Available online at www.sciencedirect.com
SCIENCE DIRECT®
Biological Conservation 123 (2005) 461–475
BIOLOGICAL CONSERVATION
www.elsevier.com/locate/biocon

# Survival, interactions with conspecifics and reproduction in 37 chimpanzees released into the wild

B. Goossens [a,b,*,1], J.M. Setchell [c,1], E. Tchidongo [b], E. Dilambaka [b], C. Vidal [b], M. Ancrenaz [d], A. Jamart [b]

[a] *Biodiversity and Ecological Processes Group, Cardiff School of Biosciences, Cardiff University, P.O. Box 915, Cathays Park, Cardiff CF10 3TL, UK*
[b] *Habitat Ecologique et Liberté des Primates (HELP) Congo, BP 335, Pointe Noire, Republic of Congo*
[c] *Department of Biological Anthropology, University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK*
[d] *Kinabatangan Orangutan Conservation Project, P.O. Box 3109, 90734 Sandakan, Sabah, Malaysia*

Received 7 April 2004

**Abstract**

We report the results of eight years of post-release monitoring of 37 wild-born, captive chimpanzees released into the Conkouati-Douli National Park, Republic of Congo. Overall survival was high, with 23 (62%) individuals remaining in the release zone, and only 5 (14%) confirmed dead. Released females regularly interacted with wild chimpanzees. Several females appeared to have integrated into wild groups for extended periods of time, and four released females gave birth to a total of five offspring. However, encounters with wild chimpanzees were a major cause of mortality in released males, and 40–50% of released males would have died without veterinary intervention. These sex differences are in accordance with knowledge of chimpanzee behavioural ecology. Our results demonstrate that wild-born, captive chimpanzees can be released into the wild successfully, under certain specific conditions. Most importantly, careful planning and preparation is critical at all stages; a suitable release area must be identified; potential risks to existing wild populations, including the possibility of disease transmission, must be minimised; and post-release monitoring is essential. Adolescent females are the most suitable candidates for release, as they appear to be able to integrate successfully into wild communities. However, males should not be released where wild chimpanzees occur, as they are likely to be attacked and killed. Release into the wild addresses the welfare of certain individual animals, although it clearly cannot address the fate of all captive, wild-born chimpanzees. Knowledge of how to successfully release chimpanzees into the wild also has both current and potential future benefits for the conservation of wild chimpanzee populations.


*Keywords:* *Pan troglodytes troglodytes*; Post-release monitoring; Social integration; Survival; Translocation

## 1. Introduction

World Conservation Union (IUCN) guidelines require that wildlife release projects must make a positive contribution to species survival in the wild (IUCN, 1998). They also emphasise the need for post-release monitoring to track the success of animal relocations (IUCN, 1998; see also Seddon, 1999). However, as is true for relocations in general (Fischer and Lindenmayer, 2000), few data exist examining the success of the release of non-human primates into the wild (Yaeger, 1997; Cowlishaw and Dunbar, 2000). In contrast to conservation-oriented relocations, the majority of primate releases occur in response to the ethical problem of orphan animals (compassionate releases), or because the

* Corresponding author. Tel.: +44 292 087 5073; fax: +44 292 087 4305.
*E-mail address:* goossensbr@cardiff.ac.uk (B. Goossens).
[1] B.G. and J.M.S. contributed equally to the work.

0006-3207/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2005.01.008

population concerned is under threat (Hannah and McGrew, 1991; Cowlishaw and Dunbar, 2000). Such projects have different goals to those of standard conservation translocations, typically involving the welfare of the individual animals concerned, and should therefore be judged according to their specified aims (e.g., survival of released animals, successful adaptation to the new environment). If release into the wild fails to maintain or actively improve the welfare of previously captive individuals, then the continuation of the release programs should be questioned.

Throughout their range, African great apes are threatened by deforestation, hunting for bush-meat and disease outbreaks (e.g., Barnes, 2002; Fa et al., 2003; Walsh et al., 2003; Leroy et al., 2004). The large-bodied chimpanzee presents a good target for the hunter, bringing a high return on the price of a shotgun cartridge. However, their long generation time means that populations are unable to survive even low levels of hunting (Butynski, 2001; Tutin et al., 2001). Hunting pressure results in increasing numbers of orphaned infants and sanctuaries have been created in response to the plight of these orphan apes. There are presently 18 ape sanctuaries in Africa, housing more than 500 great apes (Farmer, 2002a). However, keeping chimpanzees in captivity represents a long-term commitment (the life expectancy of chimpanzees in captivity being about 45 years), associated with a high financial burden. Furthermore, many sanctuaries exist in politically unstable countries and a long-term solution is required to the problem of this expanding population of captive great apes.

Returning confiscated chimpanzees to the wild may be a possibility for some captive individuals (Tutin et al., 2001). However, the natural history of chimpanzees makes their reintroduction difficult. For example, a lengthy apprenticeship with adults is needed to acquire the appropriate behaviour to survive in the wild (Custance et al., 2002), and chimpanzees respond aggressively to strangers (Goodall, 1986). Although a few chimpanzee release projects have been carried out, with various degrees of success (Hladik, 1973; Brewer, 1978; Borner, 1985; Hannah and McGrew, 1991; Treves and Naughton-Treves, 1997), most of these concerned chimpanzees originating from laboratories or zoos released onto forested islands, rather than into the wild.

In this context, HELP (Habitat Ecologique et Liberté des Primates) Congo has developed a release and post-release monitoring program for captive, wild-born chimpanzees. The initial objective of HELP Congo was to investigate whether it was possible to return chimpanzees to their natural environment and how ape release could be used as a tool for conserving wild populations and their habitat. Although we are not at the stage yet where the wild chimpanzee population is so low that it needs to be supplemented with captive chimpanzees, knowledge of how to release chimpanzees successfully in the future should be obtained now, before it is urgently needed.

To this end, long-term monitoring protocols were established to measure the success of the release. The framework and decision process behind this project have been described previously, along with preliminary results concerning the short-term fate of the first 20 chimpanzees that were released between 1996 and 1999 (Tutin et al., 2001). Importantly, releases took place in a zone where there was an existing, but low density, population of wild chimpanzees.

Since 1999, HELP Congo has released an additional 17 orphan chimpanzees into the release site, and has continued to monitor all released animals closely. After seven and half years of post-release monitoring, we are now in a position to report the mid-term results of the release of a total of 37 chimpanzees. We present data concerning the immediate fate of released individuals, mid-term survival, interactions with conspecifics (both wild and released) and reproduction. We discuss our results, and examine the conditions necessary for successful release of chimpanzees into the wild, before broadening our discussion to examine how release programs can contribute to the conservation of wild chimpanzees.

## 2. Methods

### 2.1. Release site

The Conkouati-Douli National Park (CDNP, 3°33′–4°02′S; 11°10′–11°40′E) is situated in the Republic of Congo, on the border with Gabon, about 150 km north-west of Pointe Noire. The park covers an area of 500,000 ha with a mosaic of vegetation types from mangroves, raffia palms, swamp forests, permanently and seasonally flooded forests to dry closed-canopy forests and Marantaceae forests (Hecketsweiler and Mokoko Ikonga, 1991; Doumenge, 1992).

Chimpanzee releases took place in the Triangle, a 20-$km^2$ area within the CDNP, bounded by the Ngongo and Louvandzi rivers and the Conkouati lagoon. The rivers do not isolate the Triangle completely from the surrounding forests, as natural bridges allow animals to cross the rivers easily. In 1996, the population density of wild chimpanzees in the Triangle was estimated to be 0.17–0.33 individuals/$km^2$, or an average of 3–7 individuals using the site (Tutin et al., 2001). Other wild chimpanzees were also present in neighbouring areas, with access to the Triangle via the natural bridges. Despite the low density of chimpanzees, surveys of the Triangle showed a good availability of fruiting trees and other chimpanzee foods leading Tutin et al. (2001) to conclude that extra individuals could be introduced. Reasons for the low density of wild chimpanzees were unknown, but may have included past human hunting pressure.

### 2.2. Study animals

Between 1996 and 2001, HELP Congo released 32 chimpanzees into the Triangle, and four further individuals on the opposite bank of the Ngongo river, north of the Triangle (Table 1). Released individuals had previously spent several days to five years in captivity before arriving at HELP (Table 1). Animals aged less than three years were rehabilitated in a nursery before being released onto islands in the Conkouati lagoon, while older animals were transferred directly to the islands, where they were provisioned daily for between 4.5 and 11.5 years prior to release (Table 1). In January 2001, an additional young male was introduced into a previously released group, making the total number of released individuals 37. From 1994 to 2001, HELP Congo stopped taking in new orphan chimpanzees because the sanctuary had reached its full capacity. The 2001 release terminated the current phase of the release project, although post-release monitoring will continue for at least five to 10 years, to measure the adaptation of released individuals to their release environment, monitor female reproduction, and until males are of adult size and able to defend themselves during aggressive encounters with wild chimpanzees (Tutin et al., 2001).

