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Behavioral Adaptation of *Pan troglodytes troglodytes*

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Abstract *As wild primate populations decline, numbers of orphaned primates, sanctuaries, and attempts to release primates back to the natural environment increase. Release projects frequently are poorly documented despite IUCN guidelines recommending post-release monitoring and systematic data collection as central to the process. Since 1996, Habitat Ecologique et Liberté des Primates (HELP) has been releasing wild-born orphaned chimpanzees into natural habitat in the Conkouati-Douli National Park, Republic of Congo. HELP developed a post-release monitoring system as an integral component. We present activity budgets and diet of released chimpanzees, and compared them to those of wild chimpanzee, as primary indicators of successful release. Feeding, moving, and resting dominated activity budgets, reflecting the overall patterns in wild populations. Diet was diverse and dominated by fruit, and the released chimpanzees showed specialization on a smaller number of species, as in many wild communities. The high survival rates of the chimpanzees and overall success of the release program are attributed to careful planning and post-release support facilitated via the monitoring process. Systematic post-release data collection monitoring has confirmed that wild-born chimpanzees can adjust behaviorally and nutritionally to the wild. Survival statistics of the reintroduced chimpanzees—confirmed 56%, possible 88%— reflect the behavioral adaptability.*

KEY WORDS: behavioral adaptation; chimpanzee; *pan troglodytes troglodytes*; reintroduction.

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INTRODUCTION

The largest ordinal increase of threatened and endangered species is within the Primates (Hilton-Taylor, 2000). Though the IUCN African Primate Action Plan has not recommended reintroduction as a future conservation action plan for any primate species regardless of taxon (Oates, 1996), primate releases are increasing (Soorae and Baker, 2002). As a direct consequence, the IUCN Reintroduction Specialist Group recently developed specific guidelines for reintroducing nonhuman primates into the wild (Soorae and Baker, 2002). Long-term post-release monitoring (behavioral, ecological, demographic, health, mortality, reproductive behavior, etc.) is one of the most important components of the relatively new science and conservation strategy.

The project to reintroduce golden lion tamarin (*Leontopithecus rosalia*) is one of the few primate reintroduction programs to be precisely designed and well documented. The scientific approach toward the reintroduction provided an opportunity to evaluate systematically and to assess the status and development of the tamarins in their pre- and post-release environments. Success of the program, defined by surviving monkeys and rate of reproduction, was attributable to intensive post-release monitoring that facilitated identification of sick and injured individuals needing rescue (later re-released) and provision of food and critical resources such as nest boxes (Kierulff *et al*., 2002). In contrast, many reintroduction programs are not documented and incorporate little or no follow-up. Struhsaker and Siex (1998) reported that inadequate details of methodology and lack of follow-up made it impossible to define what factors led to success or failure of the translocation of red colobus (*Procolobus kirkii*) and introduction into Zanzibar. Likewise, information on hundreds of orangutans (*Pongo abelii*; *P. pygmaeus*) released from rehabilitation centers in Malaysia and Indonesia since the 1970s, including methods used, numbers surviving, successes and failures, etc., is poorly documented (Warren and Swan, 2002).

There has been fewer attempts to reintroduce African apes; none has been made to reintroduce bonobos (*Pan paniscus*). Attempts to reintroduce western gorillas (*Gorilla gorilla gorilla*) within former specific range in the Republic of Congo and Gabon were formerly subject to poor monitoring and documentation. Post-release monitoring is now an integral component of the project and a forthcoming publication describes the framework, method, and results of the reintroduction (Farmer and Courage, in press).

Increasing numbers of young apes, particularly chimpanzees, captured illegally from the wild, are a burgeoning problem for African sanctuaries (Farmer, 2002a). Numbers of chimpanzees in African sanctuaries increased

significantly (from 438 to 737) between 2000 and 2005 (Rosen *et al*., 2003; Mills *et al*., 2005), bringing release programs into the forefront as both a welfare and a conservation strategy. Of all projects for release of African chimpanzees, 2 involved release to mainland forest, and 7, release onto islands (Farmer, 2002b). After attacks by wild conspecifics, the project transferred chimpanzees that had been released into a protected area in Senegal to islands in the Gambia (Brewer, 1978; Marsden née Brewer, 1998). An attempt to reintroduce an individual chimpanzee to a wild group in Uganda resulted in transfer to a zoo after repeated visits to villages to look for food (Treves and Naughton-Treves, 1994, 1997). Release onto islands has resulted in 2 nutritionally self-sufficient populations, and 1 in Tanzania (Borner, 1985).

