Bonobo Conservation Assessment

November 21-22, 1999
Kyoto University Primate Research Institute
Inuyama, Japan

Workshop Report

Sally Coxe, Norm Rosen, Philip Miller and Ulysses Seal, editors

A Contribution of the Workshop Participants and
The Conservation Breeding Specialist Group (IUCN / SSC)
A contribution of the workshop participants and the IUCN / SSC Conservation Breeding Specialist Group.

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28 February 2009
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Workshop Report

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Bonobo Conservation Assessment

Workshop Report

Section I
Executive Summary and Recommendations
Bonobo Conservation Assessment Workshop
Executive Summary

Introduction

Endangered, the bonobo (*Pan paniscus*) is found only in the central Congo Basin of the war-torn Democratic Republic of Congo (former Zaire). The current wild population is unknown, but definitely decreasing. Restricted in distribution, bonobos have disappeared from areas where they were abundant ten to fifteen years ago. Habitat loss, fragmentation and the catastrophic effects of the civil war in the Congo pose serious threats. Bonobos are being hunted with greater frequency for meat and profit in the commercial bushmeat trade. Traditional taboos that have protected bonobos in the past are breaking down in the face of civil war, human population pressure, and desperate economic circumstances. At this time, there is no enforced protection for the bonobo.

Conservation efforts to date have been hampered largely by political unrest, which has intensified since 1991. The intermittent presence of field researchers has provided some protection for bonobos in isolated pockets of their fragmented habitat. However, scientists have not been able to return to their study sites for one to four years, due to back-to-back civil wars that began in 1996. The frontline of the war has moved into the central part of the bonobo range, posing even more danger to the remaining bonobo population. Bonobo study groups are at particular risk because they are habituated to humans. There has been a sharp increase in the number of bonobo orphans entering the capital city, Kinshasa, and reports state that armed soldiers are hunting the apes.

On November 21-22, 1999, CBSG conducted a two-day conservation assessment workshop, hosted by the Kyoto University Primate Research Institute in Inuyama, Japan. The workshop was organized by Norman Rosen and facilitated by Dr. Ulysses Seal of CBSG. This was a satellite meeting held after the “Committee on Excellence” Symposium: *Evolution of the Apes and the Origin of Human Beings*. The workshop was held in preparation for a full-scale Population and Habitat Viability Analysis (PHVA) to be conducted in the Democratic Republic of Congo.

The objective was to identify current threats to wild bonobo communities and set priorities for action. Because PHVA workshops are not usually conducted outside of the range country and no Congolese were present, the meeting focused on sharing data, producing a first draft of a population modeling exercise using the simulation modeling package *VORTEX*, and synthesizing available information on the status of research, protected areas, and conservation activities. *The Action Plan for Pan paniscus: Report on Free-Ranging Populations and Proposals for their Preservation*, published in 1995 by the Zoological Society of Milwaukee County (Thompson-Handler et al. 1995), was used as one source of baseline information.

Twenty-two participants from five countries attended the 2-day workshop, including representatives from the active field research teams. (See List of Participants, Section V).
Background

The bonobo, also called “pygmy chimpanzee,” is registered as highly vulnerable to extinction in the IUCN/SSC Action Plan for African Primate Conservation (IUCN 1996a) and as endangered in the IUCN Red Data Book (IUCN 1996b). Bonobos are theoretically protected by Congolese and international laws. They are listed in Appendix 1 of CITES (Convention on International Trade in Endangered Species), which bans international trade of the species and any of its parts. They are also classified as endangered by the U.S. Fish and Wildlife Service.

Bonobos have been studied in the wild since the mid-1970s. Long-term study sites include Wamba, founded by Takayoshi Kano of Kyoto University in 1974 and Lomako, established in the same year by Noel and Alison Badrian. Three research projects have been conducted in the Lomako area: the Lomako Forest Pygmy Chimpanzee Project, initiated in 1980 by Randall Susman, State University of New York at Stony Brook, USA; Project Pan, established in 1990 at Isamondje by Gottfried Hohmann and Barbara Fruth of the Max-Planck Institute, Germany; and Bonobo in Situ, initiated in 1995 at Iyema and coordinated by Jef Dupain of the Royal Zoological Society of Antwerp, Belgium. Jo Thompson established the Lukuru site in 1992 in the southern portion of the bonobo range. In addition, Jordi Sabater-Pi and Vea of the University of Barcelona, Spain, conducted a brief study from 1988-1990 at the Lilungu site.

Research sites that have remained active in recent years include Isamondje and Iyema in the Lomako area, Wamba, and Lukuru. (See Appendix I). None of the field study sites falls within the boundaries of a national park. The 188 km² Luo Reserve surrounding the Wamba site was designated as an official protected area with the Centre de Recherche en Sciences Naturelles (CRSN) in 1987, and its expansion to the south is proposed. Similarly, a proposal exists for the Lomako Reserve, a 3800 km² forest block between the Yekokora and Lomako Rivers. The proposal was submitted by WWF-International to the Institut Congolais pour la Conservation de la Nature (ICCN) in 1990 and reached the ministry level in 1991, but has not yet been approved.

The Salonga National Park was originally established in 1970, in part to provide protection for bonobos, but it has never been determined if a sustainable population exists there. In cooperation with the ICCN and Zoo Atlanta’s Africa Biodiversity Program, the Zoological Society of Milwaukee launched a plan for a regional survey in 1997. Preliminary reconnaissance conducted in 1998 verified the existence of bonobos within the Salonga’s north sector, as well as evidence of poaching. A full survey of the park is pending.

Research and conservation efforts have been increasingly difficult since civil unrest began to escalate in 1991, coupled with economic collapse. In 1996, civil war broke out as forces led by Laurent Desiré Kabila challenged long-entrenched dictator Mobutu Sese Seko. In May 1997, Kabila took power and changed the name of the country from Zaire to Democratic Republic of Congo (DRC). In the summer of 1998, a second civil war erupted, spurred by rebel factions backed by Rwanda and Uganda. Troops, primarily from Zimbabwe and Angola, have supported Kabila. The conflict continues, despite the ceasefire agreed upon by all warring factions in the Lusaka Peace Accord of July, 1999. The United Nations plans to send a peacekeeping force, but their strategy remains unclear, due to the enormous complexities of the situation.
The Workshop

Norm Rosen opened the Inuyama workshop, emphasizing the importance of keeping a positive attitude, despite the war in DRC. He cited the success of CBSG workshops in developing a viable strategy for the mountain gorilla in the midst of civil unrest. Norm introduced Takayoshi Kano, the pioneer of bonobo field research, and asked him to comment. Kano emphasized the fact that bonobos are hunted for meat throughout most of their distribution and now face the most extreme difficulty in their history. With the war now in the central part of the bonobo habitat, Kano said, “villagers have probably fled into the forest. They must be hungry. They must be hunting wild animals, including *Pan paniscus*, much more heavily than they used to. Soldiers, too, must hunt them for meat. Nobody knows when this confusion will settle down. This is the worst problem. Please, let us discuss what we can do to save *Pan paniscus* in the wild.”