In the interests of releasing a cohesive group of chimpanzees, and to maximise the overall success of the release, the decision was taken to release 10 males (aged 2–11 years), in addition to 27 females, despite the risk of attack by wild chimpanzees (see Section 4). Four reasons underlay this decision. First, the low density of wild chimpanzees meant that there was a possibility for the released chimpanzees to form a new community in an unsaturated territory. Second, one case of a juvenile male transferring with his presumed adolescent sister has been observed in the wild, and the young male was not attacked by resident males (Goodall, 1986), leading to the hope that adolescent males might be less at risk of attack than adult males. Third, all released animals were monitored daily following release. The presence of human observers should act to deter attack by unhabituated wild chimpanzees, and allow swift detection of any injuries, and veterinary intervention where necessary. Finally, the alternative future for the captive males in a politically unstable country was very unattractive.

### 2.3. Release methods

Chimpanzees were released in groups (one group of six, 2 groups of five and one group of three), pairs (7) or singly (3 cases) (Table 1). Larger groups were split into smaller groups for release and led to join their group-mates after release. No supplementary food was given to the released individuals.

Individuals to be released were initially held overnight in the release cage. This delay was designed to allow them to recover fully from anaesthesia, and to become familiar with their immediate surroundings prior to release. However, the delay also allowed time for the fully awake animals to panic. Moreover, previously released chimpanzees tend to arrive at the release area and become highly agitated, making the operation highly stressful. Immediate release improved this situation: individuals were less stressed, and quickly became involved in greeting previously released animals and investigating their new environment. Familiar Congolese research assistants were present throughout the release, to reassure the newly released chimpanzees, monitor their behaviour, and lead them to other released individuals if they were not already present.

### 2.4. Post-release monitoring, data collection and analysis

Thirty-four of 37 released chimpanzees were fitted with radio-collars (Telonics Inc., USA) prior to release (in three cases radio-collars could not be fitted as the necks of certain males were too large, meaning that collars could be easily removed). Following release, chimpanzees were followed from nest to nest, seven days a week, by a team of 12–18 Congolese field assistants and several expatriate volunteers. Data collected include female reproductive status, health status and interactions with wild conspecifics. Data concerning diet, activity budget, nesting and ranging behaviour are presented elsewhere (Farmer, 2002b; Vacher-Vallas et al., submitted). Direct contact between observers and chimpanzees was minimised to avoid disease transmission (Woodford and Rossiter, 1994; Cunningham, 1996). Released females were not followed closely when they were known to be associating with wild chimpanzees, to avoid (1) disturbing interactions between released individuals and non-habituated, wild individuals and (2) any habituation of wild chimpanzees in surrounding areas which may be subject to hunting (unlike the release zone itself, which is protected from hunting by the presence of the release project).

Survival of released chimpanzees was classified as confirmed death (remains positively identified), disappearance (disappeared and not seen again as of February 2004), and present in the release zone in February 2004 (including individuals that had disappeared for a period and subsequently returned). Survival was investigated using Kaplan–Meier survival analysis (SPSS 11.0) to estimate the time from release to death or disappearance in the presence of censored cases (cases for which disappearance has not been recorded, i.e., chimpanzees still present in the release site at the end of the study). Log-rank statistics were used to compare male and female survival.

Table 1
Details of released individuals, with their immediate and mid-term fate

| ID (code) | Sex | Date of birth (month/year) | Time in captivity (pre-HELP) | Time at HELP (pre-release) | Month/year of release | Age at release | Mode of release (nb of individuals) | Status in Feb 2004 | Comments |
|---|---|---|---|---|---|---|---|---|---|
| Jeannette (Je) | F | 06/88 | 2 months | 8.5 years | 11/96 | 8 years | In group (5) | Alive | |
| Yvette (Yv) | F | 01/87 | 5 years | 4.5 years | 11/96 | 9 years | In group (5) | Disappeared (07/02) | Lost collar |
| Choupette (Cho) | F | 01/89 | Few months | 6 years | 11/96 | 7 years | In group (5) | Alive | |
| Bounie (Bou) | F | 01/87 | 2 years | 4.5 years | 11/96 | 9 years | In group (5) | Alive | |
| Mekoutou (Me) | M | 06/90 | 1 year | 4.5 years | 11/96 | 6 years | In group (5) | Alive | |
| Rosette (Ro) | F | 01/90 | Days | 6.5 years | 01/97 | 7 years | In pair (with Fa) | Alive | Disappeared 10 months in 2003, reappeared in released group 01/04 |
| Fanny (Fa) | F | 01/90 | 2 years | 5 years | 01/97 | 7 years | In pair (with Ro) | Disappeared (01/97) | Lost collar |
| Caline (Cal) | F | 01/91 | 4 months | 4.5 years | 11/97 | 6 years | In group (6) | Disappeared (11/99) | Lost collar |
| Cabinda (Cab) | F | 03/90 | 4 months | 5.5 years | 11/97 | 7 years | In group (6) | Alive | Disappeared 04/02 for 21 months, observed with wild chimpanzees 14/11/03 |
| Kakamoueka (Ka) | F | 08/91 | 1–3 weeks | 5.5 years | 11/97 | 6 years | In pair (with Ny) | Disappeared (11/97) | Lost collar |
| Massabi (Ma) | F | 01/91 | 3 weeks | 5.5 years | 11/97 | 6 years | In group (6) | Alive | Disappeared 8 months in 2003, observed with wild chimpanzees 26/01/04 |
| Mossenjo (Mo) | F | 08/91 | ? | 5.5 years | 11/97 | 6 years | In group (6) | Disappeared (05/03) | No collar |
| Nyasha (Ny) | F | 09/91 | 2-3 | 5.5 years | 11/97 | 6 years | In pair (with Ka) | Disappeared (11/97) | Lost collar |
| Dolisie (Do) | M | 03/91 | 2 months | 5.5 years | 11/97 | 6 years | In group (6) | Dead (12/97) | Killed by wild chimpanzees |
| Hinda (Hi) | M | 03/91 | 6 months | 6 years | 11/97 | 6 years | In group (6) | Dead (07/00) | Killed by wild chimpanzees |
| Sophie (So) | F | 09/89 | 2 months | 8.5 years | 01/99 | 9 years | In group (5) | Disappeared (10/00) | |
| Agathe (Ag) | F | 02/90 | 2 months | 8.5 years | 01/99 | 9 years | In group (5) | Alive | |
| Valentine (Va) | F | 12/98 | Born on island | 2 months | 01/99 | 2 months | In group (5) | Dead (05/99) | Killed by wild chimpanzees |
| David (Da) | M | 01/89 | 3 months | 10 years | 01/99 | 10 years | In group (5) | Disappeared (05/99) | No collar, likely to be dead |
| Koutou (Ko) | M | 07/89 | 7 days | 9 years | 01/99 | 9 years | In group (5) | Alive | |
| Matalila (Mat) | F | 09/89 | 2 months | 11.5 years | 06/00 | 10 years | In pair (with Pe) | Alive | Disappeared 12 months in 2002, reappeared with wild chimpanzees 02/01/03, then back in release group |
| Chinois (Chi) | M | 06/89 | 1–2 months | 11.5 years | 06/00 | 11 years | Alone | Alive | |
| Perlette (Pe) | F | 03/90 | Days | 9.5 years | 06/00 | 10 years | In pair (with Mat) | Alive | |
| Lucie (Lu) | F | 10/90 | 1 week | 9.5 years | 07/00 | 9 years | Alone | Alive | |
| Louzolo (Lo) | M | 03/99 | Few months | None | 02/01 | 23 months | In a released group | Alive | |
| Tessie (Te) | F | 01/91 | 6 months | 8 years | 07/01 | 10 years | In pair (with Em) | Alive | |
| Emilie (Em) | F | 12/93 | 3 months | 6.5 years | 07/01 | 7 years | In pair (with Te) | Alive | |
| Bateko (Ba) | M | 06/92 | 4 months | 7 years | 07/01 | 9 years | In pair (with Mf) | Alive | |
| Mfoubou (Mf) | F | 01/93 | Few days | 8 years | 07/01 | 8 years | In pair (with Ba) | Alive | |
| Dimonika (Di) | F | 03/93 | Few days | 6.5 years | 07/01 | 8 years | In group (3) | Dead (05/03) | Drowned |
| Carine (Ca) | F | 04/95 | Few days | 6.5 years | 07/01 | | In group (3) | Alive | |
| Makabana (Mak) | F | 09/92 | 3 months | 7.5 years | 07/01 | 8 years | In group (3) | Dead (04/02) | Killed by released chimpanzees |
| Bilinga (Bi) | M | 07/93 | Few days | 7.5 years | 07/01 | 8 years | In pair (with De) | Alive | |
| Derek (De) | M | 09/94 | 2 months | 6.5 years | 07/01 | 7 years | In pair (with Bil) | Alive | |
| Cheyenne (Che) | F | 03/93 | 3 months | 6.5 years | 09/01 | 8 years | In pair (with Koui) | Alive | |
| Kouilou (Koui) | F | 01/91 | Few days | 7.5 years | 09/01 | 10 years | In pair (with Che) | Alive | |
| Sibiti (Si) | F | 05/91 | Few days | 10.5 years | 11/01 | 10 years | Alone | Disappeared (11/01) | Lost collar |

