the birds used to found the captive population contained only 92% of the heterozygosity contained in the hypothetical wild base population prior to its bottleneck (Ralls and Ballou, 2004; Table 1). This equates to 6.2 founder genome equivalents (Ralls and Ballou, 2004). In the current population, (wild and captive combined) heterozygosity is 91.4%, down only slightly from the 92% of the founders (Ralls and Ballou, 2004; Table 1). Thus about 99.5% of the heterozygosity that the founders brought into the population has been retained in the current population (Ralls and Ballou, 2004). This is because condors are long-lived and the captive population has been under genetic management since its inception (Ralls and Ballou, 2004).

The average mean kinship for the total population is 0.086 with individual mean kinships ranging from 0.067 to 0.108 (Ralls and Ballou, 2004; Fig. 4). A mean kinship of 0.063 is equivalent to an individual being related to the population on average at the level of first cousin; a mean kinship of 0.125 is comparable to half-sibs (Ralls and Ballou, 2004). While all birds should be bred, birds with mean kinships below the average should be given the highest breeding priority (Ralls and Ballou, 2004). This applies, in particular, to the three birds with the lowest mean kinships (birds 1, 5, and 33; Ralls and Ballou, 2004; Fig. 4).

Genetic Structure in the Subpopulations

Retained heterozygosity is somewhat lower in the wild than in captivity (Ralls and Ballou, 2004; Table 1), which is not surprising since some of the more genetically valuable animals and their descendants have not yet been reintroduced. The level of inbreeding is less in the wild because only non-inbred birds have been reintroduced and wild birds have yet to breed (Ralls and Ballou, 2004).

There are only small to moderate differences between the wild populations in California and Arizona based on heterozygosity (Ralls and Ballou, 2004; Table 1). F_{ST}, a common measure of genetic differences between populations (Frankham et al., 2002), is only 0.009, indicating only minor differences in the frequency of founder alleles in the two populations (Ralls and Ballou 2004). We did not evaluate the wild population in Baja California because it was established with only six birds in 2002.

A more detailed genetic comparison of the wild populations in California and Arizona is provided by estimates of the proportion of each analytical founder's alleles that are present in each population (Ralls and Ballou, 2004; Fig. 6). The most obvious difference between these two subpopulations is that alleles from bird number 1 ("Tropa") are missing from the Arizona population, and alleles from bird 9 are missing from the California population (Ralls and Ballou, 2004). Number 1 is still alive and reproducing but 9 is dead (Ralls and Ballou, 2004). Its alleles are represented in the population through its offspring, 33 ("Sequoia") (Ralls and Ballou, 2004). Condor number 7 ("AC5") is also underrepresented in the Arizona population (Ralls and Ballou, 2004).

The founders' alleles also are fairly well distributed between the three current breeding facilities (Los Angeles, San Diego Wild Animal Park, and World Center for Birds of Prey), although the World Center for Birds of Prey lacks alleles from condor 9 (Ralls and Ballou, 2004; Fig. 6). Genetic deficits in specific wild or captive populations can be rectified by moving individuals carrying alleles from the underrepresented founders to the appropriate location (Ralls and Ballou, 2004).

Introduction to the Blue-headed Macaw

Until the twenty first century, the Blue-headed Macaw was not considered a conservation priority. It was rare in captivity (Cites, 2002), while specimen records and published accounts suggested that it was fairly widespread and tolerant of habitat alteration (Parker and Remsen, 1987; Juniper and Parr, 1998). Only recently has it been recognized how little is known about this species: there are few specimens, all from Peru, and it is thought to be scarce and declining throughout its range (BirdLife International, 2007a).

On the IUCN Red List of threatened species (Red List) it was reclassified from “Least Concern” to “Near Threatened” in 2004 (BirdLife International, 2004), and then jumped a rank to “Endangered” in 2006 (IUCN, 2006). These shifts are based on few data (Tobias and Brightsmith, 2006). Recent publications show the range of the Blue-headed Macaw to be in southern Amazonian Peru, with minor extensions into Brazil and Bolivia (Collar, 1997; Juniper and Parr, 1998). Using these published distributions, BirdLife International (2007a) estimated the extent of occurrence to be 373,000 km². Similarly, on the basis of a few published sources and anecdotal accounts, Lambert et al. (1993) made a rough population estimate of 10,000 individuals in 1990.