Each participant stated goals for the workshop. The primary concerns were: “What can we do to protect wild bonobos while the war continues? How can we prepare for concerted action when conditions improve?” In addition, participants suggested the following needs:

- Increase pride in bonobos among Congolese
- Coordinate conservation activities among various parties
- Assess risk of population extinction
- Establish clear goals for bonobo conservation
- Help end the war in DRC
- Maintain reserves; strengthen intervention on the local level
- Gain support of park rangers/guards
- Share perspectives on conservation
- Share information for use in bonobo conservation
- Promote public education
- Assess what has been done for bonobos
- Prepare to go back to study sites
- Focus international attention on the Congo
- Mobilize people and governments to help
- Increase awareness through media
- Collaborate with the University of Kinshasa
- Prepare for the future; be ready to act when chaos ends

Working Groups

Participants were divided into two working groups: Distribution, Threats and Activities, and Life History and Population Modeling. Discussion focused on the sites active in recent years: Wamba, Isamondje, Iyema and Lukuru sites.

(Note: Because Barbara Fruth of the Isamondje site participated in the Modeling group, much of the discussion on threats and distribution lacked her input. Gay Reinartz sent a fax outlining the status of the Salonga survey; this document can be seen in Appendix II [page 43].)
Summary of Recommendations

A key recommendation was for field researchers to return to their sites as soon as possible, with Wamba as the top priority. In addition, participants agreed to conduct coordinated surveys using GPS/GIS and to synchronize methodology for the collection of comparable data.

The group felt it was important to survey key areas of the bonobo habitat, including the area east of Lomako, between the Lopori and Tshuapa Rivers, following the Bolombo River, and the Wamba/Luo Reserve area, between the Maringa and Tshuapa Rivers. Areas in the eastern part of the bonobo range south of Kisangani were also designated for survey.

It was also agreed to hold a complete PHVA workshop as soon as possible to unify Congolese stakeholders, field researchers, zoos, conservationists, and others working for bonobos. The group agreed that Kinshasa would be the most desirable place to hold a meeting, but if this is not possible, given political circumstances in DRC, Antwerp, Belgium was recommended as an alternate venue, provided that Congolese representatives are present.

Raising local and international public awareness of bonobos and their plight was also deemed to be of utmost importance.

Conservation Priorities and Action Responsibilities

Following the reports from each working group, all participants tried to identify the information most needed, who will gather it, and actions to be taken. Focus was placed on what needs participants can take responsibility for, concentrating on actions with measurable outcomes.

General Goals And Ideas:

Assess the situation for bonobos as a whole. Coordinate bonobo surveys with other pertinent information, such as biodiversity, human demographics, land use patterns, and threats. Get satellite imagery to help determine a baseline from which to evaluate habitat status and changes over time (roads, agricultural encroachment, villages, logging). Explore possibility of using infrared photography to find bonobos in nests and coordinate with ground surveys.

Specific Recommendations:

1. Return to Wamba. Survey Luo Reserve.

2. All research teams return to their sites. Go back equipped with GPS/GIS and coordinate methodology for collection of comparable data.

3. Survey other areas (See maps, Appendix I [page 37]).
   a) East of Lomako, between Lopori and Tshuapa Rivers, following the Bolombo River (Survey Area 12)
      • Wamba area, between Maringa and Tshuapa Rivers (Survey Area 11)
      • Area between Maringa and Lopori Rivers (Survey Area 3)
   b) From western limit of south block, La Salonga to Lac Mai-Ndombe (Survey Area 9)
c) Areas south of Kisangani in the eastern section of potential range (Survey Areas 5, 1A, 1B).

d) Area between Mbandaka, Boende and Basankusu (Survey Area 13)

4. Mapping (linked to human population/impact)

5. Find out where logging concessions are already assigned and for how much money. Is selective logging or clear-cutting planned? Are contracts signed and approved? Explore ways to influence logging strategy and recommend strategies that will have the least impact on bonobos. Look toward adding eco-tourism onto the logging infrastructure.


7. Support UN Resolution for Great Apes, proposed by Richard Wrangham at COE Symposium, with a strong message for peace in the Congo.

8. Have a meeting of the entire bonobo community to unify field researchers, zoos, conservationists, and others working with bonobos. Set goals based on this meeting. Suggested venue: Antwerp in 2000. Plan PHVA in Kinshasa as soon as possible.

9. Get more publicity; raise public awareness of bonobos.

**Conclusion:** The bonobo community mobilizes!

**Commitments**

Before the meeting adjourned, participants briefly discussed what they could commit to doing to move the process forward.

Barbara Fruth: Recommend methodology for coordinated survey.

Jef Dupain: Investigate logging concessions.

Sally Coxe: Establish an e-mail discussion group to facilitate on-going communication and cooperative planning.

Sue Savage-Rumbaugh: Investigate satellite maps. Find out more about what Congolese already know about where bonobos are at certain sites. Get publicity.

Japanese team: Conduct research on the impact of research.

Jo Thompson: Investigate how to stop hunting of apes vs. other bushmeat.

Linda Van Elsacker: Work on public education. Try to gain support of Belgian government.

Because the discussion was cut short due to lack of time, participants agreed that we need to determine what else needs to be done and who will take responsibility.
Bonobo Conservation Assessment

Workshop Report

Section II
Distribution, Threats and Activities
Distribution, Threats and Activities Working Group Report

Working group participants:
Sally Coxe, Bonobo Conservation Initiative
Jef Dupain, Royal Zoological Society of Antwerp
Shiho Fujita, Primate Research Institute, Kyoto University
Miya Hamai, Primate Research Institute, Kyoto University
Chie Hashimoto, Primate Research Institute, Kyoto University
Michael Huffman, Primate Research Institute, Kyoto University
Gen’ichi Idani, Great Ape Research Institute, Hayashibara Museum of Natural Science
Takayoshi Kano, Primate Research Institute, Kyoto University
Norman Rosen, Conservation Breeding Specialist Group
Sue Savage-Rumbaugh, Georgia State University
Yasuko Tashiro, Primate Research Institute, Kyoto University
Jo Thompson, Lukuru Wildlife Research Project
Shigeo Uehara, Primate Research Institute, Kyoto University

Threats

Most threats to bonobos are the result of human activities. Participants identified the following threats to bonobos (not ranked in order of importance and with no quantitative information on actual impacts assembled as a basis for discussion):

- Human population pressure
- Agriculture
- Subsistence hunting/snaring
- Commercial bushmeat trade
- Live capture for pet trade
- Economic breakdown (i.e., no market for crops)
- Logging
- Surface Infrastructure (i.e., roads)
- Political instability
- Ignorance (lack of knowledge)
- Lack of domestic law enforcement
- Lack of laws
- Availability of weapons and ammunition
- Cultural change
- Cross-species transmission of disease

While all share similar problems, the various research sites face different situations. Threats ranked by order of severity for each site are as follows:

Wamba:
1. Political instability
2. Hunting/availability of guns
3. Cultural change (i.e., prior to intensified socio-economic and political instability in 1991, people of Wamba never ate bonobos. Since then, when villagers traveled to Kinshasa, they came back with different views and began killing bonobos.)
4. Lack of law enforcement (i.e., local authorities eat bonobos, although it is against the law)
5. Agriculture/human population increase (destroying habitat)
6. Live capture for pets

Iyema:
1. Bushmeat trade
2. Economic breakdown (i.e., no market for crops)
3. Logging
4. Political instability
5. Surface infrastructure
6. Lack of domestic law enforcement
7. Laws
8. Availability of guns and ammunition
9. Human population pressure

Threats of equal impact: ignorance, culture change, agriculture, hunting, disease.