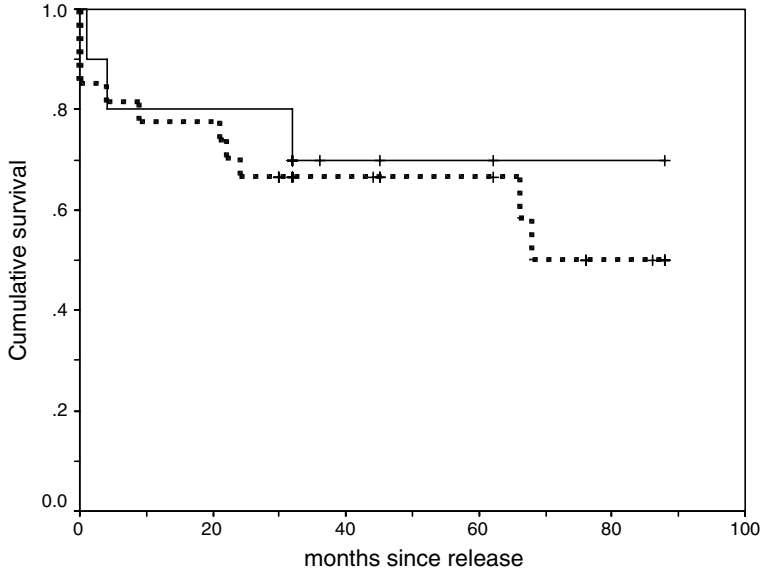


Fig. 1. Cumulative survival curve for female (solid line) and male (dashed line) released chimpanzees. Survival is defined here as still present in the release zone, and is thus a conservative estimate. Crosses indicate censored cases.

The outcome of release was assessed in terms of immediate post-release fate, and subsequent or "mid-term" fate. Immediate fate involved events (e.g., death or disappearance) directly associated with the release procedure; while subsequent fate involved events occurring once individuals were living in the release site, and that were unrelated to the release procedure itself. We consider this "mid-term" as adult life expectancy in wild chimpanzees is 30 years (Hill et al., 2001), whereas the oldest chimpanzee studied had only reached 17 years at the end of the study.

Encounters between released individuals and wild conspecifics were classed as aggressive (fighting, biting, hitting or chasing observed, or resulting in injury), or peaceful (none of the above). Wounds received by released individuals during encounters with wild chimpanzees or other released individuals were classified as fatal, severe (requiring surgery), moderate or superficial. Due to low cell counts, fatal and severe wounds were lumped together versus moderate and superficial injuries for statistical comparison using Fisher's exact test.

## 3. Results

### 3.1. Overall survival

Of 27 released females, three are known to have died (11%), eight have disappeared (30%) but are likely to have joined wild groups (see below for why these females are believed to have joined wild groups) and 16 are still followed in the release zone (59%, Table 1). Of 10 released males, two are known to have died (20%), one has disappeared and is thought to have died (10%, increasing mortality to 30%) and seven remain in the release zone (70%). Thus, the overall confirmed mortality is 14%, disappearance is 24% and known survival is 62%.

Fig. 1 shows survival curves for released males and females. Survival is defined here as present in the release zone in February 2004; however, females that have disappeared may still be alive (see above). Data are limited to 88 months (time from the first release to the end of the study period). Mean ± SEM female survival was 58 ± 7 months (11 disappearances, total 27 individuals, 95% CI 44–72 months). Mean ± SEM male survival was 65 ± 11 months (3 events, total 10 individuals, 95% CI 43–87 months). Insufficient data were available to determine median survival. There was no significant sex difference in survival (Log-rank statistic $L = 0.16$, df = 1, $p = 0.689$).

We estimate the number of chimpanzees now using the Triangle as the 23 released chimpanzees known to remain in the release zone, plus the 3–7 wild chimpanzees estimated to use the site in 1996 (Tutin et al., 2001). The density of chimpanzees using the Triangle is now therefore 1.3–1.5 individuals/km$^2$.

### 3.2. Immediate fate after release

Nine of 10 (90%) males and 23 of 27 (85%) females survived immediately following release. One male (Dolisie) fled immediately. He was radio-tracked at a distance for several days, but not observed. His radio-collar was found one month later, underwater in a swamp, and a further search revealed a skull a few meters away. The skull appeared to be at least three weeks old, and six chimpanzee nests of approximately the same age were

found within 20 m, suggesting that Dolisie may have been killed by wild chimpanzees (Paredes, unpublished report and pers. comm.), although this cannot be confirmed. A second male (Koutou) fled after release (1 February 1999) but was relocated 15 days later in a swamp area several kilometers from the release site, weak and injured. He was anaesthetised, brought back to the research station, and kept there for 8 days to recover. He was re-released on 3 March 1999 and remains in the release zone to date.

Four females also fled immediately when released and were not relocated, either because they did not have a radio-collar ($n = 1$) or due to malfunction or loss of collars ($n = 3$). The fate of these individuals is unknown.

Of the six individuals that fled immediately following release, only one was released alone, while the others were released with other individuals. Two further individuals released singly remain in the release site, indicating that release of a single individual does not necessarily lead to flight.

### 3.3. Subsequent (mid-term) fate

As of February 2004, 23 individuals (62%) were still present in the release zone: 7 males and 16 females. Fig. 2 shows the distribution of confirmed survival over the 6 releases. Although the latest two releases (June–July 2000 and July–November 2001) show high survival, this is not simply due to the recent date of release: all released animals had been free-ranging for at least 2 years and 10 months by the end of the study, and 80% of individuals released in the first group, 7.5 years before the end of the study, remain in the release zone. The young male (Louzolo) introduced into a group of previously released individuals in February 2001 is also still alive, 3 years after release.

#### 3.3.1. Confirmed deaths

Of the 23 females and nine males that survived immediately following release, two females, one male and an infant are known to have died (Table 1). One female drowned accidentally when she attempted to cross a river using overhanging branches, which broke. A second female (Makabana) was killed 9 months after release by other released individuals (see below). The male (Hinda) was attacked and killed by wild chimpanzees three years after release, and his body found in the release zone. The infant (Valentine), disappeared 5 months after release, and could not have survived alone.

#### 3.3.2. Disappearances

Four females disappeared several years after release (Table 1) and had not reappeared by the end of the study (February 2004). The fate of these individuals is unknown, but at least some may have integrated into the wild population. In support of this, additional females have disappeared for periods ranging from 8 to 21 months, before reappearing in the release zone, either back in a group of released individuals ($n = 1$), or with wild chimpanzees ($n = 3$). Six additional females also have regular contacts with wild chimpanzees, and also disappear from the release zone occasionally, reappearing days or weeks later (Table 1). By contrast, the only male that disappeared (David, 5 months after release) has never returned to the release zone and is believed to be dead.

