

Orangutan population biology, life history, and conservation

Perspectives from population viability analysis models

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22.1 Introduction

Populations of many of Southeast Asia's rainforest vertebrates are in decline due to hunting, habitat loss, and forest degradation and fragmentation. These threats are deterministic processes as they directly increase mortality or decrease fecundity, thereby lowering population growth rates. As remaining forest patches shrink and become increasingly fragmented, animal populations become smaller and more isolated. These small populations are subject to the additional threats of stochastic processes (random genetic, demographic, or environmental fluctuations that decrease rates of survivorship or reproduction) and become vulnerable to local extinction (Soulé 1980; Soulé and Wilcox 1980; Caughley 1994). Population Viability Analysis (hereafter PVA) uses mathematical simulations to estimate extinction probabilities of animal populations subject to various deterministic forces and stochastic events (e.g., Soulé 1987; Boyce 1992; Nilsson 2004). It provides a tool for identifying populations at risk of extinction, assessing the effects of different types of threats, and evaluating the potential efficacy of conservation interventions (Lacy 1993). While not without its share of controversy (e.g., Boyce 1992; Mann and Plummer 1999; Shaffer *et al.* 2002), PVA has become a cornerstone of modern conservation science and wildlife management (Brook *et al.* 2000; Sjögren-Gulve and Ebenhard 2000; Beissinger 2002).

PVA models, coupled with empirical data, have identified several attributes that make species particularly susceptible to extinction. Population size is the strongest risk factor: species living in small populations are more vulnerable to extinction than are species living in large ones—a statement that has become axiomatic in conservation biology (Soulé and Wilcox 1980; Diamond 1984; Soulé 1987). Large-bodied species are particularly vulnerable because both intrinsic and environmental extinction risks have independent effects that rise sharply in species of >3 kg body mass (Cardillo *et al.* 2005). Species with slow reproductive rates are also unusually susceptible to local extinction because their populations are slow to recover from reductions in size (Terborgh 1974; Cox 1997). In addition, species with limited geographic ranges

are more extinction-prone because they tend to be more specialized, less adaptable, and less able to survive reductions in habitat area (Brown 1995; Johnson 1998; Harcourt and Schwartz 2001). Finally, frugivores may be vulnerable because they must move between habitat patches during periods of resource scarcity (Terborgh and Winter 1980). Each of these factors suggests that orangutan populations might be expected to be especially prone to extinction. They live in highly fragmented landscapes (Rijksen and Meijaard 1999; Fuller *et al.* 2004; Goossens *et al.* 2005a) and most of their populations are small, with no populations exceeding 6500 animals (Rijksen and Meijaard 1999; van Schaik *et al.* 2001; Singleton *et al.* 2004). Orangutans are among the heaviest extant arboreal primates (Wheatley 1987) and have one of the slowest life histories of any mammal (Galdikas and Wood 1990; Knott 2001; Wich *et al.* 2004b, see Chapter 5). Their historic range extended to southern China and included most of the South East Asian mainland less than 20,000 years ago. However, presently, the geographic range of both Bornean (*Pongo pygmaeus*) and Sumatran (*P. abelii*) orangutans is each limited to a single island. Finally, orangutans are frugivorous and are known to move widely across the landscape in response to food scarcity (MacKinnon 1974; Singleton and van Schaik 2001; Buij *et al.* 2002). In sum, orangutans have a constellation of demographic, physiological, behavioral, and ecological attributes that render them highly vulnerable to extinction.

In this chapter we use PVA to consider the conservation implications of orangutan ecology, life history and population biology (see Box 22.1 for details and procedure). We present baseline models that incorporate the best available field data and that seem to accurately describe the dynamics of typical populations of Bornean and Sumatran orangutans in the absence of human-induced threats. We then use these model to examine how plausible variation in model parameters, changes in the intensity of human-induced threats (e.g., reduced habitat area or quality, greater frequency of disease, poaching), and different conservation and management interventions would affect the probability of population persistence. We briefly discuss models examining the effects of existing

threats on the extinction risk of specific orangutan populations on Borneo and Sumatra. Finally, we consider the conservation and management implications of this modeling exercise.

This chapter is largely based on information contained in the reports on a preliminary PVA data assessment and analysis session held in Singapore between 9–11 August 2003 (Ancrenaz *et al.* 2003) and a full Population and Habitat Viability Assessment (PHVA) workshop held in Jakarta between 15–18 January 2004 (Singleton *et al.* 2004). (In September 2005 a follow-up workshop for Sumatran orangutans was convened by Conservation International in Berastagi, North Sumatra. Participants expanded the modeling and conservation planning efforts of the 2004 PHVA workshop to develop a Sumatran Orangutan Conservation Action Plan.) The PHVA workshop is a process that brings together a broad range of stakeholders—including field biologists, land and wildlife managers, and also often local people or other resource users who would be impacted by conservation actions—to assess status, threats, and conservation options in order to develop a conservation plan that can be implemented and will be successful. The PHVA workshop uses PVA models as a core for compiling data, analysing trends, and assessing options, but the PHVA also includes considerations that go beyond the quantitative modeling of the PVA (Lacy 1993/4).

Both meetings drew on results and analyses presented at the first orangutan PHVA meeting held in January 1993 in Medan (Leighton *et al.* 1995). Full descriptions of the analyses and data sets described here can be found in the reports describing these meetings.

22.2 Results

22.2.1 The baseline models

The baseline models impose K through density dependent reproduction. At low to moderate population densities, the models produce low positive population growth ($r_{\text{SUMATRA}} = 0.015$; $r_{\text{BORNEO}} = 0.025$, 0.020, 0.015 in cases of best, medium, and worst natural mortality, respectively). These rates span what would be plausible rates of population growth for

large, long-lived, slow-breeding apes. Population growth rates were reduced under crowded conditions ($N = K$): $r_{\text{SUMATRA}} = -0.002$; $r_{\text{BORNEO}} = 0.001$, -0.004 , -0.009 in cases of best, medium, and worst natural mortality, respectively. Thus, the density-dependent curves we used led to essentially stable populations in the best quality habitat, while the populations would be projected to decline to a lower equilibrium size in poorer quality habitats. Although the two groups modeled mortality rather differently, both results were biologically reasonable. Moreover, when we removed all constraints on K from our models, they still stabilized at the desired population size, implying that population regulation in our model resulted from density dependence (as desired), not the upper limit K imposed on the model. When we started the population with N below 1000, the population increased to about 1000 and then stabilized (with the expected random annual fluctuations). These tests gave us confidence that we had constructed a solid baseline model that provided a reasonable representation of the dynamics of ‘typical’ orangutan populations and was an improvement on previous models (e.g., Leighton *et al.* 1995).