More recently, Gilardi (2003) commented that “the available concrete information on abundance” suggested a global population of “well under 1000 mature individuals”. The majority of principal watersheds in which this species is thought to occur “have been visited by ornithologists, birders and biologists in general”, and that they found the species to be “absent or extremely rare", (Gilardi, 2003). According to Tobias and Brightsmith (2006), these assessments have far-reaching consequences. The Red List, produced by the Species Survival Commission (SSC) of IUCN – the World Conservation Union, provides a baseline for prioritizing conservation actions (Collar, 1996; Rodriques et al, 2006), and measuring their success (Buchart et al., 2004, 2005). As the most authoritative and objective assessment of extinction risk in animals and plants, it has a growing influence on funding, legislation and research (Tobias and Brightsmith, 2006).

Tobias and Brightsmith (2006) state that the Red List carries much weight, and rightly so; but they then ask how robust are the assessments on which it is based? The criteria have been honed and re-honed (Mace and Lande, 1991; IUCN, 2001), but the assessment process still draws criticism (Possingham et al.,, 2002; Regan et al., 2005) as does the correct handling and application of population data (Broderick et al., 2006). More than a decade after the implementation of data-driven and objective criteria for estimating extinction risk (IUCN, 2001; Rodrigues et al., 2006), some critics still hold that "the Red List's categorizations are largely informed guesswork by experts: (Harcourt, 2005).

Given recent changes in status, the Blue-headed Macaw provides a useful case study of the Red List process, particularly the difficulty of classifying poorly known species (Tobias and Brightsmith, 2006). In order to re-assess the Blue-headed Macaw's global conservation status Tobias and Brightsmith (2006) reviewed all accessible information from published and unpublished sources. Tobias and Brightsmith (2006) also compiled ecological data, such as habitat preferences, clay lick usage and breeding behavior, where these were relevant to conservation. On the basis of a range-wide preview of locality data, Tobias and Brightsmith

(2006) estimated its distribution and population size, re-applied the Red List criteria, and used their findings to formulate constructive comments about the Red List process.

Locality and Record Data

Early locality records for the Blue-headed Macaw were collected from museum data and publications (Tobias and Brightsmith, 2006). Since 1930, an increase in regional research and ecotourism has produced new records, many of them unpublished, or published outside the peer-reviewed literature (Tobias and Brightsmith, 2006). Tobias and Brightsmith (2006) sought personal accounts from researchers and experienced ornithologists, including several documents published online by the Rapid Assessment Program of Conservation International, and the Rapid Biological Inventory program of the Chicago Field Museum. For a full list of sources, see the supplementary data provided by (Tobias and Brightsmith, 2006).

Where sites were tightly packed (<20 km between sites) Tobias and Brightsmith, (2006) pooled them under a single locality. Thus, while Tobias and Brightsmith (2006) used a total of 51 sources to produce a list of 61 separate localities, the actual number of sites was considerably higher (>100). To measure regional coverage, Tobias and Brightsmith (2006) noted all localities that had received recent intensive surveys (>1 week of fieldwork at a single site by experienced personnel, post 1970) but for which no records of Blue-headed Macaw are known.

Flock Size and Population Estimates

For each post-1970 locality Tobias and Brightsmith (2006) estimated minimum population size and maximum flock size. In most cases Tobias and Brightsmith (2006) assumed that non-simultaneous sightings of different flocks could involve the same birds, and therefore the maximum flock size reported is used as the minimum population size. Where flocks were seen more than 10km apart, Tobias and Brightsmith (2006) used a cumulative figure of the largest flocks at each site to generate a minimum population size; where largest flock size was not reported they made an estimate of the minimum number of birds likely to have produced the pattern of records. For localities where birds were recorded but where no population estimate was made, Tobias and Brightsmith (2006) assumed a minimum of one pair at each site. The figures in almost all cases are certain to underestimate the true number of birds present (Tobias and Brightsmith, 2006).

Range Size

The Red List criteria (IUCN, 2001) define Extent of Occurrence (EOO) as "the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon". Tobias and Brightsmith (2006) state this measure may exclude discontinuities or disjunctions within the overall distributions of taxa (e.g. large areas of unsuitable habitat). To generate an EOO for the Blue-headed Macaw Tobias and Brightsmith (2006) mapped a boundary around localities using ArcView GIS 3.2a (ESRI, 2005), and accounted for discontinuities by subtracting all major areas of inappropriate habitat (deforestation, settlements, land over 1500 m asl, large peripheral regions with no records etc.). Tobias and Brightsmith (2006) then rounded the outcome to the nearest 10,000 km^3 to produce an EOO estimate.

Habitat and Altitudinal Range

Habitat descriptions were available for >75% of post-1970 localities (Tobias and Brightsmith, 2006). In these cases Tobias and Brightsmith (2006) assigned localities to one of three habitat types (floodplain, upland, or a mix of the two), one of three anthropogenic disturbance regimes (pristine, moderately disturbed, or heavily disturbed), and one of two elevational ranges (lowlands <500m, or foothills >500 m asl). Tobias and Brightsmith (2006) chose 500 m as the cut-off point as the Andes generally rise steeply from this altitude upwards, and Amazonia drops gradually from this point downwards. Tobias and Brightsmith (2006) compared minimum population estimates and maximum flock sizes at each locality for each variable.