### 3.4. Interactions with wild chimpanzees

Of a total of 86 encounters between released and wild chimpanzees, 67 (78%) occurred when the released group contained only females and 17 (25%) when it contained both males and females. On the remaining two occasions, a released male encountered wild chimpan-

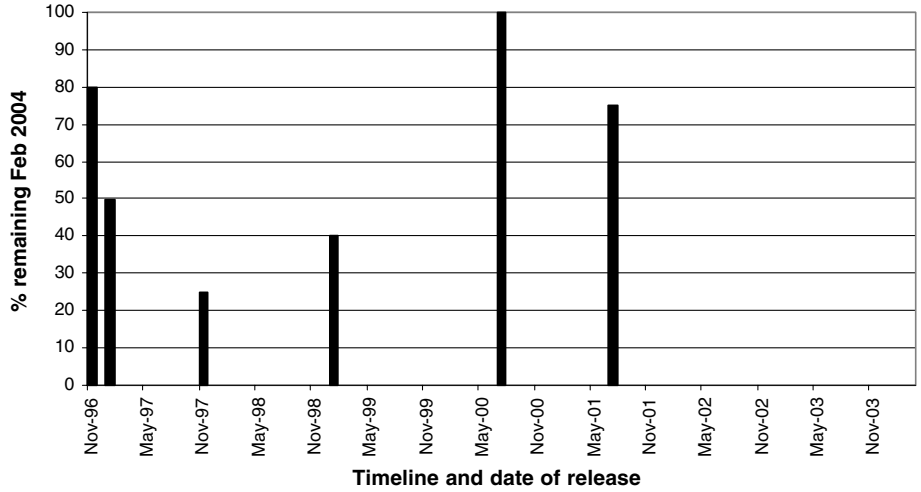


Fig. 2. Percentage of individuals still observed in February 2004 per release phase.

zees when he was alone. Seventy-three (87%) of these occasions occurred when females were showing sexual swellings. Overall, 15 of 21 (71%) successfully released females have been observed to associate with wild chimpanzee groups.

Encounters in which the released group contained both males and females were significantly more likely to involve aggression than those in which the released group contained only females (males and females: aggressive 15, peaceful 2; females only: aggressive 7, peaceful 60; $X_1^2 = 42.44$, $p < 0.001$). Both of the two encounters between solitary released males and wild chimpanzees involved aggression from the wild chimpanzees and flight by the released male.

In addition to the aggressive encounters observed between released males and wild chimpanzees, all but one of the 10 released males were attacked by wild chimpanzees (details in Table 2). In a further three cases, attacks on males would have led to death without veterinary intervention (Table 2). In contrast, no females are known to have been seriously injured or killed by wild chimpanzees. However, three of six babies (one male and two females) born to released females disappeared during interactions with wild chimpanzees, and seem likely to have been victims of infanticide.

Table 3 shows the severity of injuries received by released males and females during attacks by wild chimpanzees. Lumping fatal and severe vs. moderate and superficial or no injury, males suffered significantly more serious injury from wild chimpanzees than did females (Fisher's exact test $p = 0.018$).

Of 13 documented injury events and fatal attacks for males, six involved injury to the genital and rectal area, while on seven occasions veterinary reports did not specify the position of wounds, or the body was not recovered. In females, four events included injury to the genital and rectal area, while six involved wounds elsewhere on the body (two were unknown).

### 3.5. Interactions between released individuals

The released chimpanzees formed a fission–fusion society, similar to that observed in wild chimpanzees, and interactions between released individuals are generally peaceful. However, released chimpanzees directed 18 attacks towards other released chimpanzees. Both males (13 attacks) and females (12 attacks) participated in attacks on individuals of both sexes. Ten of the attacks (55%) were made by a single, stable released group, containing two males (Koutou, and Chinois) and 2–3 females. Notably, 13 (72%) of the attacks were directed towards the last 11 individuals to be released (summer 2001, 8 females and 3 males). Indeed one relatively recently released female (Makabana) was attacked and killed by Koutou, and bitten on the head by three females (Table 2).

Table 3 shows the severity of injuries received by released males and females during attacks by other released individuals. With the exception of Makabana, attacks by released individuals generally led to less serious injury than attacks by wild chimpanzees. Comparing fatal and severe injuries with moderate and superficial injuries, attacks by released chimpanzees were significantly less serious than those made by wild chimpanzees for males (Fisher's Exact test $p = 0.029$), but not for females ($p = 1.000$).

Of five injuries inflicted by released individuals on males, two involved injury to the genital and rectal area, while three were unspecified. In females, nine injury events included injury to the genital and rectal area, while three involved wounds elsewhere on the body.

### 3.6. Reproduction

Five offsprings were conceived and born in the wild to four of the released females (Table 4). Three of these infants were still alive at the end of the study, while two disappeared following encounters with wild chimpanzees (in addition to the infant that was released with its mother, Valentine).

## 4. Discussion

Our results show that wild-born orphan chimpanzees can be introduced into the wild successfully, with a minimum mid-term survival of 62% of individuals remaining in the release zone, and only 14% of individuals confirmed dead (i.e., a maximum survival of 86%). Non-human primate release projects are often poorly monitored and reliable survival data are therefore rare (e.g., for orang-utans: Yaeger, 1997; non-human primates in general: Cowlishaw and Dunbar, 2000). However, several projects involving the translocation of wild primate groups from one site to another have been successful (Cowlishaw and Dunbar, 2000, their Table 11.10), as have projects to release captive-bred individuals into the wild. For example, 38% (27 of 71) of golden lion tamarins (*Leontopithecus rosalia rosalia*) released in Brazil survived (Kleiman et al., 1991) and a similar percentage (5 of 13) of captive-bred black and white ruffed lemurs (*Varecia variegata variegata*) survived release in Madagascar (Britt et al., 2004). Other rehabilitation and release projects have been less successful, for example 90% of confiscated gibbons (*Hylobates muelleri*) released in Sarawak died following release (Bennett, 1989, 1992). Similarly survival and integration into wild groups was confirmed for only four (13%) of 31 captive *Hylobates lar* (the majority of which were wild-caught) released into the wild in Thailand (Tingpalapong et al., 1981). HELP Congo's survival rate is thus one of the highest for primate release programs. We attribute this success

Table 2
Attacks on released chimpanzees by wild chimpanzees or by other released individuals