22.2.2 Model exploration

N and K. Figure 22.2 shows the projections for 10 simulated Bornean populations with $N = 50$, 250, and 1000 individuals, using mortality schedules for medium quality habitats. Population size showed the predicted strong effect on extinction probability. The smallest populations were highly unstable, going extinct following catastrophe-induced declines rather than recovering. Populations in habitats suitable for 100 orangutans sometimes persisted through the simulations, but showed high fluctuations in size (not shown). Populations in habitats with K of 250 or larger always persisted (at least in these small samples of simulations) and showed reduced fluctuations as the population sizes were increased. Plots for Bornean populations in high- and low-quality habitats and for Sumatran populations showed similar patterns.

We also examined the effects of N on probabilities of population persistence (i.e., the proportion of 500 simulated populations that survived), the

Box 22.1 Methodological considerations

Over 80 conservation biologists, orangutan experts, governmental and non-governmental conservation professionals, and other stakeholders participated in the PHVA workshop in Jakarta. The Conservation Breeding Specialist Group of the Species Survival Commission of the IUCN (World Conservation Union) facilitated the workshop, where we integrated orangutan population data with estimates of human-based threats. Within separate working groups for the two orangutan species we utilized computer models to evaluate current and future risk of population decline or extinction under alternative management scenarios.

VORTEX and PVA modeling

We used the program VORTEX 9.42 for all analyses (Lacy 1993; Lacy 2000; Miller and Lacy 2003). VORTEX is one of several widely available computer packages that can be used to conduct PVA. Although these programs use different algorithms to calculate extinction probabilities, their results have been shown to be highly concordant (Brook *et al.* 2000). VORTEX is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild populations. VORTEX models population dynamics as a set of discrete sequential events that occur according to defined probabilities. The program begins by creating individuals to form the starting population that then steps through life cycle events (e.g., births, deaths, dispersal, catastrophic events), typically on an annual basis. Parameters such as breeding success, litter size, sex at birth, and survival are determined based upon designated probability distributions. Consequently, each iteration of the model gives a different result. By running the model hundreds of times, it is possible to examine the range of probable outcomes. Details on VORTEX's algorithms, structure, and assumptions can be found in Lacy (1993, 2000) and Miller and Lacy (2003).

Parameter selection and model details

The validity of our results and the plausibility of our investigations of potential threats and management interventions depended on the accuracy of our baseline model. We therefore spent considerable time compiling the best available field data, assessing its quality, and determining whether it had been appropriately analyzed. Each working group at the PHVA workshop discussed the

input parameters extensively. Below we present the input values and ranges used to model baseline populations of Bornean and Sumatran orangutans. Unless noted, values used for the two *Pongo* species were identical. General justifications and comments can be found in Leighton *et al.* (1995) and Singleton *et al.* (2004).

Number of iterations for each set of parameters tested: 500. This resulted in standard errors for probabilities of extinction and most other output values of between 1–2% of the means.

Number of years: 1000. As orangutans have long lifespans and reproduce slowly, we decided to model populations for 1000 years so that long-term population trends could be observed. It is unlikely that conditions are adequately understood or will remain constant to allow us to accurately predict population status so far into the future. Thus, both short-term and long-term results are presented.

Extinction definition: only one sex remains.

Number of populations: 1. We modeled a single isolated population in our baseline model.

Inbreeding depression: Yes. In spite of our uncertainty about the frequency of inbreeding and its likely effects, its omission could have provided overly optimistic results. Our analyses of maximum population growth rates (r_{max} below) did not incorporate any inbreeding effects, but we did include inbreeding in all models of long-term trends and extinction times. Unless directed otherwise, VORTEX assumes that matings are randomly distributed throughout the population of breeding adults. This may provide overly optimistic estimates of genetic mixing (and lack of inbreeding), but we lack sufficiently detailed knowledge of dispersal and breeding systems necessary to provide an alternative (although evidence suggests that female orangutans do not mate randomly: van Hooff [1995]; Utami *et al.* [2002]). We used an estimate of 4.06 'lethal equivalents' (a measure of the average increase in neonatal mortality for each increment in inbreeding) that was estimated by Jonathan Ballou of the US National Zoo from pedigrees of orangutans in zoos. In simulations of populations with 1000 or fewer animals, 50% of the effect of inbreeding was modeled as being due to recessive lethal alleles (which can be removed by natural selection if inbreeding occurs periodically). In populations with more than 1000 animals, the inbreeding effect was specified to be due entirely to recessive lethal alleles. We made this optimistic assumption to allow the VORTEX simulations to run more quickly. However,

continues

Box 22.1 continued

inbreeding is so rare in large populations (in the wild and in the simulation) that the results would not be noticeably affected by the value given for the proportion of inbreeding depression due to lethal alleles.

Concordance between environmental variation in reproduction and survival: Sumatra: No; Borneo: Yes. Both groups lacked sufficient data to address this parameter empirically. The Sumatran working group based their decision on the observation that large-bodied, long-lived species show little correlation between breeding and survival. The Borneo group felt that environmental factors such as food shortage could impact both survival and reproduction (although perhaps with a time lag). This difference in opinion may reflect real differences in ecology: periods of fruit scarcity appear both more frequent and more severe at Bornean research sites (see Chapter 7). However, the model outcomes for both islands were affected very little by this decision.

Mating system: Short term polygyny (animals can select new mates every year). Orangutans have a promiscuous breeding system. Both males and females may have multiple mates, although animals may breed with the same mate(s) for several years.

Age of first reproduction: Sumatra: 15 years (females), 25 years (males), data from Ketambe; *Borneo:* 15 years (females), 18 years (males), data from Tanjung Puting. The difference in male breeding age between the populations has little impact on demographic projections. In VORTEX, this parameter represents the average age of first reproduction, not the earliest age of reproduction or the onset of sexual maturity.

Maximum female age at reproduction: Sumatra: 50 years, data from Ketambe; Borneo: 45 years.

Litter size: 1. In rare cases twins are born, but at least one almost always dies.

Sex ratio at birth: 55% male. Slightly male-biased sex ratios are typically seen in polygynous mammals. In 1993 the PHVA used data from Tanjung Puting (50–55% individuals were males, out of $N = 30$). We now also have data from Suaq Belimbing (14/25 = 56% males), Ketambe (16 out of 28 were male = 57%), and infants born to rehabilitant females (10/16 = 63% males). In zoos 51.2% of 755 births were males.

Density-dependent effects on reproduction: We modeled density dependence (i.e., relationship between population density and breeding success) as a curve described by the following equation: % breeding = $[P_0 - (P_0 - P_k) * (N/K)B] * (N/(N+A))$. The variables and values

were assigned as follows: $P_0 = 18.2$ P_0 specifies the % of adult females breeding in an average year when population density is very low relative to carrying capacity (K , the size of population that can be sustained without causing long-term degradation of the habitat). To estimate this parameter, we considered the shortest weaning period observed. Data from Ketambe suggest an interbirth interval as short as 6 years; this was adjusted to 5.5 years (18.2% of females breeding annually) after correcting for females that re-breed earlier after loss of their infants.