Determining habitat associations for psittacines is complicated because they are often seen in flight above potentially suboptimal habitat; for example, a population of Blue-winged Macaws bred in relatively intact forest, but ranged daily over cleared areas and agricultural land (Evans et al., 2005). Further, although many Amazonian parrots are seen from rivers or near rivers, this may be because most surveys or expeditions do not penetrate far inland (Tobias and Brightsmith, 2006). Added to this sampling bias, there is a detectability bias as parrots are usually seen and identified most readily from rivers and clearings (Tobias and Brightsmith, 2006). As a result, the multisite analysis of habitat association done by Tobias and Brightsmith (2006) is relatively crude, especially as most localities contain a mosaic of habitats. Most birds were located and identified by voice, therefore biases affecting visual data do not apply (Tobias and Brightsmith, 2006). Blue-headed Macaws, like most parrots, call loudly and distinctively in flight and when perched (Tobias and Brightsmith, 2006).

Clay Lick Usage

To asses year round presence and seasonal fluctuations in population size at a single locality, Tobias and Brightsmith (2006) recorded at a clay lick adjacent to Tambopata Research

Center from nautical sunrise until the birds finished their morning lick use (usually before 07:30 EST) on 1468 mornings from 12 January 2000 to 31 December 2005. On every morning, observers noted the time Blue-headed Macaws were first detected near the lick; this species often visited the vicinity of the lick without actually feeding on the clay (Tobias and Brightsmith, 2006).

Encounter Rates

Tobias and Brightsmith (2006) calculated encounter rates of Blue-headed Macaws from 798.5 h of systematic parrot counts at five sites. These included over 3000 10-min point counts at Tambopata Research Center (Brightsmith and team), 83 h of observations from a 43-m tall canopy tower at Posada Amazonas (Brightsmith and team), 45 h of observations in clearing at GREES (C. Torres-Sovero and E. Tavera), 65 h of observations from a cliff-top viewpoint at Las Piedras Biological Station (A. Lee and E. Tatum-Hume), and 85 h of observations from the CICRA station clearing (JAT) (Tobias and Brightsmith, 2006).

Results and Discussion

Range Size

Tobias and Brightsmith (2006) compared their data using univariate nonparametric techniques: Mann-Whitney U-test for altitudinal variation, Druskal-Wallis tests for habitat and disturbance, ANOVA for variations in flock size, and %^{2}-tests for habitat use at CICRA. All statistical tests were carried out using SPSS (2001); *p*-values are two-tailed (Tobias and Brightsmith, 2006).

Tobias and Brightsmith (2006, Section 2) estimate a total global range of 609,494 km² and an EOO of 460,000 km². This EOO, 60% larger than the previously published estimate (BirdLife International, 2007a), is probably an underestimate. The total global range remains >90% forested, with the only significant areas of perturbation being around the largest city, Puerto Maldonado, Peru, and between Iñapari and Rio Branco, Brazil (FlashEarth, 2006). The fact that the Blue-headed Macaw is still seen on the outskirts of Puerto Maldonado suggests that anthropogenic pressures have not eliminated it from any large areas (Tobias and Brightsmith, 2006). Thus, Tobias and Brightsmith (2006) may have overestimated discontinuities in range when producing their EOO estimate. There is also a shortage of data from Acre, Brazil, and this part of the range may be considerably more extensive (Tobias and Brightsmith, 2006).

Altitudinal Range

According to Tobias and Brightsmith, (Supplementary data; 2006) localities range in elevation from 200m to 1500m, but the majority lie below 500 m (41 versus 16; 72%). This disparity reflects the fact that >90% of the range mapped in (Tobias and Brightsmith, 2006; Fig. 1) lies below 500 m. Minimum estimated population sizes and maximum flock sizes were slightly higher above 500 m, but this difference was not significant (Tobias and Brightsmith, 2006; Table 1; Fig. 2a). This result tallies with the observation that relatively dense populations are found in both foothill regions (e.g. mountains of Huánuco) and lowlands far from the base of the Andes (e.g. Los Amigos, Tahuamanu, Purús and Juruá rivers) (Tobias and Brightsmith, 2006). Similarly, the two largest flocks recorded were 60 birds at Pozuso (850 m) and 53 birds at San Lorenzo (250 m), suggesting no difference in overall abundance in lowlands versus foothills (Tobias and Brightsmith, 2006).