| ID | Date of attack | Age when attacked | Nature of attack | Attacker | Injuries | Veterinary intervention | Outcome |
|---|---|---|---|---|---|---|---|
| *Males* | | | | | | | |
| Mekoutou | 13/02/97 | 6 years | Bitten | Wild chimpanzees | Rectal prolapse; bite wounds on perineal region and fingers of both hands; superficial wounds on right eyelid, arms and right leg | Surgery | Survived |
| | 01/05/99 | 8 years | Bitten | Released male (Da) | Wounds on genitalia; portion of penis missing (~1 cm) | Stitches, antibiotics | Survived |
| | 07/09/00 | 10 years | Bitten | Released female (Yv) | Wounds on body | Disinfection | Survived |
| | 18/06/02 | 12 years | Bitten | Wild chimpanzees | Deep wounds on arms, legs, hands, feet, ears, anus and rectum; left Achilles tendon torn | Surgery | Survived |
| | 23/05/03 | 13 years | Bitten | Released males (Ko, Chi) | Superficial wounds | Disinfection, antibiotics | Survived |
| Hinda | 05/03/99 | 8 years | Bitten | Wild chimpanzees | Rectal prolapse; portion of anus missing | Surgery | Survived |
| | 10/07/00 | 9 years | Bitten | Wild chimpanzees | Wounds on body | Antibiotics | Survived |
| | 23/07/00 | 9 years | Bitten & killed | Wild chimpanzees | Bite wounds on the face, neck, hands and feet; anus torn; genitalia missing; perineal rupture | — | Death |
| Dolisie | 03/12/97 | 6 years | Killed | Wild chimpanzees | Skull found (with collar) | — | Death |
| Koutou | 08/06/00 | 10 years | Bitten | Released females (Yv, Bou) | Minor wounds | None | Survived |
| | 31/01/02 | 12 years | Bitten | Wild chimpanzees | Bite wounds on back and rectum | None | Survived |
| | 29/04/02 | 12 years | Bitten | Wild chimpanzees | Bite wounds on left biceps, right foot and right hand; numerous tooth marks on body | Disinfection, stitches, antibiotics | Survived |
| David | 19/05/99 | 10 years | Unknown | Wild chimpanzees | Disappeared following an attack on released group | — | Disappeared |
| Bateko | 20/06/02 | 10 years | Fight | Wild chimpanzees | None | None | Survived |
| | 08/07/02 | 10 years | Bitten | Wild chimpanzees | Deep wounds on rump; rectum torn; one testicle missing; portion of penis missing; numerous cutaneous wounds and muscular tears on body | Surgery | Survived |
| Dereck | 02/11/01 | 7 years | Bitten | Released male (Me) | Bite wounds on testes | Disinfection | Survived |
| Andréas | 12/06/02 | 8 months | Killed | Wild chimpanzees | | — | Disappeared |
| Louzolo | 20/12/02 | 3 years | Bitten | Wild chimpanzees | Several wounds on body | Stitches, antibiotics | Survived |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Females* | | | | | | | |
| Bounie | 21/03/97 | 10 years | Fight | 2 wild females | None | None | Survived |
| | 29/03/97 | 10 years | Bitten | Wild chimpanzees | 4 cm wound on vulva; superficial bites on right leg and hand | Antibiotics | Survived |
| | 29/05/99 | 12 years | Bitten | Wild chimpanzees | Wounds on body | None | Survived |
| Yvette | 21/03/97 | 10 years | Fight | Wild male | None | None | Survived |
| | 29/05/99 | 12 years | Bitten | Wild chimpanzees | Portion of right ear missing | None | Survived |
| Choupette | 12/06/02 | 13 years | Bitten | Wild chimpanzees | Deep wounds on right arm; vulva severely torn; wounds on face | Disinfection, antibiotics | Survived (baby killed) |
| Rosette | 01/02/03 | 13 years | Bitten | Wild chimpanzees | Wound on mouth | None | Survived |
| Sophie | 01/04/00 | 11 years | Bitten | Wild chimpanzees | Wound on right thigh | None | Survived |
| Valentine | 19/05/99 | 7 months | Unknown | Wild chimpanzees | Disappeared following an attack on released group | — | Death |
| Matalila | 27/08/00 | 10 years | Bitten | Released female (Bou) | Large wound on vulva | None | Survived |
| | 31/01/02 | 12 years | Bitten | Wild chimpanzees | Bite wounds on back | None | Survived |
| | 15/08/03 | 13 years | Bitten | Wild chimpanzees | Deep bite wounds on arms and legs | Antibiotics | Survived |
| Perlette | 31/01/02 | 12 years | Bitten | Wild chimpanzees | Bite wounds on toes, shin and labia | None | Survived |
| Lucie | 31/01/02 | 11 years | Bitten | Wild chimpanzees | Bite wounds on back (between the shoulder blades) | None | Survived |
| | 03/12/02 | 12 years | Bitten | Wild chimpanzees | Bite wound on right thigh; wounds on vulva | Antibiotics | Survived |
| Makabana | 06/04/02 | 9 years | Killed | Released indiv. (Ko, Lu) | Anus and rectum seriously torn by Ko; bitten on head by females | — | Death |
| Dimonika | 13/04/02 | 9 years | Bitten | Released indiv. (Chi, Ko, Lu, Ag) | Wounds on vulva and mouth | Disinfection, antibiotics | Survived |
| | 31/05/02 | 9 years | Fight | Released males (Ko, Chi) | None | None | Survived |
| | 07/09/02 | 9 years | Hit | Released males (Ko, Chi) | None | None | Survived |
| Emilie | 20/12/01 | 8 years | Bitten | Released indiv. (Lu, Ko, Chi, Mat, Per) | Bite wounds on left ear, hands, right ankle and right wrist | None | Survived |
| | 12/05/02 | 8 years | Bitten | Released males (Ko, Chi) | Deep wounds on rump | Disinfection, antibiotics | Survived |
| | 06/12/02 | 9 years | Bitten | Released female (Je) | Wounds on vulva | None | Survived |
| | 10/07/03 | 9 years | Bitten | Released female (Cho) | Deep wound on rump | Disinfection, antibiotics | Survived |
| Tessie | 30/01/03 | 12 years | Bitten | Released indiv. (Ko, Lu) | Wounds on vulva | Disinfection, antibiotics | Survived |
| Kouilou | 30/07/02 | 11 years | Bitten | Released female (Je) | Wounds on hands, feet and rump | Disinfection | Survived |
| | 05/03/03 | 12 years | Bitten | Released indiv. (Ko, Lu) | Skin missing on feet | Antibiotics | Survived |
| Carine | 12/05/02 | 7 years | Bitten | Released males (Ko, Chi) | Deep wounds on labia, right leg and left arm | Disinfection, antibiotics | Survived |
| Cheyenne | 07/09/02 | 9 years | Hit | Released males (Ko, Chi) | None but fell 20 m out of a tree | None | Survived |
| | 10/07/03 | 10 years | Bitten | Released female (Cho) | Superficial bite wound on toe | Disinfection | Survived |

Table 3
Severity of injuries resulting from attacks by conspecifics on released individuals

| | Fatal | Severe | Moderate | Superficial or no injury | Total |
|---|---|---|---|---|---|
| *Attack by wild chimpanzees* | | | | | |
| Males | 4 | 4 | 2 | 3 | 13 |
| Females | 1 | 1 | 3 | 9 | 14 |
| *Attack by released chimpanzees* | | | | | |
| Males | 0 | 0 | 1 | 4 | 5 |
| Females | 1 | 0 | 4 | 10 | 15 |

to careful planning (Tutin et al., 2001) and detailed post-release monitoring, including medical interventions, and the presence of research assistants reducing the risk of fatal interactions with other groups of chimpanzees, predators or hunters.

After more than seven years of post-release monitoring, we report reproduction by females of the release generation. DNA analysis identified the father of one of these offspring as a released male, demonstrating that released males also reproduced (Goossens et al., 2003). Genetic analyses are currently underway to identify the fathers of the remaining offspring, and in particular to determine whether they were sired by released or wild males.

To date, three of six infants of released females have disappeared during encounters with wild chimpanzees. This level of infant mortality is higher than in wild chimpanzee populations (about 20% during the first year of life: Hill et al., 2001), but both inter- and intra-community infanticides are also known to occur in wild populations (reviewed in Arcadi and Wrangham, 1999). Again, few data exist for other primate release programs, but wild-born, captive female orang-utans released into Gunung Leuser National Park (*Pongo abelii*) and Tanjung Puting National Park (*Pongo pygmaeus*) have also reproduced successfully (Yaeger, 1997; Utami et al., 2002). For non-great ape species, successful reproduction has been reported for released black and white ruffed lemurs (Britt et al., 2004), and for released captive-bred golden lion tamarins (Stoinski et al., 2003).

Released females regularly interacted with wild chimpanzees and several females appeared to have integrated into wild groups for extended periods of time. However, three released females that spent time with wild groups returned to the release zone when pregnant, and gave birth in their original released group. To our knowledge, such behaviour has not been reported for wild chimpanzees, where female transfer is permanent (see below), and it is possible that these females would be less likely to lose their infants to infanticidal wild chimpanzees if they stayed in the group in which they conceived.

Encounters with wild chimpanzees were a major cause of mortality in released males, and would have been more so without veterinary intervention (40–50% of released males). By contrast, females disappeared and subsequently returned to the release zone, leading us to believe that while males that have disappeared are likely to be dead, females may still be alive, but associating with wild groups. Thus, although we found no significant sex difference in the overall survival of released chimpanzees, the proportion of females still alive after eight years may be as high as 89%, as compared to 70% for males.

Sex differences in interactions with wild conspecifics are not surprising, given knowledge of wild chimpanzee behavioural ecology. Wild female chimpanzees disperse permanently into new communities at 10–12 years, around the time they reach sexual maturity (Pusey, 1979; Nishida, 1990; Gagneux et al., 1999), while male chimpanzees remain in their natal community, and cooperate in territorial defence against neighbouring communities, showing intense hostility to foreign males (Nishida et al., 1985; Goodall, 1986; Wrangham and Peterson, 1996; Wrangham, 1999). Wild females transfer when sexually attractive (Nishida, 1979), and our results also showed that encounters between released females and wild chimpanzees were particularly common when females were sexually attractive. Wild females immigrating into new communities are generally welcomed by males, but may be harassed by females (Pusey, 1980; Nishida, 1981), perhaps explaining why some released females returned to the release zone, and rejoined other released individuals after several months spent with wild chimpanzees.

Male chimpanzees are known to kill members of neighbouring communities, including infants and weaned individuals of both sexes, and inter-group vio-

Table 4
Reproduction by released females

| Mother (release date) | Date of birth | Sex | Mother's age | Fate at Feb 2004 |
|---|---|---|---|---|
| Choupette (11/96) | 22 Oct 2001 | Male | 12 years | Disappeared at 8 months, following an attack on the group by wild chimpanzees |
| Jeannette (11/96) | early March 2003 | Male | 14 years | Alive |
| Bounie (11/96) | 7 Aug 2003 | Unknown | 16 years | Alive |
| Lucie (07/00) | 17 Aug 2003 | Female | 12 years | Killed by wild chimpanzees Feb 2004 |
| Choupette (11/96) | 25 Aug 2003 | Female | 14 years | Alive |

lence is a major cause of mortality in wild chimpanzees (review in Wilson and Wrangham, 2002). Such killing seems likely to reduce competition for territory, either by directly reducing the number of competitors, or by reducing the size of rival male coalitions (see Wilson and Wrangham, 2002; Wilson et al., 2004). Infanticide by males may also serve to increase future mating opportunities (by reducing the time taken by the female to resume sexual cycles). However, data currently available for wild chimpanzees does not provide firm support for this hypothesis: infanticidal males are rarely observed to subsequently mate with the mother, and recent studies support rival reduction or resource competition hypotheses as an evolutionary explanation for intergroup infanticide (Kutsukake and Matsusaka, 2002; Newton-Fisher, 1999; Watts, 2002).