Isamondje:
1. Lack of research presence (due to war)
2. Agriculture/ population increase
3. Subsistence hunting (snaring for local consumption)
4. Logging
Not a problem: ignorance, lack of law enforcement, need to strengthen laws, immigration, culture change, x-species transmission

Lukuru:
1. Human population increase
2. Agriculture
3. Culture change
4. Political instability
5. Laws (lack of laws and enforcement)
6. Availability of guns and ammunition
7. Hunting

Distribution
Bonobos are found only in the area to the south of the Congo River. (See map, Appendix I) The distribution may extend as far east as the Lualaba River, and is bound in the south by the Kasai-Sankuru rivers. Considering these boundaries, the potential bonobo range covers an area of approximately 840,400 km². (Dupain et al. 2000; Thompson-Handler et al. 1995)

Participants discussed, in plenary session, what is now known about bonobo distribution, and extrapolated a population estimate of 60,000 to 120,000. However these estimates, built upon a systematic analysis of distribution and plausible density estimates, were so different from previous impressions that they were considered to be overly optimistic. The bonobo population is fragmented, and bonobos are known to have disappeared from several areas where they were once common (these areas were not included in the above estimates). Catastrophic threats, such
as increased hunting for the bushmeat trade and the effects of war and displaced people are also
taking a toll, the extent of which is not known. Participants reviewed the *Action Plan for Pan*
*(1995)*, noting that the situation has probably changed significantly since that report was
published five years ago. *Given the uncertainty of the data, the estimates in the Action Plan*
*(which were based on estimates from the then available data) were preferred by the editors as*
*perhaps the best estimates to use at present: 10,000 to 20,000, and possibly as few as 5,400 total*
*bonobos.*

**Status**

The current status (1999) of bonobos at Wamba, Lukuru, and Lomako is not known, due to the
continuing civil war. Based on information available, participants evaluated two issues: the
impact of habitat destruction or modification and site management. (Note: No data were
collected for the Isamondje site.)

1. **Impact of habitat destruction / modification**

   **Wamba:**
   Human population has doubled since research began in the mid-1970s. Agriculture has
   increased, but bonobos can eat secondary vegetation.

   **Iyema:**
   Permanent habitation of the Lomako forest was formerly forbidden by law. Local people
   used the forest as a temporary hunting area. However, in the past 10 years, the forest has
   become a permanent home for more people. The law did not change, but local officials allow
   people to live there. Before, people went in to gather and subsistence hunt, then went back to
   the village.
   Human population pressure poses an increasing threat, resulting in the introduction of
   permanent agriculture next to research sites.

   **Lukuru:**
   Same as Wamba with an increase in human population and agriculture.

2. **Site management**

   **Wamba:**
   Researchers have not been able to visit Wamba since 1996. Research assistants formerly
   served as guards. Now, there is no means to send salaries to them. Also, the people of
   Wamba may not be able to stay in the village now, due to the war and intruding soldiers, so
   they have probably dispersed into the forest. It is likely that the research assistants cannot
   continue their work. In 1998, Japanese researchers sent some money via missionaries. This
   was the last time salaries could be sent to the workers.

   **Lukuru:**
   As of 1998, rangers in the southern sector of the Salonga National Park had not been paid in
   5 years. In fact, the conservateur was paying park guards to track for meat. In the summer of
   1998, Jo Thompson purchased 8,401 acres south of the park through traditional local barter.
Named the Lukuru Reserve, this land located between the Lukenie and Sankuru rivers is being protected by the local people. It is in their control.

Iyema:
The research team led by Jef Dupain was last in Iyema in the autumn of 1998. It has been possible to get salaries to workers, thanks to missionaries in Basankusu. But, recently, people don’t dare come out of the forest to get their money, due to the war. It appears that bonobos remain untouched in forest. However, recent reports confirm that soldiers have come into the forest, but it is not known if they are hunting bonobos. The bonobos are habituated, so the risk of being shot is great.

Recommendations
Try to make quantitative identification of factors threatening bonobos, to assist better estimates of habitat and demographic impacts and rates of change.

Points to consider:

• Threats making a direct impact on demography / population. (Estimate frequency and effect.)

• Rate of habitat loss.

• Specify parameters of carrying capacity to assist estimates of reductions occurring.

• Information obtainable through satellite maps may assist estimates of habitat and its loss.

• Human population growth in the context of land use patterns and their projected changes over the next 25 years. (Examine reduction of habitat and its carrying capacity and forest degradation, specify measurable parameters using mapping techniques.)

• Bonobo population fragmentation with identification of barriers to movement.

• Issue regarding Lomako: Isamondje and Iyema researchers have two differing perceptions of the problem. Need to clarify.
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Section III
Life History and Population Modeling
Introduction

A primary goal of this workshop was the assembly, collation, and analysis of available demographic data on bonobo populations across the Democratic Republic of Congo. *VORTEX*, a simulation software package written for population viability analysis, was used as the primary tool to study the interaction of a number of bonobo life history and population parameters treated stochastically, and perhaps to explore which demographic parameters may be the most sensitive to threats and alternative management practices. This goal was only partially achieved since much of the field data was either unavailable or not in a form allowing systematic analysis.

The *VORTEX* package is a computer simulation of the effects of deterministic factors as well as stochastic demographic, environmental, and genetic events on wild populations. *VORTEX* models population dynamics as discrete sequential events (e.g., births, deaths, sex ratios among offspring, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or variables that follow specified random distributions. The package simulates a population by stepping through the series of events that describe the typical life cycles of sexually reproducing organisms. For a more detailed explanation of *VORTEX* and its use in population viability analysis, refer to Miller and Lacy (1999).

*VORTEX* is not intended to give absolute answers, since it is projecting stochastically the interactions of the many parameters used as input to the model and because of the random processes involved in nature. Interpretation of the output depends upon our knowledge of bonobo biology, the environmental conditions affecting the species, and possible future changes in these conditions.