Anecdotal data dominate the literature on the programs, and in some cases even survival statistics are not available because of a lack of follow-up. Exceptions include a comprehensive nutritional analysis of chimpanzee diet after release of chimpanzees onto an island in Gabon (Hladik, 1973, 1977). Hannah and McGrew (1991) systematically collected data on the introduction procedure they used when transferring wild-born chimpanzees from a laboratory in Liberia to nearby islands. Aggressive behavior of chimpanzees released onto islands often prevents follow-up.

From the outset, Habitat Ecologique et Liberté des Primates (HELP) in the Republic of Congo aimed to return wild-born orphaned chimpanzees to their natural environment. In 1991 HELP established a sanctuary on the shore of the Conkouati Lagoon, to rehabilitate chimpanzees from the physical and psychological traumas of capture. HELP gradually placed chimpanzees onto 3 forested islands where they roamed freely but provisioned them because of insufficient natural foods. By 1994, 36 chimpanzees were living on the 3 islands while 12 juveniles remained at the mainland sanctuary with accompanied visits to forest patches. At the same time, HELP investigated the long-term future of the chimpanzees at the sanctuary. The framework and decision-making process behind the release are documented elsewhere in detail, but over a 2-yr period, the organization planned a release program involving many activities that included site and candidate selection, and veterinary and genetic screening (Farmer and Jamart, 2002; Tutin *et al*., 2001). In 1996, HELP released the first group of 5 chimpanzees into the Conkouati-Douli National Park, with a total of 37 chimpanzees released back to the wild (Goossens *et al*., 2005).

To investigate if and how reintroduction could be used to conserve wild populations, HELP developed a long-term post-release monitoring system as an integral component of their project to measure the success of the reintroduction. Data include health status, female reproductive status, interactions with wild congeners, and ranging and nesting

behavior (Farmer, 2002b; Goossens *et al*., 2005). We present data on post-release activity budgets and dietary composition, and compare them to those of wild chimpanzee behavior, as primary indicators of reintroduction success. Significant deviations in time proportioned across activities, number of species consumed, and type and proportion of food classes consumed indicate difficulties in adjusting to living in the natural environment.

METHODS

Study Site

HELP includes 2 sites. The pre-release site comprises 3 forested islands (0.5, 0.3, 0.2 km^2) on the Conkouati Lagoon, bordering the Conkouati-Douli National Park (CDNP), 150 km north of Pointe-Noire in the Republic of Congo (Congo-Brazzaville). The islands provide microhabitats of natural vegetation in which the chimpanzees can forage, build nests, and live in groups with very little human interference. Though chimpanzees eat a variety of plant foods on the islands, none of them are large enough to allow nutritional self-sufficiency, and supplementary food is provided twice daily.

The CDNP (3°33′–4°02′S; 11°10′–11°, 40′E) covers 5045 km^2 and consists of dry closed-canopy forests to permanently and seasonally flooded forests, Marantaceae forests, swamp forests, mangroves, and raffia palms (Doumenge, 1992; Hecketsweiler and Mokoko Ikonga, 1991). Chimpanzee releases have been concentrated in the Triangle, an area of *ca.* 21 km^2 within the CDNP, bound by the Ngongo and Louvandzi rivers and the Conkouati Lagoon. Natural bridges allow individuals to cross the rivers to the surrounding CDNP forests. The Triangle comprises inundated, primary, and swamp forest (Tutin *et al*., 2001). In 1996, the estimated population density of wild chimpanzees in the Triangle was .17–.33 individuals/km^2 or *ca.* 37 individuals (Tutin *et al*., 2001).

Subjects

We studied 16 chimpanzees (*Pan troglodytes troglodytes*)—15 weaned individuals and 1 dependent infant—released into the Triangle in 4 separate periods between 1996 and 1999. Though 37 chimpanzees in total have been released (33 in the Triangle and 4 on the opposite bank of the Ngongo River, north of the Triangle (Goossens *et al*., 2005) we here present a data set that formed the basis of Farmer's doctorate thesis.