The number of observed cases of inter-group killing in chimpanzees remains small (Wilson et al., 2004), and some debate persists about whether this is a widespread trait among chimpanzees or is limited to certain populations, and merely represents a response to atypical conditions such as intensive provisioning (e.g., Power, 1991; Sussman, 1999). However, long-term studies of the eastern (*P. t. schweinfurthii*) and western (*P. t. verus*) sub-species of chimpanzee show intergroup killing at all sites with neighbouring communities, including those where provisioning has never occurred (Wilson and Wrangham, 2003). The attacks on released males reported here thus represent important new data on lethal aggression in the central subspecies of chimpanzee (*P. t. troglodytes*), for which no long-term data concerning inter-community relationships is yet available.

Wilson et al. (2004) discuss the predictions arising from the different evolutionary hypotheses proposed to account for intergroup violence in chimpanzees. The male-bias in both attack frequency and severity that we observed provides support for the reduction of rival coalitions hypothesis (which predicts that males should be specifically targeted). However, we cannot rule out the local resource competition hypothesis (which predicts that individuals of either sex should be targeted), due to the age of the released females: adolescent females should be less likely to be victims of aggression, as they represent future reproductive opportunities if they transfer into neighbouring communities (Wilson et al., 2004).

The high rate of male mortality due to inter-group aggression may be partly explained by the young age of released males, and also by the tendency of released chimpanzees to travel in small bi-sexual groups, with a maximum of one or two adult males (unpublished observations). Play-back experiments with wild chimpanzees suggest that lethal attacks are more likely where numerical advantage reduces the costs of attacking (Wilson et al., 2001), meaning that released individuals may be incapable of defending themselves in the face of attack from larger groups of wild conspecifics.

Interactions between released individuals were not always peaceful and one female was killed. The increase in attacks that occurred following the final release suggests that the release zone may have been saturated at least in the eyes of previously released individuals, who regarded the zone as their territory, and attacked "intruding" new releases. Here, it is also important to note that the newer individuals had previously lived on a different island to the attacking group, meaning that they were indeed strangers to one another. The current estimated density of chimpanzees (wild and released) in the release zone (1.3–1.5 individuals/km$^2$) is within the range for wild populations (1–4 individuals/km$^2$, Tutin et al., 2001), suggesting that the zone may now be saturated.

Notably, injuries to both males and females often involved the genital area. This is similar to injuries reported for captive individuals (de Waal, 1992) and wild males (Wilson et al., 2004), although little data is currently available concerning patterns of injury in wild chimpanzees. Finally, Bites and fatal attacks have also occurred between individuals living on rehabilitation islands in the Conkouati lagoon, including a fatal attack by the dominant adult male on a subordinate adult male, suggesting that release does not necessarily result in a higher risk of injury when compared to captive or semi-captive situations.

The (to date) successful introduction of a three-year-old male (Louzolo) into a previously released group of chimpanzees is an interesting case study. Treves and Naughton-Treves (1997) report a similar attempt to introduce a captive, wild-born 4–6-year-old female (Bahati) into a habituated group of wild chimpanzees. Although the early results of this release were positive, and the released female associated closely with the wild chimpanzees, after six weeks she no longer followed the wild individuals. The project was terminated after 2 months and the female returned to captivity. We suggest that the successful release of Louzolo is due to different release methods. In contrast to Bahati's abrupt "desertion" by her human caretakers (Treves and Naughton-Treves, 1997), Louzolo was introduced into his new group over a period of approximately four months, allowing him to adjust to his new situation gradually (but making the introduction extremely labour intensive). We should note here that such introduction is not to be encouraged, as it carries a very high risk of disease transmission, and requires careful health precautions.

### 4.1. Addressing the fate of wild-born, captive chimpanzees

Our results demonstrate that wild-born captive chimpanzees can be rehabilitated and released into the wild

successfully, making the project successful from a welfare perspective. However, very specific conditions are necessary for successful release (Tutin et al., 2001), and the experience gained by HELP Congo is not applicable to all other wild-born captive chimpanzees currently living in sanctuaries. First, a suitable area is necessary for relocation. Criteria include a non-existent or low existing density of wild chimpanzees, sufficient resources to sustain released individuals, and efficient protection against poachers (Tutin et al., 2001). The reason for the original decline or local extinction must be removed before release is contemplated (IUCN, 1998). However, this is rarely the case, and even national parks in chimpanzee habitat countries are often largely unprotected (e.g., Muchaal and Ngandjui, 1999; Remis, 2000; Van Krunkelsven, 2001; Waltert et al., 2002).

Second, the release zone must be far from any human habitation: wild chimpanzees have been known to attack and kill human infants (Goodall, 1986; Gavin, 2004), and released individuals are likely to be less intimidated by humans than their wild counterparts. Similarly, orang-utans released close to human habitation are known to have attacked humans (Yaeger, 1997).

Third, the risks of disturbing existing wild populations, where present, must be given the highest priority (IUCN, 1998). In particular, release of captive individuals can transmit pathogens to existing wild populations (Woodford, 2001). For example, translocated orang-utans are known to have transmitted disease from local human populations to wild orang-utans (Rijksen, 1978). A thorough pre-release health and preventive medicine program must therefore be undertaken (IUCN, 1998). Further, translocated individuals are artificial migrants, and it is essential that they originate from genetically similar populations, as genetic pollution via outbreeding depression may have serious negative consequences for existing wild populations (Goossens et al., 2002).

Fourth, as advocated by Tutin et al. (2001), adolescent females are the best candidates for chimpanzee reintroduction. Thus the size, and the age-structure, of the chimpanzee population already living in sanctuaries preclude relocation as a solution for all individuals (Farmer, 2002a). We can now confirm that while adolescent females appear to interact positively with wild conspecifics and may be accepted into wild communities, male chimpanzees should not be released where there is an existing population of wild chimpanzees, as they are very likely to be killed. Individuals to be released also require a lengthy pre-release adaptation period, including life in semi-wild conditions (in forested enclosures or on islands), allowing them to develop the social and behavioural skills needed for their survival in the wild.

A final concern relating to release programs is their cost-effectiveness. To date, the HELP Congo project has cost approximately US$33,800 per chimpanzee released, or US$54,400 per individual known to have survived (rough estimates based on annual budgets since the release process began in 1996). For comparison, each golden lion tamarin successfully released into the wild cost an estimated US$22,563 (Kleiman et al., 1991). Post-release monitoring continues to cost approximately US$5,200 per chimpanzee per year (US$1300 for Congolese field assistant salaries, $1400 for telemetry equipment, and US$2500 for other equipment, accommodation, medicine, fuel, and maintenance). Reducing the level of post-release monitoring would of course reduce these costs for future release programs. Whether this is money well spent is strongly debated (e.g., Lindburgh, 1992; Cowlishaw and Dunbar, 2000). Many argue that such large sums would be better spent on the protection of habitat and existing wild populations, and halting the pet trade (e.g., Mackinnon and Mackinnon, 1991; Struhsaker and Siex, 1998; Yaeger, 1997). This is undoubtedly true. However, the situation is complicated by the fact that the funding available for compassionate welfare programs is not always available for the conservation of wild populations (in HELP's experience).

### 4.2. Addressing the fate of wild chimpanzees

Given that the wild population of chimpanzees is currently large enough not to require reinforcement via release programs, the most important measure in the conservation of chimpanzees is clearly the protection of their habitat, and reduction of hunting pressure. However, relocation projects can contribute to conservation by attracting considerable publicity, promoting conservation, raising public awareness, and educating the public (Dodd and Seigel, 1991; Kleiman et al., 1991; Dietz et al., 1994; Yaeger, 1997; Cowlishaw and Dunbar, 2000; Tutin et al., 2001). The existence of HELP Congo in the CDNP has indeed contributed to the protection of the release zone and surrounding forests, and therefore has indirectly benefited the wild chimpanzee population. The permanent presence of the HELP Congo project has made the release zone one of the only areas of the CDNP where poaching and deforestation have been substantially reduced (Maisels and Onononga, 2000). Further, HELP Congo, together with other NGOs and stakeholders, was instrumental in drawing the attention of the Congolese government to the unique richness and biodiversity of the Conkouati Reserve, leading to its classification as Conkouati-Douli National Park in August 1999. Thus, the orphan chimpanzees released by HELP Congo have contributed to the protection of the release area and the existing population of wild chimpanzees by (1) protecting the habitat, (2) attracting public and political sup-

port (national and international), and (3) leading to the initiation of conservation measures to protect the release area. The project has therefore fulfilled the IUCN requirement that relocations make a positive contribution to survival of the species concerned in the wild (IUCN, 1998).