This pattern may not hold true on a local scale, as the species is fairly common on or near low (<1000 m) ridges in Manu National Park, but much rarer in lowlands to the east (Tobias and Brightsmith, 2006). Its distribution in this well-studied region may have given rise to speculation that the Blue-headed Macaw "possibly prefers foothill to lowland forest" (Juniper and Parr, 1998). The range-wide analysis of Tobias and Brightsmith (2006) suggests that this impression was a sampling artifact.

Association With Disturbed Habitats

Parker and Remsen (1987) stated that "this macaw seems to survive in cutover areas with scattered patches of forest and may be expanding its rather small range in south-western Amazonia". Juniper and Parr (1998) concluded on the basis of a literature review that the species preferred "disturbed or partly open habitats with birds mostly occurring at forest edge along rivers, in clearings and around partly forested settlements". Vriesendorp et al. (2004) espoused a different view, stating that it is "sensitive to human disturbance, occurring only in large tracts of primary lowland and foothill forest". The data collected by Tobias and Brightsmith (2006) suggests that the species is associated with degraded areas, at least locally, but that it occurs in many vegetation types.

Breeding

The Blue-headed Macaw is reported to have low reproductive output in the wild (CITES, 2002), but this statement is based on few data. A recent review of breeding records for south-eastern Peruvian parrots found no published or unpublished records for this species, but reported 55 nests of Scarlet Macaw Ara macao and 75 nests of Blue-and-yellow Maxaw Ara ararauna (Brightsmith, 2005). One possible nest was reportedly in a bamboo cavity (CITES, 2002), and another was in a tree cavity repeatedly visited by a pair of adults in the Cordillera Azul (Alverson et al., 2001).

In captivity, clutch size is reported to be 2 – 4 eggs (Vit, 1997). Adult longevity is unknown, but the congeneric Blue-winged Macaw can live at least 31 years in captivity (Brouwer et al., 2000). Data on reproductive output and longevity need to be confirmed by studies of birds in the wild (Tobias and Brightsmith, 2006).

If wild Blue-headed Macaws, like their captive counterparts, have a roughly annual breeding cycle and a relatively young age of first breeding, there should be only three sizeable cohorts of non-breeding birds in the population (Tobias and Brightsmith, 2006). The number of adults fluctuates according to survivorship and productivity, and the adult-immature ratio in most macaws seems likely to be between 1:1 and 5:1 (Gilardi, 2003). Given the information outlined above, Tobias and Brightsmith (2006) adopt an estimated adult-immature ratio of 4:1 for the Blue-headed Macaw.

Population Size

Summing minimum population data at each locality gives an estimated minimum global population of 545 individuals (Tobias and Brightsmith, 2006). However, this is an underestimate because: (1) repeated sightings at the same locality are likely to involve different birds; (2) many sightings are never reported; (3) the areas visited by experts make up a tiny proportion of the total range (Tobias and Brightsmith, 2006). The more widely accepted method of estimating populations of species that are too abundant and widespread to census directly involves the extrapolation of population size from density and area estimates (Bibby et al., 2000).

To assess previously published population estimates Tobias and Brightsmith (2006) suggest that we can work backwards to determine what densities they represent. BirdLife International (2007a) estimated a maximum population size of 2499 mature individuals and a range size of 373,000 km². This suggests a mean population density of one mature individual per 150 km² (Tobias and Brightsmith, 2006). Applying this published population size to the EOO estimate of Tobias and Brightsmith (2006) of 460,000 km² produces a mean density of one mature individual per 184 km². These estimates are obviously too low given that multiple individuals have been reported at most sites (Tobias and Brightsmith, 2006). Even using the earlier global population estimate of 10,000 (Lambert et al., 1993), the mean density is one individual per 46 km². This, according to Tobias and Brightsmith (2006), is more realistic but also seems too low.

Population Trend

Habitat destruction and trapping have resulted in declining populations for some Amazonian psittacids (Karubian et al., 2005), but we cannot discount the possibility that the Blue-headed Macaw is increasing with the spread of degraded forests along rivers. Tobias and Brightsmith (2006; Fig. 3b; see Section 3.1.5.) have found no evidence from sightings data of a decline in range or numbers in the wild population, and long-term data reveal a recent increase at the clay lick near Tambopata Research Center, Peru.