$P_k = 11.1$. P_k specifies the % of adult females breeding in an average year when population density is at K . The maximum interbirth interval was estimated at 10 years based on Ketambe data. After correcting for females that lose their infants, 9 years was used as the estimated interbirth interval for populations at high density, or 11.1% of females breeding each year.

$A = 1$ The Allee parameter, A , specifies the number of females in which breeding has dropped to half the normal rate because of difficulty in finding mates. Orangutans are probably able to find mates even when at low densities, so we set $A = 1$ to minimize the Allee effect in the model.

$B = 2$ This parameter defines the steepness with which breeding decreases as the population approaches K . $B = 2$ results in a relatively steady decline in breeding.

N = initial population size. We used a range of numbers, see below.

Compared to many vertebrates, the density dependence curve described by these values is relatively flat around K (Fig. 22.1).

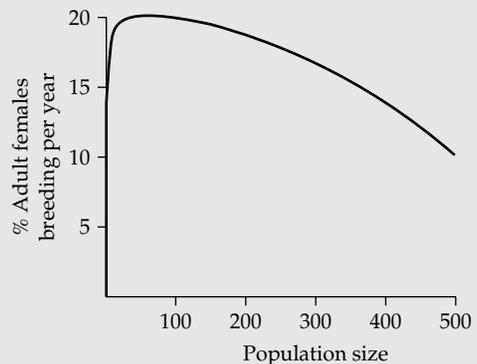


Figure 22.1 Model of density-dependent breeding in orangutans. The curve plots the relationship between population density and breeding success.

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Box 22.1 continued

This is reasonable because at high densities orangutans don't destroy the productivity of their resource base (cf. herbivores).

Environmental variation in breeding rate (percentage of females breeding per year): Sumatra: 5.5; Borneo: 10. Given the long lifespan of this species, year-to-year fluctuations in demographic rates tend to average out; therefore this value probably has little effect on population projections. However, the different values used by the two groups again reflect the observation that Bornean forests tend to be more variable in their phenology than Sumatran forests.

Monopolization of breeding (percentage of males available to breed per year): 50%. This parameter primarily affects genetics rather than demography. Sensitivity testing using higher values (75% and 100%) in small populations ($N = 50$) showed no effect on population status, so the plausible value of 50% was retained in the model.

Mortality: In general, orangutans' long lifespans and slow reproductive rates suggest low general rates of intrinsic mortality. The Sumatra and Borneo groups modeled mortality differently. The Sumatran group based mortality estimates on 30 years of long-term data from Ketambe (Table 22.1) and set environmental variation around mortality rates at 50% of the mean age-specific mortality rates. The Borneo group did not have the benefit of a long-term data set, and there was considerable disagreement over what were appropriate estimates of age-specific mortality. In addition, the group recognized that mortality rates probably vary among populations, based on habitat quality. Therefore we used three mortality schedules that represented plausible

mortality rates in undisturbed high-quality habitats, disturbed or medium-quality habitats, and very disturbed or low-quality habitats (Table 22.2).

Environmental variation around mortality was specified to the same magnitude (as a standard deviation) as the mean mortality rates, again reflecting the perception of higher variability in Bornean forests when compared with Sumatran forests.

Catastrophes: Sumatra: three types, Borneo: two types. On Sumatra the risk of a disease epidemic was modeled as a 2% probability of occurrence each year (i.e., occurring on average once every 50 years), killing 20% of the local population but having no effect on reproduction of surviving individuals. The effects of fire and landslides were modeled on Sumatra as temporary reductions in K (and therefore population size): fire events had a 0.2% annual probability of occurrence and reduced the carrying capacity by 10%, and landslides had a 2.5% annual probability of occurrence and reduced carrying capacity by 0.75%. Food shortage and effects of El Niño-related events were not modeled as catastrophic events for Sumatran orangutans. In contrast, the Borneo group recognized that many catastrophes are related to El Niño weather events and decided to collapse catastrophes into those impacts that occur with typical El Niño events, and those that occur in the more severe El Niño events. Based on observations over the last few decades, the Borneo group's model specified that moderate El Niño-related catastrophes had an annual probability of 17%, and more severe catastrophes had an annual probability of 8%. In discussing the likely severities of catastrophes, the Borneo group noted that all orangutans apparently died in some areas that were extensively burned in 1983 (e.g., parts of

Table 22.1 Estimated age-specific mortality rates for Sumatran orangutans.

Environmental variation in mortality rates (expressed as a standard deviation) were equal to one half of the estimates of age-specific mortality rates (e.g., the standard deviation of mortality rates for females between 8–11 years old in low quality habitats was set at 3)

| Age class | Mean annual mortality (%) | |
|-----------|---------------------------|-------|
| | Females | Males |
| 0–1 | 5.0 | 5.0 |
| 1–2 | 6.0 | 5.0 |
| 2–8 | 0.5 | 3.0 |
| 8–11 | 6.0 | 6.0 |
| 11–15 | 0.5 | 0.5 |
| 15+ | 1.75 | 1.25 |

continues

Box 22.1 continued

Kutai National Park), and that three orangutans died of disease thought to be related to food stress after a 1972 fire. An estimated 1000 out of 40,000 orangutans (2.5%) died from the severe fires in 1997, but this may well have been an underestimate. For the modeling, we assumed that catastrophes caused by severe El Niño events would kill an average of 3.5% of orangutans, while less severe catastrophes would kill about 1%, with no effect on reproduction.

Carrying capacity (K): Initially set at a population size of 1000, but values between 50 and 2500 were explored. We imposed a carrying capacity using the parameter *K* in the density dependent breeding function (see above). Vortex normally imposes *K* by truncating the population (i.e., killing animals) if the population size exceeds *K*. To avoid such a mortality-imposed carrying capacity, the level at which this truncation would occur was set arbitrarily high (at 2× the desired *K*) in the VORTEX simulations. For our baseline scenario, we assumed that habitat would not be lost or gained. Later, we examined the impacts of expected rates of habitat loss or gain for some specific populations. The parameter for specifying environmental variation in *K* was set to 0, because variation in habitat quality was already accounted for in the variation in annual mortality and reproduction.

Harvest: None. We assumed no planned harvests for management purposes. Losses due to poaching were modeled later with scenarios in which we examined impacts of hunting.

Supplementation: None. Although supplementation may be considered in the future to increase gene flow

or rescue declining populations, we did not model any animals being added to the populations from captive or other sources.

Analyses and model exploration

We used the above parameters in VORTEX to determine the potential for population persistence under baseline conditions. We also explored the effects of variation in several key parameters on the stability of populations of various sizes. Because the Sumatran and Bornean working groups were separate and independent, the range of parameters tested and the scenarios examined differed between the two groups. We examined variation in the following parameters:

N and K. We examined scenarios with *N* and *K* set at 50, 100, 250, 500, and 1000 (also 1500 and 2500 for Sumatran orangutans). These scenarios model the effects of a reduction in habitat availability (without compression effects). We examined the effects of *N* and *K* on the probability of population persistence, mean population size, and genetic diversity.