As primate species continue to head for extinction, and habitats become increasingly fragmented, the importance of release projects will increase (Cowlishaw and Dunbar, 2000). Confirmation that wild-born, captive chimpanzees can be reintroduced into the wild successfully has implications for the future conservation of wild populations. Although wild chimpanzees are not at imminent risk of extinction, increasing habitat fragmentation has already led to the isolation of small communities (e.g., Galat-Luong et al., 1999-2000; Reynolds et al., 2003). Cultural differences between chimpanzee populations make conservation of as many individual populations as possible even more important (Whiten et al., 1999). Our results suggest that re-introduction of males and females (where local populations are extinct) or re-stocking with females (where small populations remain) may have potential as a method of increasing the numbers and the genetic variability of small populations. However, as population extinction tends to co-occur with high hunting pressure and human population encroachment on chimpanzee habitat, these factors must first be addressed before any release program is attempted. Finally, chimpanzee release programs may also be of use in relocating populations that have no future in their current habitat.

## 5. Conclusions

Rigorous and long-term post-release monitoring of a chimpanzee relocation project provides evidence in support of two important conclusions. First, wild-born, captive chimpanzees can be successfully released into the wild, under certain specific conditions. This is important, due to the large number of orphaned chimpanzees accumulating in sanctuaries across Africa, and also to the mixed success of previous attempts to release chimpanzees. Second, as predicted from knowledge of chimpanzee behavioural ecology, male chimpanzees face severe risks of attack by conspecifics and should not be released into areas with wild chimpanzees. While release into the wild clearly cannot address the fate of all captive, wild-born chimpanzees, it addresses the welfare of individual animals, and has both current and potential future benefits for the conservation of wild chimpanzee populations. However, the priority for chimpanzee conservation must clearly be improved protection of their natural habitat, and reduction of hunting pressure.

## Acknowledgements

HELP Congo works in collaboration with the authorities of the Republic of Congo (Ministry of Forest Economy and Environment), and we are grateful for their collaboration and support. We are indebted to Mr. Ondaye for his support for the project, and for authorization to work in the Conkouati-Douli National Park. We also thank G. Bonassidi (Conservateur of the CDNP) and N. Blondel (Wildlife Conservation Society) for their support in the CDNP. We are grateful for financial support from the US Fish and Wildlife Service (Great Ape Conservation Fund, Grants No. 98210-1-GO94 and No. 98210-3-G562), Cleveland Zoological Society, Columbus Zoo and Aquarium, Lincoln Park Zoo, International Primate Protection League, Arcus Foundation, Pan African Sanctuaries Alliance, Fondation Brigitte Bardot, Fondation Bourdon, Société Protectrice des Animaux, One Voice, Beauval Zoo, Amneville Zoo, La Barben Zoo, Gorilla and F. Martinez, Air Gabon, and Cardiff University. We thank C. Tutin and M. Vacher-Vallas for their valuable comments on the manuscript. Data were compiled from reports by the following veterinarians and researchers: M. Ancrenaz, S. Mahé, J. Paredes, C. Sourmail, C. Tutin, M. Vacher-Vallas and C. Vidal. We are grateful to the members of HELP International for their support. Finally, we thank the HELP Congo field assistants for their continuing hard work in monitoring the released chimpanzees.

## References

Arcadi, A.C., Wrangham, R.W., 1999. Infanticide in chimpanzees: Review of cases and a new within-group observation from the Kanyaware study group in Kibale National Park. Primates 40, 337–351.

Barnes, R.F.W., 2002. The bushmeat boom and bust in West and Central Africa. Oryx 36, 236–242.

Bennett, J., 1989. Gibbon rehabilitation in Sarawak. Sarawak Gazette 116, 14–22.

Bennett, J., 1992. A glut of gibbons in Sarawak: Is rehabilitation the answer?. Oryx 26, 157–164.

Borner, M., 1985. The rehabilitated chimpanzees of Rubondo Island. Oryx 19, 151–154.

Brewer, S., 1978. The Chimpanzees of Mt Assirik. Alfred A. Knopf, New York, pp. 293—295.

Britt, A., Welch, C., Katz, A., Iambana, B., Porton, I., Junge, R., Crawford, G., Williams, C., Haring, D., 2004. The re-stocking of captive-bred ruffed lemurs (*Varecia variegata variegata*) into the Betampona Reserve, Madagascar: Methodology and recommendations. Biodiversity and Conservation 13, 635–657.

Butynski, T.M., 2001. Africa's great apes. In: Bec, B.B., Stoinski, T.S., Hutchins, M., Maple, B., Norton, A., Rowan, E.F., Stevens, A., Arluke, A. (Eds.), Great Apes and Humans: The Ethics of Coexistence. Smithsonian Institution Press, Washington and London, pp. 3–56.

Cowlishaw, G., Dunbar, R., 2000. Primate Conservation Biology. University of Chicago Press, Chicago.

Cunningham, A.A., 1996. Disease risks of wildlife translocations. Conservation Biology 10, 349–353.

Custance, D.M., Whiten, A., Fredman, T., 2002. Social learning and primate reintroduction. International Journal of Primatology 23, 479–499.

de Waal, F.B.M., 1992. Chimpanzee Politics. Jonathan Cape, London.

Dietz, J.M., Dietz, L.A., Nagagata, E.Y., 1994. The effective use of flagship species for conservation. In: Olney, P.J.S., Mace, G.M., Feistner, A.T.C. (Eds.), Creative Conservation. Chapman & Hall, London, pp. 32–49.

Dodd Jr., C.K., Seigel, R.A., 1991. Relocation, repatriation and translocation of amphibians and reptiles: Are they conservation strategies that work? Herpetologica 47, 336–350.

Doumenge, C., 1992. La Réserve De Conkouati, Congo. Le Secteur Sud-ouest. World Conservation Union, Gland, Switzerland.

Fa, J.E., Currie, D., Meeuwig, J., 2003. Bushmeat and food security in the Congo Basin: Linkages between wildlife and people's future. Environmental Conservation 30, 71–78.

Farmer, K.H., 2002a. Pan-African Sanctuary Alliance: status and range of activities for great ape conservation. American Journal of Primatology 58, 117–132.

Farmer, K.H., 2002b. The behavior and adaptation of reintroduced chimpanzees (*Pan troglodytes troglodytes*) in the Republic of Congo. PhD thesis, University of Stirling, UK, 415 pp.

Fischer, J., Lindenmayer, D.B., 2000. An assessment of the published results of animal relocations. Biological Conservation 96, 1–11.

Gagneux, P., Boesch, C., Woodruff, D.S., 1999. Female reproductive strategies, paternity and community structure in wild West African chimpanzees. Animal Behaviour 57, 19–32.

Galat-Luong, A., Galat, G., Ndiaye, I., Keita, Y., 1999-2000. Fragmented distribution and current status of chimpanzees *Pan troglodytes verus* at the extreme of distribution in Senegal. African Primates 4, 71–72.

Gavin, M., 2004. Primate versus primate. BBC Wildlife 22 (1), 50–52.

Goodall, J., 1986. The Chimpanzees of Gombe: Patterns of Behaviour. Harvard University Press, Cambridge.

Goossens, B., Funk, S.M., Vidal, C., Latour, S., Jamart, A., Ancrenaz, M., Wickings, E.J., Tutin, C.E.G., Bruford, M.W., 2002. Measuring genetic diversity in translocation programs: Principles and application to a chimpanzee release project. Animal Conservation 5, 225–236.

Goossens, B., Setchell, J.M., Vidal, C., Dilambaka, E., Jamart, A., 2003. Successful reproduction in wild released orphan chimpanzees (*Pan troglodytes troglodytes*). Primates 44, 67–69.

Hannah, A., McGrew, W., 1991. Rehabilitation of captive chimpanzees. In: Box, H. (Ed.), Primate Responses to Environmental Change. Chapman & Hall, London, pp. 167–186.

Hecketsweiler, P., Mokoko Ikonga, J., 1991. La Réserve De Conkouati, Congo. Le Secteur Sud-est. World Conservation Union, Gland, Switzerland.