BirdLife International (2007a) inferred a population decline for the Blue-headed Macaw because (1) sightings in Bolivia were reported to have dwindled, with "few reports in the north (mainly Pando), but none in the last 8-9 years, despite a number of studies in the area", and (2) the number of birds traded locally and internationally was apparently increasing. These factors were causally linked in the suggestion that the species is “declining owing to unsustainable exploitation for the cagebird trade” (BirdLife International, 2007a). The supplementary data provided by Tobias and Brightsmith (2006) shows that it has been encountered quite consistently in Bolivia after its discovery there in 1986, with records in 1989-1992 (2), 1997 (2), 2002, 2004, and 2005 (3). As for trapping pressure, it is possible that it is currently sustainable because the global population is fairly large, and much of the global range is remote and rarely visited by trappers (Tobias and Brightsmith, 2006). Thus, current trends remain highly uncertain, but for the purposes of assessing conservation status Tobias and Brightsmith (2006; see Section 3.2.2) tentatively assume a decline on the basis of an apparent increase in trade.

Conservation

Levels of Protection and Changes in Forest Cover

The Blue-headed Macaw occurs in at least 10 major protected areas in Brazil (Serra do Divisor National Park), Bolivia (Madidi National Park and Reserva Nacional Amazónica Manuripi-Heath), and Peru (Cordillera Azul National Park, Manu National Park, the Alto Purús Communal Reserve and National Park, Los Amigos Conservation Concession, Tambopata National Reserve and Bahuaja Sonene National Park) (Tobias and Brightsmith, 2006). These protected areas cover a combined area of 110,216.5 km², which constitutes 18.7% of the estimated global range size (Tobias and Brightsmith, 2006). This figure, though impressively high, is misleading because three national parks (Cordillera Azul, Manu and Madidi) contain a large area of unsuitable habitat (Tobias and Brightsmith, 2006).

In Peru and Bolivia, the most accessible Andean foothills are being rapidly degraded, but very large areas remain remote and untouched (Tobias and Brightsmith, 2006). In western

Amazonia the proportion of forest cover is still high (Nepstad, 1999), although extensive patches of forest have been cleared around some major towns, and large areas in all range states have experienced, or are slated for, selective logging; Tobias and Brightsmith (2006) have no evidence that this activity removes habitat for the Blue-headed Macaw.

Forest loss is likely to escalate in future as regional development intensifies (Tobias and Brightsmith, 2006). In Brazil, the states of Rondônia and Acre are suffering from massive conversion to agriculture and cattle ranching (Tobias and Brightsmith, 2006). This type of clear-felling has hardly affected the neighboring department of Pando, Bolivia, as can be seen by viewing recent aerial and satellite imagery (FlashEarth, 2006). Perhaps most alarmingly, a major new road project (the Transoceanica Highway) will connect the Brazilian State of Acre to the Peruvian coast, via Puerto Maldonado (Conover, 2003), bisecting the range of the Blue-headed Macaw. Given the impact of roads elsewhere in Amazonia (Nepstad et al., 2001), these projects are likely to cause an increase in habitat loss, human settlement, and associated exploitation.

Captive Breeding Programs

The avicultural community plans to “establish a breeding program for conservation purposes” (CITES, 2002). Tobias and Brightsmith (2006) suggest that no additional individuals be taken from the wild, but efforts should be made to bring together birds already in captivity in accredited institutions and breeding consortia. Towards this end, governments and international institutions should encourage collaboration and exchange of individuals among established programs (Tobias and Brightsmith, 2006).

Applying Red List Criteria

The Blue-headed Macaw is listed as Endangered under criterion C2a(i) of the IUCN Red List (BirdLife International, 2007a), and it is therefore “considered to be facing a very high risk of extinction in the wild” (IUCN, 2001). Conversely, Tobias and Brightsmith (2006) argue that it faces a very low risk of extinction, even in the long term. To qualify for the Endangered category under criterion C2a(i) a species has to have a declining global population of <2500 mature individuals, with “no subpopulation estimated to contain more than 250 mature individuals” (IUCN, 2001). BirdLife International (2007a) stated that the species lives in >1 subpopulation, the largest of which contains 50-249 birds.

The evidence for a decline is weak and largely inferred from trade reports according to Tobias and Brightsmith (2006; se Section 3.1.11 *Population Trend*). Tobias and Brightsmith (2006) also state that the population structure given by BirdLife International (2007a) is inaccurate. All Blue-headed Macaws probably belong to a single population given that lowland and foothill populations are apparently contiguous and western Amazonian forests are not yet fragmented into blocks (Tobias and Brightsmith, 2006). The mobility of macaws, and their ability to disperse over broad rivers and open areas, is illustrated by the high genetic similarity of Blue-and-yellow Macaws Ara ararauna collected over 2000 km apart in Amazonia (Caparroz, 2003). This implies that the Blue-headed Macaw does not meet subcriterion C2a(i) (Tobias and Brightsmith, 2006). Field data collected by Tobias and Brightsmith (2006) suggests that the estimated population size of <2500 mature individuals is unduly pessimistic. Although Tobias and Brightsmith (2006) can account for a minimum number of 545 individuals, a conservative extrapolation across the available habitat produces a higher population estimate (9200-46,000 mature individuals).