Table I. Sex, mean age (±SD) of chimpanzees at arrival to HELP, time spent on pre-release island, and age at release for each stage in the release process

Release stage	Release date	Sex		Age at arrival to HELP		Time spent on pre-release island		Age at release	
		♂	♀	Mean	± SD	Mean	± SD	Mean	± SD
1	24.11.96	1	4	3 yr 0 mo	2 yr 1 mo	5 yr 8 mo	1 yr 6 mo	8 yr 8 mo	1 yr 3 mo
2	25.02.97	0	1	1 yr 5 mo	—	6 yr 8 mo	—	8 yr 1 mo	—
3	28.22.97	1	4	1 yr 3 mo	0 yr 6 mo	5 yr 4 mo	0 yr 5 mo	6 yr 7 mo	0 yr 6 mo
4	01.02.99	2	2	0 yr 8 mo	0 yr 3 mo	9 yr 0 mo	0 yr 7 mo	9 yr 8 mo	0 yr 8 mo

SD, standard deviation.

HELP released chimpanzees primarily within groups (3 groups of 5 individuals), but led 1 chimpanzee released alone to join a group of 5 individuals that originated from the same island and were released *ca.* 2 months earlier. We fitted 14 chimpanzees with telemetric radio collars (Telonics) pre-release to facilitate post-release monitoring. The neck morphology of 1 male (R4) made it impossible to fit a collar. We did not fit the dependent infant with a collar.

Group composition at each release, including number, sex, mean age at arrival to HELP, mean time spent on island, and mean age at release, are in Table I. HELP released 1 female (R4) with a 2-mo-old female that had been conceived and born on the island (figures in Table I do not include the dependent infant). We did not collect data on the infant because it would not be routinely performing many activities and its activity profile would be very closely linked to that of its mother. HELP had previously rehabilitated the chimpanzees on 2 of the 3 islands (Yombe Island: 0.5 km^2; Yvette Island: 0.3 km^2). All chimpanzees were wild-born and had spent on average 5–9 yr on the island and had an average age of 6–10 yr at release.

Post-release Monitoring and Data Collection

General Activity

We did not collect data on pre-release behavior because it was impossible to enter the islands because of territorial aggressive behaviors of the adolescent and adult chimpanzees. Post-release, we recorded each individual's activity every 10 min via scan sampling with instantaneous recording. We adapted behavioral categories and definitions from Nishida *et al.* (1999). The definitions of behaviors that we recorded are in Table II.

A team of Congolese and expatriate field assistants (including Farmer) followed chimpanzees from nest to nest, 7 d/wk. We recorded observations from 0500 h to 1920 h. To assess interobserver reliability, we used the index

Table II. Behavior classifications and description

Category label	Definition of activities included within category
Feed	Remove food item (fruit, leaves, stem pith, etc.,) from the substrate, process, put into mouth, bite and chew, wadge and swallow it
Rest	Remain immobile (sit, lie) both on the ground and in trees. Noted if rest was within a nest
Move	Walk, run, jump, somersault, climb and descend between two locations on the ground and within trees
Groom	Hair pulled back with the thumb or finger of 1 hand and holding it back while picking at the exposed skin with the nail or finger of the other hand. Grooming may occur while sitting or lying. Indicated whether self or social
Aggression	Attack (aggressive physical contact between 2 or more chimpanzees) or threaten (repertoire of behaviors (e.g., arm wave, hit towards, branch wave, charge, slap, etc.) to elicit submissive behavior
Play	Divided into lone and social play. Can involve locomotor (e.g., dangle, leap, swing, somersault, tickle, chase, slap, etc.) and object play (e.g., pick up, throw, drag, drape etc.)
All other behaviors	a) Copulation (intromission and pelvic thrusting between a male and estrous female). b) Drinking (drinking of water or other liquids by directly leaning over source, dripping water from fingers, licking water from substrates, etc.). c) Coprography (eating of feces). d) Urine drinking (drinking of urine from substrate or from own up-jetted stream). e) Nest building (construction of a bed by bending branches). f) Urinating. g) Defecating

Adapted from Nishida *et al.*, 1999.

of concordance (Martin and Bateson, 1998). We compared the total number of agreements and disagreements between Farmer and 5 field assistants (responsible for the majority of observations), and the interobserver reliability score at its lowest was 86% and highest 100% (Farmer, 2002b).