The working group decided to consider the central region within the current bonobo range in the Democratic Republic of Congo (Lomako, Wamba) and in Lukuru and Salonga separately in the demographic modeling process for the following reasons:

Wamba – Lomako
- Known demographic data
- Threats from human population growth

In our development of the bonobo demography, we treated only the known geographic areas and extrapolated from these models later to include the unknown areas.
The Salonga region was not explicitly modeled in this workshop but was simply treated as a larger variant of the first population.

**Input Parameters for Simulations**

*Inbreeding Depression:* In the current set of simulations, inbreeding depression was not included as the extent of occurrence of bonobos in the region is quite large. However, information presented at the workshop by Jo Thompson suggests that bonobo populations within this area now may be highly fragmented and, therefore, become susceptible to inbreeding by random drift and its deleterious consequences. Working group participants identified this issue as uncertain and requiring further deliberation and analysis.

*Concordance in environmental variability between survival and female fecundity:* The group assumed that covariance between these processes does not exist because of a significant reproductive buffering that compensates for reproductive losses in a given year and the dissociation of environmental effects on survival and reproduction.

*Catastrophes:* Catastrophes are singular environmental events that are outside the bounds of annual environmental variation affecting reproduction and/or survival. Natural catastrophes can be tornadoes, floods, droughts, disease, or similar events. These events are modeled in VORTEX by assigning an annual probability of occurrence and a pair of severity factors describing their impact on mortality (across all age-sex classes) and the proportion of females successfully breeding in a given year. These factors range from 0.0 (maximum or absolute effect) to 1.0 (no effect), and are imposed during the single year of the catastrophe, after which time the demographic rates are returned to their baseline values.

The group identified the following as potential catastrophic events:
- War and subsequent refugee problems
  - Lomako [only secondary effects]
  - Wamba [serious effects]
- Disease
- Logging

The specific characteristics of disease and logging were not quantified so they were not included in these demographic models. Additional analysis with use of information from other primate – especially chimpanzee - populations necessary in order to provide a more complete picture of these events and their potential impacts on bonobo populations. Disease events were modeled for the mountain gorilla (Werikhe et al. 1998) and their omission here makes it likely that the impact of this threat to the bonobo populations is being underestimated and their risk of extinction underestimated. Logging effects on habitat may be modeled by changes in K.
Ultimately, the group derived two catastrophic events to use in this modeling exercise, with the following characteristics:

- Excessive hunting: 3% annual probability of occurrence, leading to 75 percent mortality in local areas.
- Large-scale human civil disorder: 14.4% annual probability of occurrence, leading to 15 percent mortality over more extended areas.

Note: disorder mortality was excluded from the annual average adult female mortality estimates.

**Breeding System:** Polygynous.

**Age of First Reproduction:** *VORTEX* precisely defines reproduction as the time at which offspring are born, not the age of sexual maturity. In addition, the program uses the mean age rather than the earliest recorded age of offspring production. Field data indicate that bonobos begin breeding on average at age 15.

**Age of Reproductive Senescence:** *VORTEX* assumes that animals can reproduce (at the normal rate) throughout their adult life. Observations suggest that bonobos will not reproduce beyond about 40 years of age. This value was used in all of the models.

**Density-Dependent Reproduction:** Density dependence in reproduction (proportion of females breeding in a given year) is modeled in *VORTEX* according to the following equation:

\[
P(N) = \left[ P(0) - \left( P(0) - P(K) \right) \left( \frac{N}{K} \right)^B \right] \frac{N}{N + A}
\]

in which \(P(N)\) is the percent of females that breed when the population size is \(N\), \(P(K)\) is the percent that breed when the population is at carrying capacity \((K,\) to be entered later), and \(P(0)\) is the percent of females breeding when the population is close to 0 (in the absence of any Allee effect). \(B\) can be any positive number. The exponent \(B\) determines the shape of the curve relating percent breeding to population size, as population size gets large. If \(B\) is 1, the percent breeding changes linearly with population size. If \(B\) is 2, \(P(N)\) is a quadratic function of \(N\). The term \(A\) in the density-dependence equation defines the Allee effect, in which reproduction can be reduced in a low-density population simply because of difficulty in finding suitable mates across the landscape. One can think of \(A\) as the population size at which the percent of females breeding falls to half of its value in the absence of an Allee effect (Akçakaya 1997).

The group agreed that, at carrying capacity, an average of 21.7% of adult females breed annually. This is derived directly from estimates of interbirth intervals from wild population studies. Moreover, as many as 25% of adult females breed annually when the population is far below carrying capacity, regardless of age-specific survival rates (see discussion below on mortality). In order to simulate the desired functional relationship, exponential steepness is equal to 2. The group concluded that bonobos would not suffer from Allee effects at low population densities. Therefore, \(P(0) = 25\%, \ P(K) = 21.7\%, B = 2,\) and \(A = 0.\)
Annual variation in female reproduction is modeled in *VORTEX* by specifying a standard deviation (SD) for the proportion of adult females that reproduce within a given year. The group derived a standard deviation in this parameter of 4%; this level of annual variability translates in a range of female breeding success from one year to the next from roughly 17% to 33% over time (when the population is below carrying capacity).

**Mortality:** Field data from Wamba indicate the following simplified mortality schedule over the age ranges indicated with no differences between the sexes:

<table>
<thead>
<tr>
<th>Age</th>
<th>% Mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 – 1</td>
<td>4.0</td>
</tr>
<tr>
<td>1 – 7</td>
<td>4.0</td>
</tr>
<tr>
<td>8 – 14</td>
<td>4.6</td>
</tr>
<tr>
<td>15 – 40</td>
<td>4.0 (Adults)</td>
</tr>
</tbody>
</table>

A working group member suggested that these mortality estimates for Wamba are optimistic, particularly with respect to infant survival and suggested some factors to consider:
- Provisioning [1-2 months/year] helps bonobos which may affect infant survival during the first year. But note that mortality in Lomako was not higher either.
- Perhaps the lack of infanticide in bonobos as compared to chimpanzees results in lower rates.
- Researchers probably aid survival of bonobos

Values of 4, 6, and 8% for infant mortality were analyzed in a sensitivity analysis for this parameter. Values of 2, 4, and 7% for adult mortality were simulated in a sensitivity analysis for this parameter.

**Results of Simulations**

**Reported Results and Their Interpretation**

The scenario simulation reports include values for deterministic population growth rates, generation time, and the initial population age and sex structure. The results, reported here, of the simulations at specified time intervals included stochastic population growth rates with standard deviations (SD), mean extant population size with SD, probability of extinction, and age and sex structure of the population. Other information in the reports, not included here, is provided on the loss of heterozygosity and allelic losses over the time interval of the simulation.