This exceeds the threshold for Endangered under criterion C (2500 mature individuals), but – applying the precautionary principle – it falls below the threshold for Vulnerable (10,000 mature individuals) (Tobias and Brightsmith, 2006). Tobias and Brightsmith (2006) therefore recommend that the species be reclassified as Vulnerable under criterion C2a(ii), on the grounds that the population may contain fewer than 10,000 mature individuals, “at least 95% of which occur in one subpopulation” (IUCN, 2001), and may be undergoing a continuing decline.

ESA vs. Red List

The ESA and Red List have many similarities and differences. Both are lists on which animals are put when there is a concern about their survival. They are both equally quantitative and have within them multiple classifications (i.e. “Least Concern” and “Near Threatened” for the Red List and “Threatened” and “Endangered” for the ESA). The criteria for the Red List are continuously being honed, but the assessment process continues to draw criticism.

Both take into account the type of decline, including declines in geographic range, number of populations, and overall abundance. The Red List, however, cannot have a global population of more than 2500 individuals, or a subpopulation estimated to contain more than 250 mature individuals on its endangered list.

Once a species is on the ESA, the Secretary of the Interior must develop a recovery plan that outlines the management actions needed for the conservation and survival of that species, whereas the Red List requires no such action to be taken. The Red List merely provides a baseline for prioritizing conservation actions.

It is difficult to assess a species that little is known about, regardless of which criteria are being used. It is for this reason that the case study on the Blue-headed Macaw may or may not be an accurate representation of that species. More is known about the California Condor and therefore a recovery plan was able to be created under the ESA and can be considered to this point to be tremendously successful. The Blue-headed Macaw is still a work in progress so to speak.

Little is known about the Blue-headed Macaw and its status on the Red List has been disputed. Until more is known about the species, it cannot be possible to know whether or not it meets the criteria for being endangered on the Red List. Hopefully the true status to the Blue-headed Macaw will be discovered, lest they do actually become extinct.

The ESA, to me, seems a more effective "protector" of endangered species. This is not simply because the California Condor is considered to be a huge success. I say this because once on the ESA, no matter what category, a recovery plan must be made unless such a plan will not promote conservation of the species. On the Red List, the most threatened species take top priority in conservation.

The ESA can have failed endeavors, I just feel as though it does more to conserve the species on its list. I believe that if the Red List were more than the priority-based list that it seems to be, that it would be on par with the ESA and seemingly as effective. Effectiveness as a whole, however, depends on the recovery plans. A good recovery plan can only be written if enough is known about the species it is being written for. It is for this very reason that we need to learn as much as possible about the species on these lists.

Works Cited

Alverson, W.S., Rodríguez, L.O., Moskovits, D.K., 2001. Perú: Biabo, Cordillera Azul. The Field Museum, Chicago, IL.

Ballou, J.D. 1983. Calculating inbreeding coefficient from pedigrees, p. 509-520. *In* C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas [$^{\text{EDS.}}$], Genetics and conservation: a reference for managing wild animal and plant populations. Benjamin/Cummings, Menlo Park, CA.

Ballou, J.D. and T.J. Foose. 1996. Demographic and genetic management of captive populations, p. 263-283. *In* D.G. Kleiman, M. Allen, K. Thompson, S. Lumpkin, and H. Harris [$^{\text{EDS.}}$], Wild mammals in captivity. University of Chicago Press, Chicago.

Ballou, J. and R.C. Lacy. 1995. Identifying genetically important individuals for management of genetic diversity in captive populations, p. 76-111. *In* J.D. Ballou, M. Gilpin, and T. Foose [$^{\text{EDS.}}$], Population management for survival and recovery. Columbia University Press, New York.

Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S.H., 2000. Bird Census Techniques, 2nd ed. Academic Press, London

BirdLife International, 2004. Threatened Birds of the World 2004, CD-ROM. BirdLife International, Cambridge, UK.

BirdLife International 2007a. Species factsheet: *Primolius couloni*. Downloaded from http://www.birdlife.org on 12/3/2007

Brightsmith, D., 2005. Parrot nesting in southeastern Peru: seasonal patterns and keystone trees. Wilson Bulletin 117, 296-305.

Broderick, A.C., Frauenstein, R., Glen, F., Hays, G.C., Jackson, A.L., Pelembe, T., Ruxton, G.D., Godley, B.J. 2006. Are green turtles globally endangered? Global Ecology and Biogeography 15, 21-26.