Diet

For post-release feeding records, we noted the plant species and part consumed. If we could not identify the plant species, we collected, numbered, and preserved a sample for later identification. We could not identify all plant parts consumed to specific level and where necessary used the plant genera, family, or life form for descriptive purposes. As an indication of the number of species consumed, we counted as 1 species the ones identified to genera, family, or life form, assuming that subjects consumed a minimum of 1 species. Such a conservative method probably underestimates the number of species consumed. We categorized plant parts as fruit, leaf, stem pith, seed, flower, sap, shoots, and bark. We measured diet in terms of time spent feeding on each food class, plant species, and part.

Analyses

Activity Budgets

We collapsed behavioral data (Table II) into 4 main core categories for analysis (Dunbar, 1988; Teleki, 1977). We performed analyses on mean percentage scores as observations (total of 240,673 data points) across chimpanzees, and months were uneven. We pooled monthly mean percentage scores for each chimpanzee and activity to get the overall mean budget for each activity and to ensure statistical independence. We analyzed data for the first 14 mo post-release except for 2 males from R4; 1 male disappeared during mo 4, and we included 12-mo data for 1 male that was not observed during mo 2 and mo 13.

We compared seasonal variation in activity levels and consumption of each main food class. Regional climate is characterized by a dry season between May and September, and a rainy season between October and May (Doumenge, 1992; Dowsett, 1991; Hecketsweiler and Ikonga, 1991). We collected climatic data at the release site consistently during 1998 and early 1999, which we used to determine site-specific seasonality.

Comparative data on wild chimpanzees are in Table III. We show multiple studies from the same site to illustrate variations within and between sites. Influencing factors such as habitat type, season, age, and sex of chimpanzee and type of budget measurement are included to facilitate comparison. However, there are caveats because not all studies present data in the same format.

Diet

We selected 3 studies presenting comparative data on wild chimpanzee diet on the basis of similar habitat type to CDNP (all lowland tropical forest within central Africa): Lopé Reserve, Gabon (Tutin *et al.*, 1994); Nouabalé-Ndoki, Republic of Congo (Moutsamboté *et al.*, 1994); and Itebero region in Kahuzi-Biega, Democratic Republic of Congo (Yumoto *et al.*, 1994). The most comprehensive dietary analysis is that on a group of released chimpanzees on an island of lowland tropical forest in Gabon and is included here as an additional comparison (Hladik, 1973, 1977).

We analyzed variables via repeated measures ANOVA and Bonferroni *post hoc* tests. We provide exact values of probability up to 4 decimal places; lower values are displayed as $p < 0.0001$.

Table III. Activity budgets of wild and released chimpanzee populations

Wild chimpanzee populations				Released chimpanzee populations										
Country	Tanzania	Tanzania	Tanzania	Uganda	Uganda	Uganda	Uganda	Eq. Guinea	Ivory Coast	Ivory Coast	Gabon	Republic of Congo		
Study site	Gombe	Gombe	Gombe	Budongo	Budongo	Budongo	Kibale	Rio Muni	Tai Forest	Tai forest	Ipassa (Sonso)	Conkouati (Sonso)		
Reference	Goodall, 1965	Wrangham, 1975	Teleki, 1981	Reynolds and Reynolds, 1965	Newton-Fisher, 1999	Fawcett, 2000	Ghiglieri, 1984	Sabater-Pi, 1979	Doran, 1997	Boesch and Boesch-Achermann, 2000	Hladik, 1973	Current data		
Habitat	E/SD/G/BW	E/SD/G/BW	E/SD/G/BW	CL/MF/CF/S	CL/MF/CF/SF	CL/MF/CF/SF	PF/G/SF/SC	PF/RF/SF/MF	LRF	LRF	SF	IF/PF/SF	IF/PF/SF	
Season	D/R	D/R	D/R	R	D/R	D/R	D/R	D/R	D/R	D/R	D/R	D/R	D/R	
n	MD	14	31	MD	MD	36	MD	MD	30	MD	8	15	15	
Age	M/IM/I	P/PP	8–35 yr	ALL	NS	A/AD	A/SA/J/I	ALL	ALL	ALL	4–8 yr	6–10 yr 6-10 yr		
Sex	M/F	M	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	
Measurement	HD	O	D (15 h)	HD	O	O	D	D	D	O	HD	O	D	
ACTIVITY:														
Feeding	6–7	55.7%	42.8%	6-8	48.8%	52.8%	62.1% (♂)	40.8%	43%	45%	4.5–5.5[f]	50.75%	50.22%	52.5% (♀)
Moving	–	13.8%	13.5%	–	–	7.5%	12.1% (♂)	27.5%	12%	22%	–	14.96%	14.77%	10% (♀)
Resting	–	24.1%[a]	18.9%	–	–	25.0%	25.8%[e] (♂)	–	39%	22%[e]	–	26.67%	26.90%	37.6%[e] (♀)
Grooming	–	6.2%[b]	–	–	–	14.3%	–	–	–	–	–	2.57%	2.20%	
Social	–	–	24.9%[c]	–	–	0.04%[d]	–	–	– –	–	2.88%[g]	2.45%[g]		