The population growth rate (‘r’) provides a measure of the rate of growth of the population under the specified values of the parameters in the simulation scenario remembering they will vary stochastically from year to year as a result of intrinsic and environmental variation. A positive value of 1% (r ~ 0.01) yields a population doubling time of about 70 years. It is a mean over the time interval (100 years in these simulations) of the rate calculated for each year. A standard deviation is also calculated to provide an indication of the dispersion of the values given that they will vary from year to year because of the stochastic variation in the parameter values from year to year. An approximately stable population will have an r = 0.000. Declining populations will be indicated by negative values and growing populations by positive values. A
negative r value if sustained will always lead eventually to the extinction of the population being simulated. Recommended management actions are intended to reverse negative values. The time interval required for the final extinction of the last population may be quite long depending upon the value of r, the size of the initial population, and the life expectancy of the species.

The probability of extinction, P(E), is a measure of the extinction risk (or the probability of survival) over the specified time interval, in the case of this report this is 100 years. A value of zero may be obtained in the face of declining populations simply because the negative growth rate is relatively low, the bonobos have a relatively long life expectancy, and the initial population size is relatively large. Thus starting populations of 3,000 will survive for much longer time intervals than starting populations of 300 or 30 at the same rate of decline. The challenge posed for detecting these declines is that census and survey methodologies have relatively large confidence limits. Thus detecting a 1% rate of decline (or increase) with annual fluctuations with methods that have 20% margins of error may require many years and relatively large sample sizes and consistent methods with known accuracy and precision – conditions rarely met. These considerations are of importance for the bonobo because of the low rates of increase (1–2%) that appear possible even under optimal conditions. Depleted populations with available habitat will take a long time to recover by manager time scales.

Mean population numbers (N) provide a useful indicator of the direction and rate of change of simulated populations over time. In this case with 100 time intervals it is possible to see that a under a given set of conditions populations are either unstable or declining. Small population sizes greatly increase the risk of extinction because of the variations that occur from year to year and the risk that several years of bad luck or a single catastrophic event may result in extinction. This is readily seen in these scenarios with comparisons of starting population sizes of 30 with those of 300 or 3,000 under the same set of starting conditions.

**Base Scenario**

A base scenario was built from information collected in the plenary session and then developed further in the working group. However, it must be emphasized that much field distribution and demographic information was not available or had not been prepared properly for analysis in this workshop. The field studies have not had the collection of demographic information as a primary or even intended purpose. This means that observational data need to be examined in detail with demographic questions in mind. Means need to be recalculated as annual rates with standard deviations to provide estimates of environmental (and methodological) variation and to allow examination for unusual event years that may reflect catastrophic events. This kind of analysis has not been done for any of the bonobo data and we were able to make only crude estimates during the workshop. It is our impression that there are substantial observational data potentially available that might contribute to such an analysis and that this analysis needs to be a priority.

The base scenario developed had the following global and local parameter values: The simulations were for 100 years with 200 repetitions; inbreeding depressions was not included; the maximum age of reproduction was 40 years; a single population was modeled (no metapopulations); density dependence was included with values of 25% and 21.7% for proportion of females breeding; litter size = 1; sex ratio at birth = 1:1; K was set at 3,000 in all
scenarios with no variation or change; age of first reproduction = 15 years for males and females; starting population sizes of 3,000, 300, or 30; the mortality rate schedule was the same for both sexes, with annual mortality of 4.0% for 0-7 years of age, 4.6% for subadults (8-14 years of age), and 4.0% for adults.

For sensitivity analyses the age of first reproduction was varied from 15 to 14, and 13, adult mortality rates of 2, 4, and 7%; 0-1 year mortality rates of 4, 6, and 8%, and addition of a single catastrophe with frequency of 14.7%, no effects on reproduction, and a 15% increase in mortality rates (severity = 0.85).

This base scenario yielded growth rates close to zero at all three initial population sizes, Table 1, lines 2, 5, and 8. This set of values may approximate present conditions with adult mortality increased above ‘natural’ levels by hunting or other human induced disruptions and removals. These conditions are only approximately stable as evidenced by a P(E) of .015 in the smallest population. Any increase in mortality or reduction in reproduction would result in negative growth rates and declining populations with eventual extinction of the even the largest population. The long time required for complete extinction of all simulated populations was noted by Furuchi in analyses undertaken after the workshop (Appendix I).

Reduction of adult mortality to 2%, which may be closer to natural levels, (Table 1, lines 1, 4, and 7), produced positive growth rates and a near tripling in population size over 100 years for those populations not limited by the set carrying capacity of 3,000. The population doubling time at a 1% growth rate is about 70 years. An increase of adult mortality to 7% (Table 1, lines 3, 6, and 9) resulted in negative growth rates in all scenarios and population declines.

Table 1. Effects of adult female mortality rates on mean stochastic population growth rate, mean final population size, and probability of extinction after 100 years. The 0-1 year mortality rate was set at 4%, the age of first reproduction at 15 years, and no catastrophes were included. Carrying capacity K is 3000 in all scenarios. All other parameter values were those of the base scenario described in the text. The results presented are mean stochastic population growth rate, mean final population size, and probability of extinction after 100 years of simulation.

<table>
<thead>
<tr>
<th>Variable Conditions</th>
<th>Results – 100 Years</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>File</td>
</tr>
<tr>
<td>1. H.040</td>
<td>2%</td>
</tr>
<tr>
<td>2. O.040</td>
<td>4</td>
</tr>
<tr>
<td>3. G.040</td>
<td>7</td>
</tr>
<tr>
<td>4. H.043</td>
<td>2</td>
</tr>
<tr>
<td>5. O.043</td>
<td>4</td>
</tr>
<tr>
<td>6. G.043</td>
<td>7</td>
</tr>
<tr>
<td>7. H.043</td>
<td>2</td>
</tr>
<tr>
<td>8. O.043</td>
<td>4</td>
</tr>
<tr>
<td>9. G.043</td>
<td>7</td>
</tr>
</tbody>
</table>
A check on the approximation of the parameter values to conditions in the wild population is available from a comparison of the simulated age and sex structures with those reported for the wild populations (1995 report). The proportion of infants in the population is reported as 5.2% and the model estimates 5.0%.

Variation in first year mortality rates from 4 – 8% were tested for their effects on population growth rates with adult mortality at 2%. There was a small effect on population growth rates and final mean population sizes of doubling the infant mortality rate under these conditions. This was only detectable at the lower starting population sizes (Table 2). A doubling of infant mortality changed ‘r’ by 0.001 whereas a doubling of adult female mortality decreased ‘r’ by about 0.009. This result indicates that increased loss of females from a bonobo population requires special attention for risks of population extinction.

**Table 2.** Effects of first year mortality rates on mean stochastic population growth rate, mean final population size, and probability of extinction after 100 years. The adult mortality rate was set at 2%, the age of first reproduction at 15 years, and no catastrophes were included. Carrying capacity K is 3000 in all scenarios. All other parameter values were those of the base scenario (Table 1).