Hunting. Orangutans are a long-lived, slowly reproducing species, so even very low rates of hunting (or other sources of extrinsic mortality) might strongly threaten population growth, stability, and persistence. We modeled the effects of hunting at different intensities using elevated mortality values. We modeled hunting on Bornean populations by adding 1%, 2%, or 3% to the mortality of each age class, such that fewer total animals are removed as population size declines. Hunting was not modeled for Sumatra populations.

Table 22.2 Estimated age-specific mortality rates for Bornean orangutans. Estimates of mortality schedules were made for high-quality, medium-quality, and low-quality habitats. Environmental variation in mortality rates (expressed as a standard deviation) were equal to estimates of age-specific mortality rates (e.g., the standard deviation of mortality rates for females greater than 5 years old was set at 1.5)

| Habitat quality | High (%) | Medium (%) | Low (%) |
|-------------------|----------|------------|---------|
| Female age | | | |
| 0–5 | 1.0 | 1.5 | 2.0 |
| 5+ | 0.5 | 1.0 | 1.5 |
| Male age | | | |
| 0–5 | 1.0 | 1.5 | 2.0 |
| 5–12 | 0.5 | 1.0 | 1.5 |
| 12+ | 1.0 | 1.5 | 2.0 |

continues

Box 22.1 continued

Logging. We modeled logging of Sumatran orangutan habitat as a permanent annual percentage reduction in K , assuming that logged areas cannot support orangutans. Current annual logging rates are estimated to be 2–20%, so sensitivity testing explored annual reductions in K of 0, 1, 2, 3, 5, 10, 15 and 20%. Unabated logging, regardless of the intensity, will eventually drive any orangutan population to extinction; but the trajectory of the decline will vary due to population size and logging rate. We modeled Sumatran orangutan populations from 50 to 1000 individuals to investigate this relationship. As this scenario is a generic model of habitat loss, reduction in habitat caused by other factors (e.g., conversion to oil palm) would provide identical results. The Bornean group did not specifically model the effects of logging.

Inbreeding. Because the impact of future inbreeding on survival (and other aspects of fitness) is uncertain, we examined values for the number of lethal equivalents of 0 (no effect of inbreeding), 2, and 6. These values for lethal equivalents cover the range often measured in mammalian populations, although some species have been observed to be more severely affected (Lacy 1997; Ralls *et al.* 1998). These varying impacts of inbreeding depression were tested for Bornean orangutan populations with $N = K = 100$. While the Sumatran group included inbreeding in its model, it did not specifically examine the effects

of variation in the value used for the number of lethal equivalents.

Modeling of specific populations

After creating baseline models for both *P. abelii* and *P. pygmaeus* and examining the effects of alteration in various parameters in these models, we modeled specific orangutan populations. Sumatran orangutan populations are well documented and few in number, so the Sumatra group conducted detailed explorations of models for each of the 13 remaining orangutan populations on Sumatra. The Borneo group split into 4 subgroups that modeled the larger populations in East Kalimantan ($n = 6$ populations, each with $n \geq 400$ individuals), Central Kalimantan ($n = 5$ populations, each with $n \geq 1000$ individuals), West Kalimantan and Sarawak ($n = 6$ populations, each with $n \geq 350$ individuals), and Sabah ($n = 6$ populations, each with $n \geq 250$ individuals). For each population, we then specified N , K , habitat quality (and therefore the natural mortality schedule expected to be most applicable to the population) for Bornean populations, ongoing or foreseen trends in habitat availability or quality, threats, and potential management interventions. While presentation of the details of each analysis is beyond the scope of this chapter, we summarize the major results of these models.

mean population sizes (i.e., the means of the 500 projections), and the mean genetic diversity (as a proportion of the starting gene diversity). We calculated values for each of these indices after 50 years, 100 years, and 1000 years (Table 22.3).

Patterns were similar between Borneo and Sumatra. Not surprisingly, given orangutans' long lifespans, even small populations were relatively stable over the first half century. After 1000 years small populations lost a substantial amount of genetic diversity and were subject to high extinction probabilities. Although it is not known how much genetic variation orangutan populations will need to maintain high individual fitness (i.e., lack of inbreeding depression) and population adaptability to environmental change, a commonly used goal for endangered species management is to strive to maintain gene diversity of at least 90% of

the initial level (Soulé *et al.* 1986). By this criterion, the populations with $N \geq 500$ remained genetically healthy.

Hunting. We examined models with 1%, 2%, and 3% additional mortality in all age classes, running 500 iterations with populations of 250 individuals of Bornean orangutans (Fig. 22.3). In the best quality habitats, annual hunting rates of 1% did not cause population extinction (but did decrease population size), while even this low level of hunting caused declines to extinction if natural mortality is at the levels estimated for less than optimal habitat. Higher rates of hunting are unsustainable even in the highest quality habitats. Although the Sumatran group did not explicitly model its effects, hunting does occur on Sumatra and its effects are expected to be similar to the effects of hunting on Bornean populations.

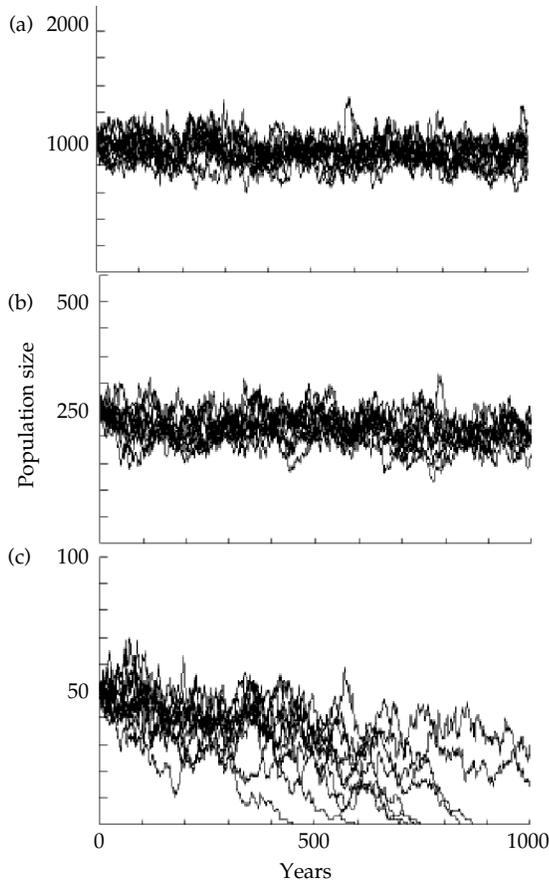


Figure 22.2 Plots of 10 VORTEX simulations for Bornean populations in medium-quality habitats with starting population sizes (N) of 1000 (a), 250 (b) and 50 (c) individuals. All y-axes show population size, but scales differ. Plots for Sumatra and in habitats of different quality in Borneo show similar patterns.