Habitat: E = Evergreen forest; SD = semideciduous forest; G = grassland; BW = *Brachystegia* woodland; CF = colonizing forest; MF = mixed forest; CF = *Cynometra* forest; SF = swamp forest; PF = primary forest; SC = scrub; RF = regenerating forest; MF = montane forest; LRF = lowland rain forest; IF = inundated forest. Season: D = dry; R = rainy; n: MD = missing data. Age: NS = not specified; ALL = all ages; M = mature; IM = immature; I = infant; P = prime; PP = past prime; A = adult; AD = adolescent; SF = subadult; J = juvenile
Sex: M = male; F = female. Measurement: O = overall; D = daily; HD = hours per day

[a] Sit/stand inactive 17.8% and lie (not in night nest) 6.3% = total 24.1%.

[b] Allogroom only.

[c] Includes all instances of self-groom and solitary play in addition to social instances.

[d] Includes all instances of social behaviours except groom such as copulation, dominance and vocalization.

[e] Includes social time.

[f] Chimpanzees were provisioned in this study accounting for *ca.* 30% of their diet. Hladik argues that if movements necessary to locate food are included then the time involved in feeding would rise to 6.5–7.5 h. However, he does not describe how he distinguishes feeding from nonfeeding movements.

[g] Includes social grooming, social play, aggression and copulation.

RESULTS

Survivorship

As of February 2004, of the 16 chimpanzees released, 9 were alive (7 females and 2 males) including 7 that were released >5 yr ago. The status of 5 chimpanzees is unknown (4 females and 1 male): researchers have not observed 1 male since 5 mo post-release (R4), 2 females after 2 yr (R3 and R4), and 2 females after 5 yr post-release (R1 and R3). It is unlikely that researchers following wild chimpanzees would fail to see a well-habituated male for >3 yr, and therefore it seems certain that he died. It is plausible, though also unlikely, that one would not see wild females for long periods of time unless they were immature and subsequently transferred into a neighboring community. However, we observed 2 females with wild chimpanzees that we had not seen for 21 and 8 mo, respectively. A third female reappeared to a released group after we had not seen her for 10 mo. There have been 2 confirmed deaths; 1 male died as a direct result of injuries inflicted by wild chimpanzees nearly 4 yr post-release and the dependent infant disappeared 5 mo post-release and is presumed dead. The release program therefore has a confirmed 56% success rate and 88% (as of February 2004) if all status unknown cases are included.

Activity Budgets

Feeding, moving, and resting accounted for 92% of all time (Fig. 1). Subjects devoted very little time to social activities but groom predominated (85%, $n = 5237$). The majority of groom (97%, $n = 5065$) and play (77%, $n = 436$) were social.

Activity budget data of wild and released chimpanzees are in Table III. Released chimpanzees spent 51% of their time overall, and 50% daily, eating. The values fall within the range for wild chimpanzees, as does the estimated 7.5 h/d spent feeding (Table III). Chimpanzees released into Ipassa spent 4.5–5.5 h/d feeding. Time spent moving and resting also fell within ranges to similar wild chimpanzee budgets.