Hill, K., Boesch, C., Goodall, J., Pusey, A., Williams, J., Wrangham, R.W., 2001. Mortality rates among wild chimpanzees. Journal of Human Evolution 40, 437–450.

Hladik, C.M., 1973. Alimentation et activité d'un groupe de chimpanzés réintroduits en forêt gabonaise. La Terre et la Vie 27, 343–413.

IUCN, 1998. Guidelines for Re-introductions. IUCN/SSC Re-introduction Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Kleiman, D.G., Beck, B.B., Dietz, J.M., Dietz, L.A., 1991. Costs of a reintroduction and criteria for success: accounting and accountability in the Golden Lion Tamarin Conservation Program. Symposium of the Zoological Society of London 62, 125–142.

Kutsukake, N., Matsusaka, T., 2002. Incident of intense aggression by chimpanzees against an infant from another group in Mahale Mountains National Park, Tanzania. American Journal of Primatology 58, 175–180.

Leroy, E.M., Rouquet, P., Formenty, P., Souquière, S., Kilbourne, A., Froment, J.-M., Bermejo, M., Smit, S., Karesh, W., Swanepoel, R., Zaki, S.R., Rollin, P.E., 2004. Multiple ebola virus transmission events and rapid decline of Central African wildlife. Science 303, 387–390.

Lindburgh, D.G., 1992. Are wildlife reintroductions worth the cost? Zoo Biology 11, 1–2.

Mackinnon, K., Mackinnon, J., 1991. Habitat protection and reintroduction programmes. In: Gipps, J.H.W. (Ed.), Beyond Captive Breeding: Re-introducing Endangered Mammals to the Wild. Symposia of the Zoological Society of London No. 62. Clarendon Press, Oxford, pp.173—198.

Maisels, F., Onononga, J.R., 2000. Conkouati-Douli National Park – conservation status, Jan/Feb 2000 large mammals and human impact. Unpublished report by NYZW/The Wildlife Conservation Society, Republic of Congo.

Muchaal, P.K., Ngandjui, G., 1999. Impact of village hunting on wildlife populations in the Western Dja Reserve, Cameroon. Conservation Biology 13, 385–396.

Newton-Fisher, 1999. Infant killers of Budongo. Folia Primatologica 70, 167–169.

Nishida, T., 1979. The social structure of chimpanzees of the Mahale Mountains. In: Hamburg, D., McCown, E.R. (Eds.), The Great Apes. Benjamin/Cummings, Menlo Park, CA, pp. 73–122.

Nishida, T., 1981. The World of Wild Chimpanzees. Chuokoronsha, Tokyo.

Nishida, T., 1990. Demography and reproductive profiles. In: Nishida, T. (Ed.), The Chimpanzees of the Mahale Mountains. University Press of Tokyo, Tokyo, pp. 63–97.

Nishida, T., Hiraiwa-Hasegawa, M., Hasegawa, T., Takahata, Y., 1985. Group extinction and female transfer in wild chimpanzees in the Mahale Mountains. Zeitschrift für Tierpsychologie 67, 284–301.

Power, M., 1991. The Egalitarians – Human and Chimpanzee: An Egalitarian View of Social Organization. Cambridge University Press, Cambridge, UK.

Pusey, A., 1979. Intercommunity transfer of chimpanzees in Gombe National Park. In: Hamburg, D., McCown, E.R. (Eds.), The Great Apes. Benjamin/Cummings, Menlo Park, CA, pp. 465–480.

Pusey, A., 1980. Inbreeding avoidance in chimpanzees. Animal Behaviour 31, 363–377.

Remis, M.J., 2000. Preliminary assessment of the impacts of human activities on gorillas *Gorilla gorilla gorilla* and other wildlife at Dzangha-Sangha Reserve, Central African Republic. Oryx 34, 56–65.

Reynolds, V., Wallis, J., Kyamanywa, R., 2003. Fragments, sugar, and chimpanzees in Masindi district, western Uganda. In: Marsh, L.K. (Ed.), Primates in Fragments. Kluwer Academic/Plenum Publishers, New York, pp. 309–320.

Rijksen, H.D., 1978. A Field Study on Sumatran Orang-Utans (*Pongo Pygmaeus Abelii* Lesson 1827): Ecology, Behaviour and Conservation. Veenman and Zonen, Wageningen.

Seddon, P.J., 1999. Persistence without intervention: assessing success in wildlife reintroductions. Trends in Ecology and Evolution 14, 503.

Stoinski, T.S., Beck, B.B., Bloomsmith, M.A., Maple, T.L., 2003. A behavioral comparison of captive-born, reintroduced golden lion tamarins and their wild-born offspring. Behaviour 140, 137–160.

Struhsaker, T.T., Siex, K.S., 1998. Translocation and introduction of the Zanzibar red colobus: success and failure with an endangered island endemic. Oryx 32, 277–284.

Sussman, R.W., 1999. The myth of man the hunter, man the killer and the evolution of human morality (evolutionary and religious perspectives on morality). Zygon 32, 453–472.

Tingpalapong, M., Watson, W.T., Whitmire, R.E., Chapple, F.E., Marshall, J.T., 1981. Reactions of captive gibbons to natural habitat and wild conspecifics after release. Natural History Bulletin of the Siamese Society 29, 31–40.

Treves, A., Naughton-Treves, L., 1997. Case study of a chimpanzee recovered from poachers and temporarily released with wild conspecifics. Primates 38, 315–324.

Tutin, C.E.G., Ancrenaz, M., Paredes, J., Vacher-Vallas, M., Vidal, C., Goossens, B., Bruford, M.W., Jamart, A., 2001. The conservation biology framework of the release of wild-born orphaned chimpanzees into the Conkouati Reserve, Congo. Conservation Biology 15, 1247–1257.

Utami, S.S., Goossens, B., Bruford, M.W., de Ruiter, J., van Hooff, J.A.R.A.M., 2002. Male bimaturism and reproductive success in Sumatran orang-utans. Behavioral Ecology 13, 643–652.

Vacher-Vallas, M., Goossens, B., Farmer, K.H., Vallas, P., Ancrenaz, M., Paredes, J., Vidal, C., Jamart, A., submitted. Feeding behaviour of reintroduced chimpanzees, Conkouati-Douli National Park, Republic of Congo. American Journal of Primatology.

Van Krunkelsven, E., 2001. Density estimation of bonobos (*Pan paniscus*) in Salonga National Park, Congo. Biological Conservation 99, 387–391.

Walsh, P.D., Abernethy, K.A., Bermejo, M., Beyers, R., De Wachter, P., Ella Akou, M., Huijbregts, B., Idiata Mambounga, D., Kamdem Toham, A., Kilbourn, A.M., Lahm, S.A., Latour, S., Maisels, F., Mbina, C., Mihindou, Y., Ndong Obiang, S., Ntsame Effa, E., Starkey, M.P., Telfer, P., Thibault, M., Tutin, C.E.G., White, L.J.T., Wilkie, D.S., 2003. Catastrophic ape decline in western equatorial Africa. Nature 422, 611–614.

Waltert, M., Lien, Faber, K., Muhlenberg, M., 2002. Further declines of threatened primates in the Korup Project Area, south-western Cameroon. Oryx 36, 257–265.

Watts, D., 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. Behaviour 139, 343–370.

Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. Nature 399, 682–685.

Wilson, M.L., Hauser, M.D., Wrangham, R.W., 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees. Animal Behaviour 61, 1203–1216.

Wilson, M.L., Wallauer, W.R., Pusey, A.E., 2004. New cases of intergroup violence among chimpanzees in Gambe National Park, Tanzania. International Journal of Primatology 25, 523–549.

Wilson, M.L., Wrangham, R.W., 2003. Intergroup relations in chimpanzees. Annual Review of Anthropology 32, 363–392.

Woodford, M.H., 2001. Quarantine and Health Screening Protocols for Wildlife Prior to Translocation into the Wild. OIE/IUCN SSC Veterinary SG Publications, Paris.

Woodford, M.H., Rossiter, P.B., 1994. Disease risks associated with wildlife translocation projects. In: Olney, P.J.S., Mace, G.M., Feistner, A.T.C. (Eds.), Creative Conservation. Chapman & Hall, London, pp. 178–200.

Wrangham, R.W., 1999. Evolution of coalitionary killing. Yearbook of Physical Anthropology 42, 1–30.

Wrangham, R.W., Peterson, D., 1996. Demonic Males. Houghton Miflin, New York.

Yaeger, C.P., 1997. Orangutan rehabilitation in Tanjung Putting National Park, Indonesia. Conservation Biology 11, 802–805.