<table>
<thead>
<tr>
<th>File</th>
<th>0-1 Mortal.</th>
<th>Initial N</th>
<th>r(stoc)</th>
<th>N</th>
<th>P(E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>H.040</td>
<td>4%</td>
<td>3000</td>
<td>.006</td>
<td>2957</td>
<td>0</td>
</tr>
<tr>
<td>I.0400</td>
<td>6</td>
<td>3000</td>
<td>.005</td>
<td>2955</td>
<td>0</td>
</tr>
<tr>
<td>J.040</td>
<td>8</td>
<td>3000</td>
<td>.004</td>
<td>2952</td>
<td>0</td>
</tr>
<tr>
<td>H.043</td>
<td>4</td>
<td>300</td>
<td>.011</td>
<td>893</td>
<td>0</td>
</tr>
<tr>
<td>I.043</td>
<td>6</td>
<td>300</td>
<td>.010</td>
<td>827</td>
<td>0</td>
</tr>
<tr>
<td>J.043</td>
<td>8</td>
<td>300</td>
<td>.009</td>
<td>753</td>
<td>0</td>
</tr>
<tr>
<td>H.043</td>
<td>4</td>
<td>30</td>
<td>.010</td>
<td>95</td>
<td>0</td>
</tr>
<tr>
<td>I.043</td>
<td>6</td>
<td>30</td>
<td>.009</td>
<td>83</td>
<td>0</td>
</tr>
<tr>
<td>J.043</td>
<td>8</td>
<td>30</td>
<td>.008</td>
<td>75</td>
<td>0</td>
</tr>
</tbody>
</table>

**Table 3.** Effects of inclusion of a single a catastrophe on bonobo population dynamics with all other parameter values the same as in Table 2. The catastrophe had a frequency of 14.7% (approximately 7 year interval but stochastic), no effect on reproduction, and a 0.85 severity on survival (15% decrease in survival across all age classes). First year mortality rates were variable at 4 or 6 or 8%. The adult mortality rate was set at 2%, the age of first reproduction at 15 years. Carrying capacity K is 3000 in all scenarios. All other parameter values were those of the base scenario (Table 1).

<table>
<thead>
<tr>
<th>File</th>
<th>0-1 Mortal.</th>
<th>Initial N</th>
<th>r(stoc)</th>
<th>N</th>
<th>P(E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>H.058</td>
<td>4%</td>
<td>3000</td>
<td>-.015</td>
<td>778</td>
<td>0</td>
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<tr>
<td>I.058</td>
<td>6</td>
<td>3000</td>
<td>-.015</td>
<td>709</td>
<td>0</td>
</tr>
<tr>
<td>J.058</td>
<td>8</td>
<td>3000</td>
<td>-.016</td>
<td>678</td>
<td>0</td>
</tr>
<tr>
<td>H.061</td>
<td>4</td>
<td>300</td>
<td>-.022</td>
<td>42</td>
<td>.01</td>
</tr>
<tr>
<td>I.061</td>
<td>6</td>
<td>300</td>
<td>-.023</td>
<td>43</td>
<td>.02</td>
</tr>
<tr>
<td>J.061</td>
<td>8</td>
<td>300</td>
<td>-.022</td>
<td>42</td>
<td>.03</td>
</tr>
<tr>
<td>H.064</td>
<td>4</td>
<td>30</td>
<td>-.015</td>
<td>14</td>
<td>.33</td>
</tr>
<tr>
<td>I.064</td>
<td>6</td>
<td>30</td>
<td>-.019</td>
<td>13</td>
<td>.50</td>
</tr>
<tr>
<td>J.054</td>
<td>8</td>
<td>30</td>
<td>-.017</td>
<td>14</td>
<td>.42</td>
</tr>
</tbody>
</table>
The addition of a single catastrophe (occurring on average every seven years and affecting only mortality with a 15% mortality increase) to the scenarios with 2% adult mortality resulted in negative growth rates for all of the populations (Table 3) including the base scenarios (lines 1, 4, and 7). Extinction probabilities have increased substantially and population sizes declined from the initial levels and extinction for all simulations would eventually result. Bonobo populations cannot sustain this level of loss.

The age of first reproduction was suggested in the 1995 report to be 14 years rather than the 15 years we used in these analyses. The potential impact of variations in this parameter was examined in the scenario with 4% adult mortality, 4% first year mortality, and no catastrophes which produces approximately zero ‘r’ values. Reduction by one year yielded an increase in ‘r’ of 0.003 and higher final mean population sizes at 100 years. The average lower age of first reproduction might occur in populations at low densities relative to habitat carrying capacity.

Table 4. Effects of age of first reproduction on mean stochastic population growth rate, mean final population size, and probability of extinction after 100 years. The 0-1 year mortality rate was set at 4%, the adult mortality rate at 4%, and no catastrophes were included. Carrying capacity K is 3000 in all scenarios. All other parameter values were those of the base scenario (Table 1).

<table>
<thead>
<tr>
<th>Variable Conditions</th>
<th>Results – 100 Years</th>
</tr>
</thead>
<tbody>
<tr>
<td>File Age First Reproduction</td>
<td>Initial N</td>
</tr>
<tr>
<td>O.040 15 3000</td>
<td>-.002</td>
</tr>
<tr>
<td>O.041 14 3000</td>
<td>.000</td>
</tr>
<tr>
<td>O.042 13 3000</td>
<td>.002</td>
</tr>
<tr>
<td>O.043 15 300</td>
<td>.002</td>
</tr>
<tr>
<td>O.044 14 300</td>
<td>.005</td>
</tr>
<tr>
<td>O.045 13 300</td>
<td>.008</td>
</tr>
<tr>
<td>O.046 15 30</td>
<td>.000</td>
</tr>
<tr>
<td>O.047 14 30</td>
<td>.003</td>
</tr>
<tr>
<td>O.048 13 30</td>
<td>.006</td>
</tr>
</tbody>
</table>

Given the sensitivity of the bonobo population dynamics to adult female mortality, what is the effect of removing females from populations of different sizes? Given the approximate proportion of adult females as 25% then it is possible to estimate how many additional females need to be removed to increase the mortality rate from 2 to 4 to 6%. The population will grow at 2%, be approximately stable at 4% and decline at 6% adult female mortality. The loss of an additional female every two years from a population of 30 is sufficient to guarantee its extinction (Table 5). A loss of only 1.5 to 3.0 additional females per year from a population of 300 will produce a negative population growth rate and eventual extinction (Table 5). These estimates indicate that bonobo populations cannot sustain even what might appear to be small additional losses on a continuing basis. The numbers can also assist design of the management scenarios needed to sustain viable wild populations over the long term. This rate of change is not measurable with the census techniques being used over short research time periods.
Table 5. Expected numbers of adult female bonobos dying per year, as a function of population size, at three rates of mortality. About 23% of the population is expected to be adult females. (About 5% of the population is expected to be in the 0-1 year age class). Removal of about 3 adult females per year, above natural mortality, from a population of 300 bonobos would increase the adult female mortality from 2 to 6% (an increase of 4%) and produce a negative growth rate of about 1% per year.