Two studies of wild populations provided data on social activity. The discrepancies between them are attributable in part to differences in categorization, i.e., 25% includes all instances of self-groom and solitary play in addition to social instances (Teleki, 1981), whereas .04% excludes all grooming (Fawcett, 2000). However, chimpanzees in our study spent

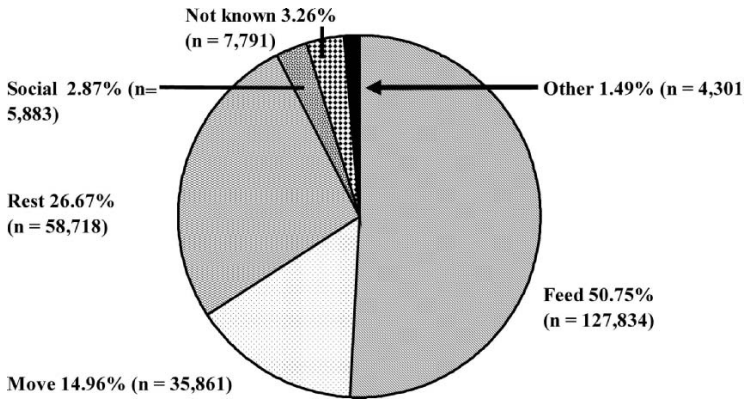

Fig. 1. Overall mean time releases engaged in core activities (number of scans in brackets).

considerably less time grooming (all instances of groom) than either of the 2 wild populations.

Sex Differences in Activity Budgets

Four of 10 wild chimpanzee studies in Table III provided data on sexual differences (Table IV). Doran (1997) noted little difference between females and males, whereas Fawcett (2000) and Ghiglieri (1984) noted that females moved less than males did, and Ghiglieri (1984) also documented that males fed more and rested less than female chimpanzees did. Our female subjects spent significantly more time than males feeding (F (3, 39) = 8.85, $p < 0.001$).

Seasonal Variation in Activity Budgets

We examined effects of season on activity budgets. Chimpanzees spent significantly more time feeding but less time resting in the dry season (F (3, 39) = 37.04, $p < 0.001$) (Fig. 2). There is no significant difference in time spent moving or within social activities in the dry and wet season.

Diet of Released Chimpanzees

Pre-release chimpanzees ate $\geq$23 plant parts from $\geq$14 species. Post-release the chimpanzees ate $\geq$239 plant parts from $\geq$122 species. We identified 62 species, from 3 orders, 39 families, and 55 genera (Table V) and identified another 22 food plants, from 2 orders and 17 families, to the

Table IV. Activity budgets and results of comparisons made between female and male wild and released chimpanzees

Activity	Chimpanzee group	Reference	*N*		Activity budget%		Significance
			♀	♂	Females	Males	
Feed	Wild	Fawcett, 2000	19	17	54.73	50.60	NS
		Ghiglieri, 1984	MD	MD	52.50	62.10	$p < 0.05$
		Doran, 1997	23	7	43	43	NS
		Teleki, 1981	13	18	51.80	40.10	NT
	Released	Current data	11	4	53.45	43.32	$p < 0.001$
Move	Wild	Fawcett, 2000	19	17	6.33	8.83	$p < 0.01$
		Ghiglieri, 1984	MD	MD	10	12.10	$p < 0.05$
		Doran, 1997	23	7	12	12	NS
		Teleki, 1981	13	18	14.60	13	NT
	Released	Current data	11	4	14.76	15.52	NS
Rest	Wild	Fawcett, 2000	19	17	24.58	25.49	NS
		Ghiglieri, 1984	MD	MD	37.6	25.8	$p < 0.05$
		Doran, 1997	23	7	39	39	NS
		Teleki, 1981	13	18	15.50	20.10	NT
	Released	Current data	11	4	24.56	32.48	NS
Groom	Wild	Fawcett, 2000	19	17	13.90	14.76	NS
	Released	Current data	11	4	2.23	2.81	NS
Social	Wild	Fawcett, 2000	19	17	0.04	0.03	NS
		Teleki, 1981	13	18	18.10	26.80	NT
	Released	Current data	11	4	2.98	3.27	NS

MD = missing data; NS = nonsignificant; NT = not tested.