Logging. High annual rates of habitat loss (15% and higher) result in certain extinction in all Sumatran orangutan populations within 50 years. At this rate only about 1–4% of orangutan habitat on Sumatra remains after 20 years. Moderate rates of logging (5–10% annually) drive most populations to extinction with 100 years; although initially large populations ($n = 1000$) persist, they consist of very few individuals at 100 years and are not viable. Low rates of logging can be sustained for 100 years, although all populations eventually go extinct within several hundred years. An annual loss of 1% results in a 63% reduction in K

over 100 years, while a 3% loss removes over 95% of the habitat in 100 years.

Inbreeding. Our model explored the effects of variation in the number of lethal equivalents in small populations ($n = 100$) of Bornean orangutans. In the best quality habitats, inbreeding had relatively small effects (e.g., 6.0 lethal equivalents reduced population size by 28%, Table 22.4).

In medium- or poor-quality habitat, inbreeding depression caused extinctions if lethal equivalents were ≥ 4.06 , the value that has been estimated from zoo records. The impact of inbreeding depression is greatest in those scenarios with higher natural mortality, because the populations are less able to withstand moderate reductions in infant survival.

22.2.3 Modeling of specific populations

22.2.3.1 Sumatra: initial analyses

Of the 13 remaining orangutan populations on Sumatra, only seven are estimated to have 250 or more individuals. Of these seven relatively large populations, six are believed to be subject to 10–15% annual habitat loss due to logging. All six populations disappeared within 50 to 100 years in our simulations. Only the West Batang Toru population was sufficiently large (about 400 individuals) and had a sufficiently low estimated rate of habitat loss (2% annually) to persist for more than 150 years. However, even this population was pushed to extinction within 275 years. Assuming the life history parameters and estimated continued logging rates and impacts used in this model are realistic, simulation results suggest that the Sumatran orangutan population may decline by about 97% in the next 50 years (mean projected population size of 234 individuals) and that Sumatran orangutans may be extinct within 300 years (Fig. 22.4). In contrast, if logging and hunting of orangutans could be halted today, the number of Sumatran orangutans expected to remain in 50 years would be about 6570. It is unlikely that logging could be eliminated immediately in Sumatra. A more realistic timeline might be to end all logging within 5 years. Projections under this management scenario suggest that about 2758 orangutans would still remain after 1000 years, probably in 5–9 different populations. Although a delay of 5 years in ending

Table 22.3 The effects of population size on population viability after 50, 100, and 1000 years. Results are mean values obtained from 500 iterations. For Sumatran orangutan populations only one mortality schedule was used; for Bornean orangutans values are computed for populations experiencing mortality rates in high-, medium-, and low-quality habitats

| Input parameters | Starting N | 50 years | | | 100 years | | | 1000 years | | |
|------------------------|------------|----------|------|-----|-----------|------|-----|------------|------|----|
| | | PE | N | GD | PE | N | GD | PE | N | GD |
| Sumatra | 50 | 0 | 41 | 96 | 1 | 36 | 92 | 99 | 7 | 40 |
| | 100 | 0 | 83 | 98 | 0 | 78 | 96 | 64 | 28 | 59 |
| | 250 | 0 | 210 | 99 | 0 | 203 | 99 | 2 | 142 | 85 |
| | 500 | 0 | 417 | 100 | 0 | 404 | 99 | 0 | 342 | 93 |
| | 1000 | 0 | 839 | 100 | 0 | 808 | 100 | 0 | 732 | 97 |
| | 1500 | 0 | 1269 | 100 | 0 | 1206 | 100 | 0 | 1149 | 98 |
| | 2500 | 0 | 2085 | 100 | 0 | 2020 | 100 | 0 | 1947 | 99 |
| Borneo | | | | | | | | | | |
| High-quality habitat | 50 | 0 | 48 | 97 | 0 | 46 | 94 | 27 | 18 | 48 |
| | 100 | 0 | 98 | 98 | 0 | 96 | 97 | 0 | 81 | 74 |
| | 250 | 0 | 249 | 99 | 0 | 246 | 99 | 0 | 235 | 89 |
| | 500 | 0 | 501 | 100 | 0 | 494 | 99 | 0 | 482 | 95 |
| | 1000 | 0 | 1000 | 100 | 0 | 1006 | 100 | 0 | 974 | 97 |
| Medium-quality habitat | 50 | 0 | 44 | 96 | 0 | 41 | 93 | 87 | 2 | 33 |
| | 100 | 0 | 91 | 98 | 0 | 87 | 97 | 1 | 60 | 67 |
| | 250 | 0 | 229 | 99 | 0 | 226 | 99 | 0 | 209 | 88 |
| | 500 | 0 | 460 | 100 | 0 | 452 | 99 | 0 | 433 | 94 |
| Low-quality habitat | 1000 | 0 | 924 | 100 | 0 | 916 | 100 | 0 | 896 | 97 |
| | 50 | 0 | 40 | 96 | 0 | 36 | 92 | 99 | 0 | 25 |
| | 100 | 0 | 82 | 98 | 0 | 77 | 96 | 44 | 17 | 56 |
| | 250 | 0 | 207 | 99 | 0 | 202 | 98 | 0 | 167 | 85 |
| | 500 | 0 | 421 | 100 | 0 | 416 | 99 | 0 | 377 | 93 |
| | 1000 | 0 | 838 | 100 | 0 | 832 | 100 | 0 | 787 | 96 |

PE, % probability of extinction; N, mean population size; GD, genetic diversity of initial gene diversity.

logging might not result in species extinction, it could lead to over a 50% reduction in the number of orangutans that can be maintained in Sumatra under the conditions modeled. Therefore, quick action to reduce and stop logging can have long-term implications for orangutan populations.

22.2.3.2 Sumatra: subsequent analyses

In the September 2005 follow-up workshop for Sumatran orangutans, more refined estimates were made for the type (illegal logging, legal logging, encroachment), rate, and duration of habitat alteration and their estimated impacts on carrying capacity for orangutans. These resulted in an estimated loss of 40% of total carrying capacity for Sumatran orangutans over the next 20 years. These revised model results indicate that habitat loss and other factors will cause Sumatran orangutan

populations to decline about 18–25% in the next 10 years (depending upon conditions) and about 50% over the next 50 years. Of the 7 habitat units that were then estimated to contain 250 or more individuals, 5 are projected to retain suitable habitat to sustain at least 250 orangutans in the future and were associated with long-term viability in VORTEX model projections. The remaining eight populations are subject to population decline and risk of extinction, depending upon the degree of threats to each population. Opening of additional logging concessions, population fragmentation, and hunting would lead to additional population decline and risk of extinction.