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

Butchart, S.H.M., Stattersfield, A.J., Bennun, L.A., Akcakaya, H.R., Baillie, J.E.M., Stuart, S.N., Hilton-Taylor, C., Mace, G.M., 2005. Using Red List indices to measure progress towards the 2010 target and beyond. Philosophical Transactions of the Royal Society, London B 1454, 255-268.

Butchart, S.H.M., Stattersfield, A.J., Bennun, L.A., Shutes, S.M., Akcakaya, H.R., Baillie, J.E.M., Stuart, S.N. Hilton-Taylor, C., Mace, G.M., 2004. Measuring global trends in the status of biodiversity: Red List Indices for birds. PLoS Biology 2, 2294-2304. doi:10.1371/jounal.pbio.002038

Caparroz, R., 2003. Filogeografia, estrutura e variabilidade genetic da Araracanindé (*Ara ararauna*, Psittaciformes: Aves) no Brasil baseadas na análise de DNA mitocondral e de DNA nuclear. PhD Thesis, University of São Paulo, Brazil.

CITES, 2002. Consideration of proposals for amendment of appendices I and II. Prop 12.18. http://www.cites.org/eng/cop/12/prop/E12-P18.pdf.

Collar, N.J., 1996. The reasons for Red Data Books. Oryx 30, 121-130

Collar, N.J., 1997. Family Psittacidae (Parrots). In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.), Handbook of the Birds of the World, Sandgrouse to Cuckoos, vol. 4 Lynx Edicions, Barcelona, pp. 280-477.

Conover, T., 2003. Peru's long haul: highway to riches or ruin. National Geographic (June), 80-111.

Dobson, A.P., J.P. Rodriguez, W.M. Roberts, and D.S. Wilcove. 1997. Geographic distribution of endangered species in the United States. Science 275:550-553.

Emslie, S.D. 1987. Age and diet of fossil California Condors in Grand Canyon, Arizona. Ccience 237:768-70. CrossRef, PubMed

ESRI, 2005. ArcGIS Version 9.1 for Windows. Environmental Systems Research Institute, Redlands, CA.

Evans, B.E.I., Ashley, J., Mardsen, S.J., 2005. Abundance, habitat use, and movements of blue-winged macaws (*Primolius maracana*) and other parrots in and around an Atlantic Forest reserve. Wilson Bulletin 117, 154-164

Falconer, D.S.. and T.F.C. Mackay. 1996. Introduction to quantitative genetics. 4th ed. Longman, Harlow, UK.

FlashEarth, 2006. Downloaded on 10 November 2006 from http://www.flashearth.com

Flather, C.H., L.A. Joyce, and C.A. Bloomgarden. 1994. Species endangerment patterns in the United States. General technical report RM-241. U.S. Forest Service, Fort Collins, Colorado.

Frankham, R., J.D. Ballou, and D. Briscoe. 2002. Introduction to conservation genetics. Cambridge University Press, Cambridge, UK.

Gerber, L.R., and L.T. Hatch. 2002. Are we recovering? An evaluation of recovery criteria under the U.S. Endangered Species Act. Ecological Applications 12:668-673

Greyer, C.J., O.A. Ryder, L.G. Chemnick, and E.A. Thompson. 1993. Analysis of relatedness in the California Condors from DNA fingerprints. Molecular Biology and Evolution 10:571-589. CSA

Gilardi, J., 2003. Letters to the Globally Threatened Bird Forums. BirdLife International, Cambridge, UK. Downloaded on April 20, 2005 from http://www.birdlife.org/action/science/species/global_species_programme/gtb_forums.html

Haig, S.M. and J.D. Ballou. 2002. Pedigree analyses in wild populations, p. 388-405. *In* S.R. Beissinger and D.R. McCullough [EDS.], Population viability analysis. University of Chicago Press, Chicago.

Harcourt, A.H., 2005. Problems of studying extinction risks. Science 310, 1276-1277.

IUCN, 2001. IUCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission. IUCN, Gland< Switzerland and Cambridge, UK. http://app.iucn.org/webfiles/doc/SSC/RedList/redlistcatsenglish.pdf

IUCN, 2006. 2006 IUCN Red List of Threatened Species. Downloaded from http://www.iucnredlist.org on 4 May 2006.

Juniper, T., Parr, M., 1998. A Guide to the Parrots of the World. Pica Press, Robertsbridge, UK.

Karubian, J., Fabara, J., Yunes, D., Jorgenson, J.P., Romo, D., Smith, T.B., 2005. Temporal and spatial patterns of macaw abundance in the Ecuadorian Amazon. Condor 107, 617-626.

