Western Gorilla (Gorilla gorilla)

Appendix 1

Supplementary documentation for Gorilla gorilla Red List assessment

Based on correspondence from Damien Caillaud to Liz Williamson (5th May 2007):
Generation length of Gorilla gorilla gorilla Maya Nord, Congo = 22 years

A method to estimate the generation time of Western Lowland Gorilla is outlined below.

The main issue is the lack of long-term data on this species. The longest, ongoing study
is Mbëli Baï, launched in 1995. Some life history trait estimates from this population (and
also from habituated groups and from Maya Nord population) were published in 2004
(Robbins et al., Int. J. Prim.). Though this publication does not provide estimates of adult
mortality, which would be necessary to estimate the mean generation time, it gives
some interesting evidence that inter-birth interval could be longer in Western Gorilla than
in Mountain Gorilla. As in mammals inter-birth interval is positively correlated with life
expectancy, this observation could indicate that the generation time may be longer in
Western Lowland Gorilla than in Mountain Gorilla.

So, which available dataset may be useful to estimate Western Lowland Gorilla adult
survival and some other life history traits? Does longitudinal observation data constitute
the only source of information? Under the main assumption that the few populations
studied in clearings are demographically stable (i.e., their structure has reached an
equilibrium and does not change with time anymore), we can imagine that population
structure data conveys information concerning the life history traits they result from. D.
Caillaud has developed a method to extract this (life history) information, using a
Bayesian statistical method that has been developed in population genetics (which is not
strange since one of the aims of population genetics is to infer historical events from
cross sectional data, namely DNA sequences). The purpose of Caillaud’s work was
mainly to estimate age-specific migration parameters in Western Lowland Gorilla, but it
was also used to estimate age-specific survivals.

This work used the population structure data from Lokoué: 365 individuals observed
from October 2003 to January 2004 (just before the Ebola outbreak). However, as a part
of this dataset is useless to answer the question we are interested in here (composition
of each group or number of adult males for example), Caillaud simplified it. The other
published population structure data from Mbëli (Parnell 2002, Am. J. Prim.) and Maya
Nord (Magliocca et al. 1999) was also included. Finally, the method was simplified,
giving up the Bayesian algorithm as it is not necessary to estimate the generation time.
The assumptions made to estimate the adult female survival are:

- The populations are demographically stable.

- It is assumed initially that individuals could be assigned one of the following age classes: infant (< 3.5 years), juveniles (< 6 years), subadult (< 8 years) and adult (≥ 8 years). The infant age class is slightly extended.

- The annual survival of adult females varies according to their age (senescence). It is assumed that this variation follows the same pattern as that observed in Mountain Gorillas (Robbins and Robbins 2005, agent based model). This does not mean that the age specific survivals are assumed to be the same, but that the decrease of the annual survival is assumed to follow a similar pattern (notably with a max age of 40 years).

- The sex-ratio of immatures (namely, infants+juv+subadults) is 1.

- The survival of infants (to the age of 3) varies between 0.3 and 0.5 (following Robbins et al. 2004).

- The survival of juveniles equals the survival of subadults. This assumption would not be necessary if we knew exactly at what age juveniles become subadults. The 6 years transition age will probably be revised in a next future (or the morphological criteria it is based on).

Caillaud also first assumed that the transition age between infants and adults was 8 years old. However this assumption led to an important site-dependant variation of the adult survival estimates, which is interpreted as an effect of the observer (as this variation is very large, it is very unlikely to be a consequence of ecological difference). The morphological criteria currently used are probably not reproducible enough (i.e, they are too subjective). Basically, it seems that Caillaud’s morphological criteria imply a transition age of 7 years rather than 8 years at Lokoué, and an inverse bias at Mbeli, where the subadult-adult transition age seems to be 9 years. Maya Nord seems somewhere between 8 and 9 year. So Caillaud chose to suppress the distinction between subadults and adults, and set the annual immature survival probability to an arbitrary but plausible value of 0.95 (0.98 was also tested). The results were as follows:

**Case 1:** Infant survival probability to the age of 3 equals 0.7, juv and sub annual survival probability both equal 0.98.

<table>
<thead>
<tr>
<th>infancy duration</th>
<th>3.5 years</th>
<th>4 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>model1</td>
<td>19.8</td>
<td>20.8</td>
</tr>
<tr>
<td>model2</td>
<td>20.1</td>
<td>21.1</td>
</tr>
<tr>
<td>model3</td>
<td>20.4</td>
<td>21.3</td>
</tr>
</tbody>
</table>

**Case 2:** Infant survival probability to the age of 3 equals 0.7, juv and sub annual survival probability both equal 0.95.
<table>
<thead>
<tr>
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<th>4 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>model1</td>
<td>21.0</td>
<td>22.0</td>
</tr>
<tr>
<td>model2</td>
<td>21.2</td>
<td>22.1</td>
</tr>
<tr>
<td>model3</td>
<td>21.4</td>
<td>22.3</td>
</tr>
</tbody>
</table>

**Case 3:** Infant survival probability to the age of 3 equals 0.5, juv and sub annual survival probability both equal 0.98.

<table>
<thead>
<tr>
<th>infancy duration</th>
<th>3.5 years</th>
<th>4 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>model1</td>
<td>20.8</td>
<td>21.7</td>
</tr>
<tr>
<td>model2</td>
<td>21.4</td>
<td>22.2</td>
</tr>
<tr>
<td>model3</td>
<td>21.9</td>
<td>22.6</td>
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</table>

**Case 4:** Infant survival probability to the age of 3 equals 0.5, juv and sub annual survival probability both equal 0.95.

<table>
<thead>
<tr>
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<th>3.5 years</th>
<th>4 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>model1</td>
<td>21.9</td>
<td>22.8</td>
</tr>
<tr>
<td>model2</td>
<td>22.4</td>
<td>23.2</td>
</tr>
<tr>
<td>model3</td>
<td>22.8</td>
<td>23.5</td>
</tr>
</tbody>
</table>

The above tables provide estimates of the mean age of females aged 10 years or more, obtained using population structure data from 3 sites (Lokoué, Mbeli, MayaN). The 3 models denoted model1, model2 and model3 correspond to three different ways to parameterize the survivals of the immature individuals. Caillaud also tested two durations for the infant age class (3.5 and 4 years). The generation time estimates, defined as the mean age of females aged 10+, range from 20.8 to 23.5 years.

Caillaud therefore advises using **22 years** as the (temporary) reference value for the generation time of Western Lowland Gorilla.

It is important to note that that these estimates mainly rely on three assumptions. The first is that the populations are demographically stable. The second is that the decrease of adult female survival depends on their age in a similar pattern to that observed in *G. beringei beringei*. The third is that the duration of the infant age class varies between 3.5 and 4 years. Among these three assumptions, the second one is the most likely to be invalidated in the future. The maximum life duration is indeed likely to differ among the two gorilla species.

**References**