22.2.3.3 East Kalimantan

Orangutans persisted in each of the six major habitat units through 1000 years in the simulation,

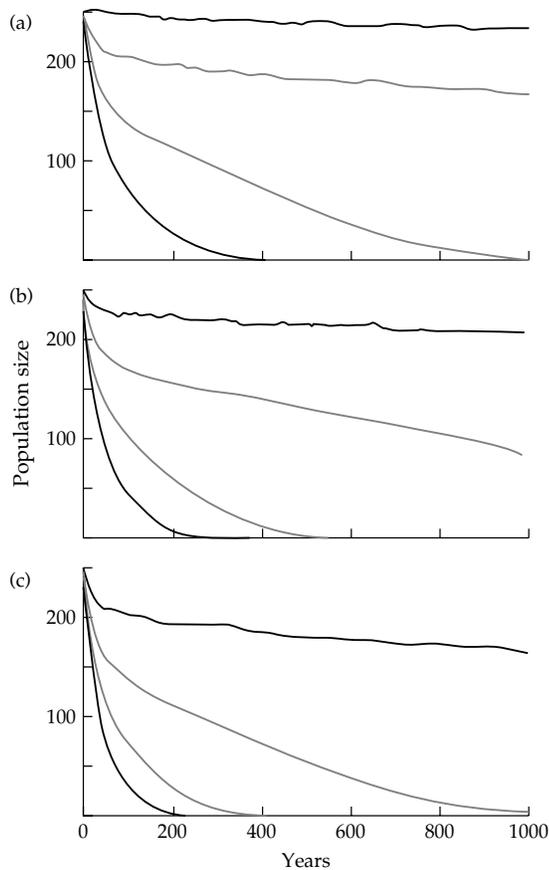


Figure 22.3 Impacts of hunting on population size. Traces show the effects of different hunting rates on VORTEX models of Bornean orangutan populations in high-quality (a), medium-quality (b), and low-quality habitats (c). In each plot lines show, from top to bottom, the effects of hunting that removes 0%, 1%, 2%, and 3% of the population annually. Lines plot mean population size of 500 iterations. Each population started with 250 individuals.

assuming no habitat loss from logging. However, populations of fewer than 300 individuals lost more than 10% of their genetic diversity, and declined in population size toward the end of the 1000 year period due to inbreeding.

22.2.3.4 Central Kalimantan

Overall, the populations in the major Central Kalimantan habitat units are sufficient in size that they would be expected to remain large and genetically healthy if the habitat remains and if hunting or other direct threats are avoided. Two

populations are expected to experience habitat loss and reduction in K (Arut Belantikan, 60% decline, and Samba-Kahayan, 20% decline). Two other populations, Mawas and Sebangau, may steadily lose habitat until the orangutan populations are extirpated. An increase in available habitat is possible at Tanjung Puting, which would be expected to lead to increase in population size there.

22.2.3.5 West Kalimantan and Sarawak

Six of the habitat units in West Kalimantan and Sarawak are estimated to be sufficiently large to be capable of continuing to support demographically and genetically healthy populations. A smaller habitat unit at Bukit Baka ($N = 175$ individuals) also appears able to persist, although with diminished genetic diversity.

22.2.3.6 Sabah

The survey work of Ancrenaz and colleagues provides evidence that some populations in managed forests (e.g., Tabin, Trus Madi, and Sabah Foundation) are likely currently below K (Ancrenaz *et al.* 2004b, 2005). In contrast, the population at Kulamba is estimated to be at a size that is more than double the carrying capacity of the habitat. Similarly, the populations in the fragmented forests of Lower Kinabatangan are thought to be above K , and to currently have an excess of males, due to the sex bias in dispersal between fragments. We examined the impact of complete and partial isolation of fragments. When completely isolated, the smallest fragments do not contribute to the long-term populations in the province. Low rates of dispersal among fragments (as low as 1% to 3%; i.e., 7 to 21 animals moving between fragments annually) do provide considerable stability to the metapopulation. However, for such dispersal to occur, orangutans would have to be able to move safely among the forest fragments. If there were high mortality during dispersal, then the effect of 1–3% attempted dispersal events could be the same as 1–3% hunting—steady decline of the currently large population to extinction.

Two final notes. First, there are many small patches of forest on Borneo that contain very small populations of orangutans. These populations, smaller than any we modeled, would be very

Table 22.4 Impacts of varying levels of the severity of effects of inbreeding, with 0.0, 2.0, 4.06 (the number, derived from zoo data, that we used in our baseline model), or 6.0 lethal equivalents, in Bornean orangutan populations with initial and maximum population sizes of 100 individuals. Results are presented using the three different mortality schedules corresponding to high-, medium-, and low-quality habitats

| Input parameters Mortality schedule | Lethal equivalents | 50 years | | | 100 years | | | 1000 years | | |
|----------------------------------------|--------------------|----------|----|----|-----------|----|----|------------|----|----|
| | | PE | N | GD | PE | N | GD | PE | N | GD |
| High-quality habitat | 0.00 | 0 | 99 | 98 | 0 | 98 | 97 | 0 | 97 | 76 |
| | 2.00 | 0 | 98 | 98 | 0 | 98 | 97 | 0 | 91 | 76 |
| | 4.06 | 0 | 98 | 98 | 0 | 96 | 97 | 0 | 81 | 74 |
| | 6.00 | 0 | 97 | 98 | 0 | 95 | 97 | 0 | 66 | 72 |
| Medium-quality habitat | 0.00 | 0 | 90 | 98 | 0 | 90 | 97 | 0 | 91 | 73 |
| | 2.00 | 0 | 91 | 98 | 0 | 88 | 97 | 0 | 78 | 71 |
| | 4.06 | 0 | 91 | 98 | 0 | 87 | 97 | 1 | 60 | 67 |
| | 6.00 | 0 | 91 | 98 | 0 | 87 | 97 | 25 | 27 | 62 |
| Low-quality habitat | 0.00 | 0 | 82 | 98 | 0 | 79 | 96 | 0 | 80 | 68 |
| | 2.00 | 0 | 83 | 98 | 0 | 78 | 96 | 4 | 57 | 64 |
| | 4.06 | 0 | 82 | 98 | 0 | 77 | 96 | 44 | 17 | 56 |
| | 6.00 | 0 | 81 | 98 | 0 | 75 | 96 | 93 | 1 | 55 |

PE, % probability of extinction; N, mean population size; GD genetic diversity of initial gene diversity.