<table>
<thead>
<tr>
<th>Pop Size (N)</th>
<th>#Adult Fems.</th>
<th>2%</th>
<th>4%</th>
<th>6%</th>
</tr>
</thead>
<tbody>
<tr>
<td>3000</td>
<td>750</td>
<td>15</td>
<td>30</td>
<td>45</td>
</tr>
<tr>
<td>300</td>
<td>75</td>
<td>1.5</td>
<td>3.0</td>
<td>4.5</td>
</tr>
<tr>
<td>30</td>
<td>7.5</td>
<td>.15</td>
<td>.3</td>
<td>.45</td>
</tr>
</tbody>
</table>

Suggested Actions / Recommendations:

- Collect demographic information that is needed
- Conduct surveys:
  - determine degree of fragmentation
  - coordinate methods
  - investigate/evaluate priorities that have been indicated in the 1995 Action Plan
- Evaluate (review literature?) the impact of presence of researchers on female migration and group size (in the context of cost-benefit of having researchers in the wild vs. conservation);
- Educate about different population effects of commercial hunting and hunting for subsistence;
- Get logging rate [area / time] from the logging company.

Who will do what?

- Barbara Fruth: Coordinate methodology
- Jef Dupain: Information on logging companies
- Sue Savage: Satellite maps
- Kano/Furuichi: Research on effect of research on primate population
- Everybody: Educate
References


Bonobo Conservation Assessment

Workshop Report

Section V
Workshop Participants
### Bonobo Conservation Assessment Workshop

**List of Participants**

<table>
<thead>
<tr>
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</thead>
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Appendix II:
Update of status of pending survey of the Salonga National Park
(Fax transmission sent to Inuyama by Project Coordinator Gay Reinartz)

I have some bonobo sighting data for the Salonga’s north sector taken during a preliminary
reconnaissance to the park – please note that these data are so few, that no statistically valid density
estimates can be obtained (contrary to unauthorized reports). Nevertheless, we are preparing the data into
a preliminary note for publication. For purposes of the workshop, I can say from our analyses of
encounter rates taken by Inogwabini Bila Isia that signs of poaching along access routes in Salonga are as
numerous as sings of large mammals. Bonobo nest sights were encountered, thus confirming a resident
population in the northeast portion of the northern sector- density appears to be low, but we refrain from
actual estimates.

Our future plans:
Zoological Society of Milwaukee Programs in Congo (as announced at IPS Congress 1996):
(1) Survey of Pan paniscus: The most urgent conservation need for the bonobo is to obtain critical
information on the distribution and size of wild bonobo populations - only then will it be possible to
develop an effective conservation strategy to protect the species. Therefore, in 1997 in collaboration with
the Institut Congolais pour la Conservation de la Nature (ICCN) and Zoo Atlanta’s Africa Biodiversity
Program, the ZSM launched the first regional quantitative survey to determine the status of bonobos in
the Salonga National Park, Democratic Republic of Congo. The Salonga, the only federally protected
area for the bonobo, was created in 1970 specifically to protect bonobos, but it has never been determined
whether a sustainable population actually lives there. The Salonga represents one of Africa’s most
important regions of biodiversity and harbors many species of conservation concern. Preservation of
bonobos in the Salonga and elsewhere in Congo means protection of a broad range of rare, endemic or
threatened species.

The first phase of this project, a reconnaissance of the Salonga’s northern sector completed in
1998, verified the existence of bonobos within the Salonga north sector and the feasibility of a
comprehensive survey. The next phase, the full-scale survey, will span approximately 12-18 months and
will use the latest techniques in wildlife surveys to estimate bonobo density throughout sectors of the
park. The survey will lay groundwork for regional bonobo population monitoring and will serve as a
model for future surveys needed throughout the bonobo’s range. Delayed by the civil war, the fieldwork
will resume as soon as possible when peace returns to the region. In the meantime, we continue
fundraising efforts to ensure as early a start date as possible.

(2) Training Field Biologists: In order for the Congolese to lead bonobo conservation efforts and make
informed decisions, they must be given technical training in biological inventory and wildlife surveys.
Therefore, in tandem with the survey, up to 20 Congolese trainees, 9 or more will be chosen to conduct
the survey. Such skills are the basis for and effective wildlife-monitoring program and can be transferred
to other species and conservation sites. Support and collaboration with ICCN: The ZSM currently
supplies direct technical and financial assistance to the ICCN central office with oversight by the German
Technical Cooperation and provides information relevant to conservation and the Salonga National Park
Moreover, as an ICCN partner we are providing direct field expertise to survey elephants during the
bonobo survey as part of the international program, Monitoring of Illegal Killing of Elephants
(CITES/IUCN).

(3) Habitat Protection: The Salonga National Park is currently receiving little or no financial support
because of the war currently underway in the Congo. The ZSM is exploring means to help support
approximately 50 park guards for one year and pay an equivalent of their annual salary. Remote Sensing
Study: As part of the survey, the ZSM is collaborating with the University of Maryland to conduct a vegetation analysis of satellite images of the Salonga region. From these studies, we develop a tool to identify the forest types in which bonobos and other large mammals most likely occur. Once forest types are verified over the course of the field survey, we will be able to extrapolate these findings to predict the occurrence of species throughout their range. The satellite images are also important to monitor forest degradation and human impact. At the moment, war is escalating and there is heavy fighting reported in the region of Basankusu, Boende, and the east. The Salonga appears to be nearly surrounded by the rebel advance.

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Zoological Society of Milwaukee
Appendix III:
T. Furuichi and C. Hashimoto Post-Workshop Modeling Report

Procedure and results

1. Making a basic model
First we set the initial population to 3000 and carrying capacity to 6000 while assuming a contiguous population around the Luo Reserve. We set the basic parameters, including birth rate, mortality, age at first birth, to those obtained from the study at Wamba, without any catastrophe (Table 1, List 1, see Furuichi et al., 1998, IJP). This model showed a slight increase to reach the carrying capacity.

Then we adjusted the probability and severity of catastrophe 1 (bad year) so that the population is kept at a stable level around 3000 (Fig. 1, Base 3000). We used this "Base 3000" model as the basic model for the following analyses.

2. Effect of initial population
To examine effects of the initial population size, we changed the initial population size to 300 and 30, while keeping other parameters as same as the basic model (Table 1, Fig. 1). Models Base 3000 and Base 300 were endurable for at least 1000 years, but the Base 30 model might extinct within 100 years and had to be extinct within 600 years.

3. Effect of bad years
We examined the effect of bad years, while changing its probability of occurrence and severity (Table 1, Fig. 2). In the "frequent" model, the population size decreased but it did not become extinct within 1000 years. However, the "severe and frequent" model became extinct within 600 years.