Lacy, R.C. 1989. Analysis of founder representation in pedigrees: founder equivalents and founder genome equivalents. Zoo Biology 8:111-123. CrossRef, CSA

Lacy, R.C. 1995. Clarification of genetic terms and their use in the management of captive populations. Zoo Biology 14:565-578. CrossRef, CSA

Lambert, F.R., Wirth, R., Seal, U.S., Thomsen, J.B., Ellis-Joseph, S., 1993. Parrots: An Action Plan for their Conservation 1993-1998. BirdLife International, Cambridge, UK.

Leidner, Allison K., and Maile C. Neel. "Taxonomic and Geographic Patterns of Decline for Threatened and Endangered Species in the United States." *Conservation Biology* 25.4 (2010): 716-25. Print.

Mace, G.M., Lande, R., 1991. Assessing extinction threats – toward a re-evaluation of IUCN threatened species categories. Conservation Biology 5, 148-157.

Neel, M.C. 2008. Conservation planning and genetic diversity. Pages 283-298 in S.P. Carroll and C.W. Fox, editors. Conservation Biology: evolution in action. Oxford University Press, New York.

Nepstad, D., 1999. Large-scale impoverishment of Amazonian forests by logging and fire. Nature 398, 505-508.

Nepstad, D., Carvalho, G., Barros, A., Alencar, A., Capobianca, J., Bishop, J., Moutinho, P., Lefebvre, P., Lopes, S.U., Prins, E., 2001. Road paving, fire regime feedbacks, and the future of Amazon forests. Forest Ecology and Management 154, 395-407.

Parker, T.A., Remsen Jr., J.V., 1987. Fifty-two Amazonian bird species new to Bolivia. Bulletin of the British Ornithologists’ Club 107, 94-107.

Pollak, J.L., R.C. Lacy, and J.D. Ballou. 2002. PM2000: population management software. Cornell University, Ithaca, NY.

Possingham, H.P., Andelman, S.J., Burgman, M.A., Medellin, R.A., Master, L.L., Keith, D.A., 2002. Limits to the use of threatened species lists. Trends in Ecology and Evolution 17, 503-507.

Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. 1995. The future of Biodiversity. Science, 269, 347-350.

Ralls, Katherine, and Jonathan D. Ballou. "Genetic Status and Management of California Condors." *The Condor* 106.2 (2004): 215-28. Print.

Regan, T.J., Burgman, M.A., McCarthy, M.A., Master, L.L., Keith, D.A., Mace, G.M., Andelman, S.J., 2005. The consistency of extinction risk classification protocols. Conservation Biology 19, 1969-1977.

Relva, M.A., Nunez, M.A. & Simberloff, D. 2010. Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown. Biological Invasions, 12, 303-311.

Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M., Brooks, T.M., 2006. The value of the IUCN Red List for conservation. Trends in Ecology and Evolution 21, 72-76.

Ruledge, D.T., C.A. Lepczyk, J.L. Xie, and J.G. Liu. 2001. Spatiotemporal dynamics of endangered species hotspots in the United States. Conservation Biology 15:475-487.

Snyder, N.F.R., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, S.B., Toone, W.D. & Miller B. 1996, Limitations of captive breeding in endangered species recovery. Conservation Biology, 10:338-348.

Snyder, N. and H. Snyder. 2000. The California Condor: a saga of natural history and conservation. Academic Press, San Diego, CA.

Tear, T.H., J.M. Scott, P.H. Hayward, and B. Griffith. 1995. Recovery plans and the Endangered Species Act – are criticisms supported by data. Conservation Biology 9:182-195.

Thompson, E.A. 1986. Ancestry of alleles and extinction of genes in populations with defined pedigrees. Zoo Biology 5:161-170. CrossRef

Tobias, Joseph A., and Donald J. Brightsmith. "Distribution, Ecology and Conservation Status of the Blue-headed Macaw Primolius Couloni." *ScienceDirect* 139 (2007): 126-38. Print.

Vit, R., 1997. Der Blaukopf-oder Gebirgsara. Gefiederte Welt 11, 375-376.

Vriesendorp, C., Chávez, L.R. Moskovits, D.K., Shopland, J.M., 2004. Perú: Megantoni. The Field Museum, Chicago, IL.

Wallace, M. and W. Toone. 1992. Captive management for the long-term survival of the California Condor, p. 744-766. *In* D.R. McCullough and R.H. Barrett [EDS.], Wildlife 2001: populations. Elsevier Applied Science, London.

Wilcove, D.S., M. McMillan, and K.C. Winston. 1993. What exactly is an endangered species? An analysis of the U.S. Endangered Species list: 1985-1991. Conservation Biology 7:87-93.

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607-615.

Wilson, Conor D., and Dai Roberts. "Modelling Distributional Trends to Inform Conservation Strategies for an Endangered Species." *Diversity and Distributions* 17 (2011): 182-89. Print.