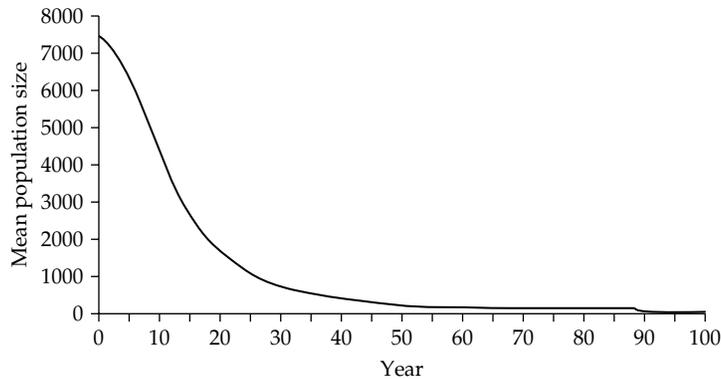


Figure 22.4 Mean population size of all surviving orangutan populations in Sumatra over the next 100 years given estimates current rates of logging.

vulnerable to extirpation and are unlikely to add anything to long-term viability of *P. pygmaeus* populations without active management and relocation of individuals. Second, some of the forest areas that we considered to be single 'habitat units' (e.g., areas in central and west Kalimantan) are partly to severely fragmented. It is not known if orangutans can move among these forest fragments. If not, populations in these forest units will be much less stable and less secure than they appear to be in our models.

22.3 Discussion

22.3.1 Summary and general considerations

We used the best available data from long-term field studies to estimate basic vital rates for orangutan populations. We used these estimates as parameters in a PVA to assess extinction probability of populations on Borneo and Sumatra under current conditions, and to ascertain the sensitivity of the populations to various threats. Our analyses improved on the model used at the 1993 PHVA

held in Medan because we incorporated more realistic measures of density dependence, considered Sumatra and Borneo separately, modeled the trajectories of actual orangutan populations, and used a longer set of long-term data to estimate parameters. Despite these extensions and refinements, our results generally confirm those of the earlier PHVA workshop (see Leighton *et al.* 1995).

The Sumatran and Bornean working groups at the 2004 PHVA workshop used different parameters for some models. Some of this variation reflects differences in field data. Differences in field data are presumably partly due to random sampling errors associated with small field samples and partly due to real differences between the two *Pongo* species. More data are required before we can assess the relative importance of these two sources of variation. In other instances, experts in the Sumatran and Bornean group provided different informed estimates for certain parameters. These differences partly reflect perceived differences in habitat quality between the two islands (Wich *et al.* in review; Chapter 7), which may affect *Pongo* population demography on the two islands (Wich *et al.* 2004b, Chapter 5). In our models, *P. pygmaeus* had lower mortality and faster reproductive rates, and consequently exhibited more rapid population growth than *P. abelii*. In general, these differences were small and the results for the two orangutan species are largely congruent.

Although we used the best available data from field studies of wild orangutans, it is important to remember that most studies are conducted in high-quality habitats. Therefore estimates of key demographic and life-history parameters might provide unrealistically optimistic estimates of population viability (Marshall in press). As noted above, it is also possible that demographic rates vary across the species' ranges. We need data from multiple studies to help document the extent of this variation, the degree of flexibility of the two species, and the relationships between habitat characteristics and orangutan demography and population dynamics.

It is also important to recognize that our models for Bornean orangutans assume that the habitat units will remain largely unchanged and will not be subjected to stresses larger than (or even, in some cases, as large as) those that they are currently

experiencing. Yet many of these forests will be cleared or badly degraded unless urgent and forceful action is taken soon. These models should be seen not as predictions of what will happen, but rather as projections of the expected stability of the existing large populations of orangutans if the habitat units are preserved and other threats (e.g., hunting) are eliminated.

Our modeling shows that it may take a long time for the consequences of population fragmentation and isolation to have noticeable effects. Even populations that are most likely destined for extinction in several hundred years would appear to be stable after 50 or even 100 years (see Table 22.3). This is particularly worrying, given that our current methods for monitoring orangutan populations (i.e., nest counts) are relatively imprecise and inaccurate. It would probably be decades before we would realize that a population was in decline, at which time it may be too late to save the population without prohibitively high costs. This suggests that we need better ways to monitor orangutan populations, and that we take a preventative perspective on orangutan protection.

22.3.2 Threats and conservation actions

The biggest threats to orangutans are well known: habitat loss and hunting. Selective logging, especially at high levels, degrades habitat, but its effects on orangutan populations are less severe than complete loss of habitat or poaching (see Chapter 6). We therefore discuss only these two most severe threats below.

Loss of habitat due to clear-cutting or conversion to oil palm reduces the carrying capacity of forest fragments. Although the loss of habitat may be easily visible on satellite images, its effects on orangutan populations may not be immediately obvious. Orangutan densities may temporarily be extremely high in areas near logging operations due to compression effects (e.g., Marshall *et al.* 2006; see Chapter 6), potentially leading to dangerous overestimates of population size. In these compressed populations (i.e., those above K), we expect more intense intraspecific competition, which will depress fecundity and/or elevate mortality, and in time reduce population size. In other

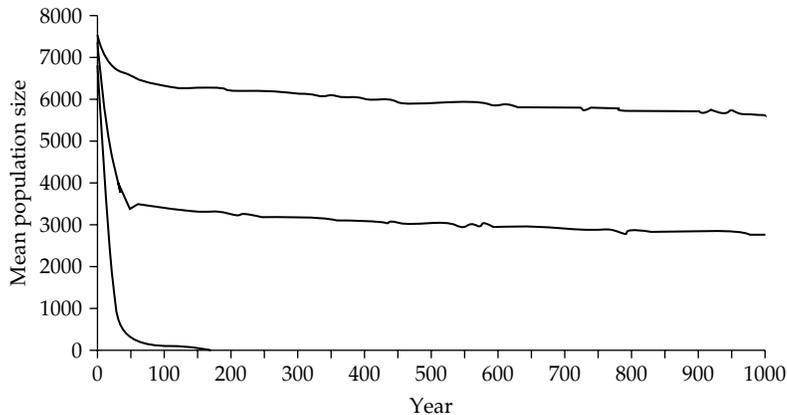


Figure 22.5 Mean population size of all surviving orangutan populations in Sumatra over the next 1000 years given estimates current rates of logging (bottom line), cessation of logging in 5 years (middle line), and immediate cessation of logging (top line).

words, although clear-cutting may not directly kill many orangutans, it does create an unavoidable ‘extinction debt’ (*sensu* Tilman *et al.* 1994). Clearly the complete removal of orangutan habitat has major negative effects, and additional clear-cutting should be prohibited from around the limited number of large orangutan populations that will be the last strongholds of wild orangutans.

Our models indicate that even very low hunting rates have strongly deleterious effects, a result confirmed by recent field surveys (Marshall *et al.* 2006). Simulation results suggest that in the best-quality habitats 1% annual hunting rates may be sustainable, but 2% or 3% annual offtake rates drive all populations to extinction. Nobody would claim to be able to detect the difference between 1% and 2% hunting rates in the field, yet the future of orangutan populations hangs on this minute difference. Therefore, current legal bans on hunting of orangutans should be strictly enforced. The current numbers of orangutan infants (and associated deaths of their mothers) estimated to be removed annually for the pet trade are far higher than is sustainable. Nijman (2005) estimated that between 200–500 infant orangutans were lost to the pet trade annually in Kalimantan alone, with an associated loss of 3–4% of reproductive females annually. Additional killings of orangutans for food, ritual purposes, or in response to crop raiding would further accelerate decline.