4. Effect of human impact
We examined the effects of human impact, such as the continuous small-scaled hunting by local people, and the large-scaled hunting during the war (Table 1, Fig. 3). Although we assumed a moderate impact (1% decrease of survivorship) in the continuous hunting model, the population decreased rapidly and became extinct within 1000 years. For the war model, we assumed the catastrophe would occur once a 7 years and decreased the survivorship by 20%. In this model, the population decreased much more rapidly, and became extinct within 300 years.

5. Single vs. Metapopulation
All the above mentioned models assumed a single population. To examine the difference in robustness between a single and meta-population, we compared two models: single population of 300 individuals and meta population of 10 groups of 30 individuals between which females transfer at the age of 7 to 9 years old, both with the catastrophe by wars (Table 1, Fig. 4). Though there was no big difference, the metapopulation model showed more quick decrease and extinction.
### Parameters in each model

<table>
<thead>
<tr>
<th>Models</th>
<th>N₀</th>
<th>K**</th>
<th>Probability of occurrence</th>
<th>Effect on birth rate</th>
<th>Effect on survival</th>
<th>Probability of occurrence</th>
<th>Effect on birth rate</th>
<th>Effect on survival</th>
<th>Population and environment assumed</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Base model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Base 3000</td>
<td>3000</td>
<td>6000</td>
<td>10%</td>
<td>-5%</td>
<td>-2%</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>A contiguous population around the Luo Reserve</td>
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<tr>
<td><strong>Comparison on initial population</strong></td>
<td></td>
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<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Base 300</td>
<td>300</td>
<td>600</td>
<td>10%</td>
<td>-5%</td>
<td>-2%</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>10 groups</td>
</tr>
<tr>
<td>Base 30</td>
<td>30</td>
<td>600</td>
<td>10%</td>
<td>-5%</td>
<td>-2%</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1 group</td>
</tr>
<tr>
<td><strong>Comparison on bad years</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequent</td>
<td>3000</td>
<td>6000</td>
<td>20%</td>
<td>-5%</td>
<td>-2%</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Rainforest with a bit severe environmental fluctuation</td>
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<tr>
<td>Severe &amp; fr</td>
<td>3000</td>
<td>6000</td>
<td>20%</td>
<td>-10%</td>
<td>-4%</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Marginal area of rainforest to savanna-woodland</td>
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<td><strong>Comparison on Human impact</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>War</td>
<td>3000</td>
<td>6000</td>
<td>10%</td>
<td>-5%</td>
<td>-2%</td>
<td>15%</td>
<td>-</td>
<td>-20%</td>
<td>Large-scaled hunting during the war etc.</td>
</tr>
<tr>
<td>Hunting</td>
<td>3000</td>
<td>6000</td>
<td>10%</td>
<td>-5%</td>
<td>-2%</td>
<td>100%</td>
<td>-</td>
<td>-1%</td>
<td>Continuous small-scaled hunting by local people</td>
</tr>
<tr>
<td><strong>Comparison between single and meta-population</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Single</td>
<td>30</td>
<td>600</td>
<td>10%</td>
<td>-5%</td>
<td>-2%</td>
<td>15%</td>
<td>-</td>
<td>-20%</td>
<td>10 groups between which females age 7 to 9 transfer</td>
</tr>
<tr>
<td>Meta</td>
<td>0 x 10</td>
<td>600</td>
<td>10%</td>
<td>-5%</td>
<td>-2%</td>
<td>15%</td>
<td>-</td>
<td>-20%</td>
<td></td>
</tr>
</tbody>
</table>

* Initial Population Size

** Carrying Capacity
Figure 1. Effect of Initial Population

Figure 2. Effect of Catastrophe 1 (Bad Year)

Figure 3. Effect of Catastrophe 2 (Human Impact)
Figure 4. Robustness of single population model and metapopulation model against the “war” catastrophe.

Sample VORTEX Input File

```
TEST.OUT  ***Output Filename***
Y  ***Graphing Files?***
N  ***Details each Iteration?***
20 ***Simulations***
1000 ***Years***
10 ***Reporting Interval***
0 ***Definition of Extinction***
1 ***Populations***
N ***Inbreeding Depression?***
N ***EV concordance between repro and surv?***
2 ***Types Of Catastrophes***
P ***Monogamous, Polygynous, or Hermaphroditic***
14 ***Female Breeding Age***
14 ***Male Breeding Age***
40 ***Maximum Breeding Age***
50.000000 ***Sex Ratio (percent males)***
1 ***Maximum Litter Size (0 = normal distribution) *****
Y  ***Density Dependent Breeding?***
Basic
24.700000 ***Density dependence term P(0)***
18.700000 ***Density dependence term P(K)***
2.000000 ***Density dependence term B***
1.000000 ***Density dependence term A***
5.80 ***EV-breeding***
4.000000 *FMort age 0
1.100000 ***EV
4.000000 *FMort age 1
1.100000 ***EV
4.000000 *FMort age 2
1.100000 ***EV
4.000000 *FMort age 3
1.100000 ***EV
4.000000 *FMort age 4
1.100000 ***EV
4.000000 *FMort age 5
1.100000 ***EV
4.000000 *FMort age 6
```
Sample VORTEX Input File (Contd.)

4.600000 *FMort age 7
1.200000 ***EV
4.600000 *FMort age 8
1.200000 ***EV
4.600000 *FMort age 9
1.200000 ***EV
4.600000 *FMort age 10
1.200000 ***EV
4.600000 *FMort age 11
1.200000 ***EV
4.600000 *FMort age 12
1.200000 ***EV
4.600000 *FMort age 13
1.200000 ***EV
4.000000 *Adult FMort
1.100000 ***EV
4.000000 *MMort age 0
1.100000 ***EV
4.000000 *MMort age 1
1.100000 ***EV
4.000000 *MMort age 2
1.100000 ***EV
4.000000 *MMort age 3
1.100000 ***EV
4.000000 *MMort age 4
1.100000 ***EV
4.000000 *MMort age 5
1.100000 ***EV
4.000000 *MMort age 6
1.100000 ***EV
4.600000 *MMort age 7
1.200000 ***EV
4.600000 *MMort age 8
1.200000 ***EV
4.600000 *MMort age 9
1.200000 ***EV
4.600000 *MMort age 10
1.200000 ***EV
4.600000 *MMort age 11
1.200000 ***EV
4.600000 *MMort age 12
1.200000 ***EV
4.600000 *MMort age 13
1.200000 ***EV
4.000000 *Adult MMort
1.100000 ***EV
10.000000 ***Probability Of Catastrophe 1***
0.950000 ***Severity--Reproduction***
0.980000 ***Severity--Survival***
0.000000 ***Probability Of Catastrophe 2***
Y ***All Males Breeders???
Y ***Start At Stable Age Distribution???
3000 ***Initial Population Size***
6000 ***K***
0.000000 ***EV--K***
N ***Trend In K???
N ***Harvest???
N ***Supplement???
N ***AnotherSimulation???