The biggest threats to orangutans apply to orangutan populations on both islands, although hunting is a larger threat in some parts of Borneo than Sumatra, and much less orangutan habitat remains on Sumatra than on Borneo. On the most basic level, hunting could be addressed effectively simply by the enforcement of existing laws. Enforcement of existing laws would also halt the loss of habitat in formally protected areas, although it is interesting to note that although killing of orangutans is forbidden anywhere, destruction of their habitat, which leads to their death, is legal outside protected areas. Despite the importance of and urgent need for enforcement, simultaneous implementation of complementary conservation interventions is likely to yield more favorable outcomes.

Issues of natural resource management and conservation are inherently multifaceted and a broad set of initiatives, incentives, and enforcement is required to adequately address them. The two PHVA working groups discussed a wide range of options: stopping construction of roads in protected areas, funding existing conservation projects, improving law enforcement, monitoring of orangutan populations, reconnecting isolated populations with corridors, developing education and outreach programs, maintaining concession moratoriums indefinitely for legal logging, establishing helicopter patrols, encouraging the participation and collaboration of local non-governmental organizations,

promoting forest restoration, providing incentives for people to move out of important orangutan habitat, removal of illegal settlers in formally protected areas, working more closely with local governments and traditional community leaders, developing alternative income-generating activities for local people, establishing new research sites, developing innovative tourism opportunities, using remote sensing to monitor forest loss, initiating international and national media campaigns, and building local capacity. Issues related to the conservation of orangutan populations are broad in scale, both temporally and spatially, but also require solutions appropriate to local conditions. Finding and implementing these solutions will require substantial political will and investment at all levels.

22.3.3 Sumatra

It is clear that *P. abelii* is in more immediate threat of extinction than is *P. pygmaeus*. In comparison with Borneo, fewer Sumatran orangutans live in the wild, less suitable habitat remains, and forest is being lost at faster rates (Wich *et al.* 2003a). In addition, much of the current wild Sumatran orangutan population lives in Aceh, a province in which political unrest and environmental catastrophe have severely hampered conservation efforts in recent years. Fortunately, the political unrest is over and as a result there is again hope for implementation of conservation initiatives. The Ladia Galaska road project threatens to further divide one of Sumatra's largest remaining orangutan populations. It was against this backdrop that the Sumatra group considered how the conservation and management of orangutans on the island could be best effected. They concluded that many of the recommendations listed above could be usefully applied to the management and protection of Sumatran orangutan populations. Several additional possibilities were considered: gaining World Heritage Site status for the Leuser ecosystem, continuing efforts to connect the Trumon-Singkil and west Leuser populations, reconnecting the west and east Leuser habitat units, and reactivating research at Ketambe. We feel that implementation of these recommendations must be considered a major priority in global efforts to preserve wild populations of great apes.

22.3.4 Borneo

At the end of our PHVA meeting, the Borneo working group was faced with the prospect of conveying a complicated message. On one hand, there are far more wild orangutans on Borneo than was previously thought. On the other hand, far more orangutans have been lost in Borneo over the last century than we had previously realized. This message is at once both sobering and hopeful, and indicates that the first orangutan population counts probably underestimated their true abundance by several orders of magnitude. The current situation in Borneo is not as dire as in Sumatra, but the plight of *P. abelii* provides a glimpse of what the future for *P. pygmaeus* may hold. Very few orangutan habitats in Borneo are immune from logging, and most are also subjected to hunting, either directly for meat and pets, or indirectly when displaced orangutans are killed as agricultural crop pests. Only timely and effective interventions will prevent Bornean populations from facing the imminent extinction that now confronts Sumatran ones.

22.3.5 PVA and the realities of orangutan conservation

Population Viability Analyses have been part of the conservation biologist's toolkit for over two decades. Over this time, more sophisticated analytic techniques and more fully developed theoretical considerations have been incorporated into PVA (e.g., Gilpin and Soulé 1986; Beissinger and Westphal 1998; Sjögren-Gulve and Ebenhard 2000; Sæther and Engen 2002; White *et al.* 2002), changes which are assumed to have increased the accuracy and precision of our estimates of extinction probabilities. Despite these refinements, PVA results are only as accurate as the data upon which they are based (Lindborg and Ehrlén 2002). Estimates of mean vital rates are notoriously difficult and time-consuming to obtain for wild vertebrate populations (Thomas 1990; Münzbergová and Ehrlén 2005), and the equally important measures of variance in these rates are even more difficult to assess (Beissinger and Westphal 1998; Sæther and Engen 2002). This could scarcely be more true than for orangutans, who live at low population densities,

have long lifespans, reproduce slowly, and for whom few long-term data exist. In addition, climate, governance, and land-use policies are likely to change in important but unknown ways in the next decades in Indonesia and Malaysia, limiting the extent to which we can project current models into the future.

We recognize that our estimates of basic life history variables and the intensity of important threats are not as accurate nor as precise as we would like. However, we also recognize that unless current threats are quickly and drastically reduced, Sumatran orangutans will be extinct long before we have the chance to collect such specific data. Conservation biology, the new 'dismal science', is full of dire predictions and urgent calls to arms. In few cases is the situation more dire and the need for action more urgent than for Sumatran orangutans. Unless bold and courageous action is taken soon, we will have stood by as one of our closest living relatives went extinct in the wild.

We conclude this chapter by summarizing the main results and indicating management implications emerging from the analyses.

1. Indonesian and Malaysian forests are disappearing and orangutans on both islands are becoming increasingly isolated into forest fragments. Populations in fragments for which we have good data are in decline. Orangutans are particularly vulnerable to population decline and local extinction because of their life histories. The biggest threats are hunting and habitat loss.

2. Our initial exploration of some scenarios representing typical populations on Borneo suggests that orangutan populations restricted to habitats capable of supporting only about 50 animals can persist for a considerable number of years, but are unstable and vulnerable to extirpation. Habitats capable of supporting more than 250 orangutans appeared necessary to ensure good demographic and genetic stability.

3. At typical population densities, 500–1000 km² of habitat is required to maintain a demographically and genetically healthy population of Bornean orangutans. As some Sumatran forests

appear to support higher orangutan densities, a slightly smaller area may be sufficient on Sumatra. Regardless, relatively few protected areas contain 500 km² of good orangutan habitat. This means that protection and management of orangutans outside formally protected areas is required to maintain viable populations.

4. Simple calculations indicate that orangutan populations under no external threats can grow at a maximum of 2% annually ($r_{\max} \approx 0.02$). Probably very few wild populations achieve this maximum theoretical rate. This means that the loss only a few individuals per year can mean the difference between persistence and extinction.

5. Orangutan life history and population biology result in strong time lags between insults and detectable reduction in population size. Once we detect that a population is in decline, it may be too late to save it. Therefore, a precautionary approach is necessary to avert the extinction of orangutan populations.

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