generic level. We did not identify the remaining 38 to genus or family. Of the 62 identified species, 45 are trees, 8 lianas, 5 herbs, 3 palms, and 1 fern. Those identified to genus comprise 11 trees, 4 lianas, 5 herbs, 1 palm, and 1 shrub. Of nonidentified species, 8 are liana and 1 tree. Chimpanzees also ate ≥ 1 species of fungi. Though the diet of reintroduced chimpanzees was diverse, the vast majority of time spent feeding (>70%) was accounted for by consumption of relatively few species (Farmer, 2002b): *Elaeis guinnensis*, *Irvingia gabonensis*, *Scytopetalum klaineanum,* and *Staudia gabonensis*, plus ≥ 1 species of *Vitex* and *Dialium*, Marantaceae, and liana. They ate fewer species than chimpanzees at Ipassa and Lopé did, but more than individuals at Nouabalé-Ndoki and Kahuzi-Biega.

Composition of Diet

Fruit dominated the diet of the reintroduced chimpanzees, followed by leaf and stem pith that together constituted a major component of the diet (Table VI). Chimpanzees ate sap, seed, shoots, and bark in small amounts,

Table V. Number of plant order, family, genera, species and parts consumed by released and wild chimpanzees

		Released chimpanzees				Wild chimpanzees					
Reference		Present data		Hladik, 1973, 1977		Tutin *et al.*, 1994		Moutsambote *et al.*, 1994		Yumoto *et al.*, 1994	
Site		Conkouati		Ipassa		Lopé		Nouabalé-Ndoki		Kahuzi-Biega	
Study Duration		1996–2000		1971–1972		1983–1994		1988–1992		1987–1991	
Diet (*n*)	Order	3		2		2		2		3	
	Family	39		38		36		28		28	
	Genera	55		90		85		49		41	
	Species	122		151		141		64		48	
Parts eaten		%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
	Fruit	42	101	67	116	66	116	80	53	74	39
	Leaves	26	62	10	18	12	21	3	2	8	4
	Seeds	8	19	9	16	9	16	8	5	1.5	1
	Stem/pith	8	19	3	6	6	11	6	4	15	8
	Flower	7	17	4	7	4	7	3	2	–	–
	Sap	7	17	–	–	–	–	–	–	–	–
	Shoots	2	4	6	10	–	–	–	–	–	–
	Bark	–	*	1	1	2	4	–	–	1.5	1
	Galls	–	–	–	–	1	1	–	–	–	–
	Total		239		174		176		66		53

* = not known.

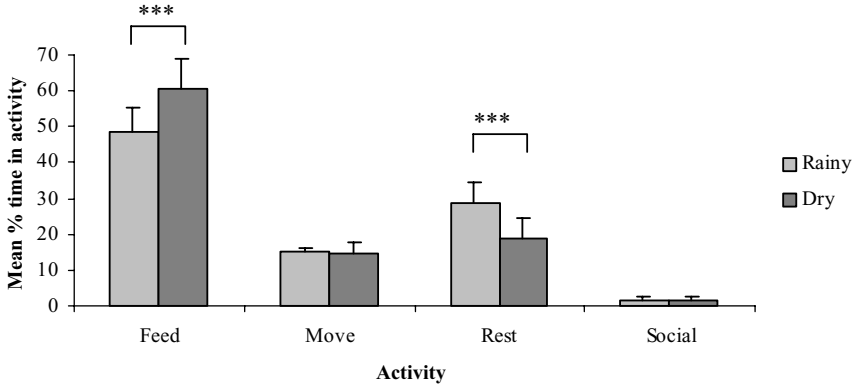

Fig. 2. Mean percentage time spent in each activity and season (±SD). $^{***}p < 0.001$.

and did not eat any food type significantly more or less across dry and rainy seasons (F (4,50) = 0.68, $p = 0.612$). Each chimpanzee consumed nonplant food that consisted primarily of invertebrate prey and parts, e.g., ant nest, honey. Though all chimpanzees received some supplementary food (primarily to encourage post-release exploration), overall the amount constituted a very small proportion of the diet.

Table VI. Mean percentage time (±SD) spent feeding on plant parts by the released chimpanzees

Food part	Overall mean%	±SD	*n* (chimpanzee)
Fruit	54.97	8.28	15
Leaf	19.27	4.61	15
Stem	16.87	4.69	15
Flower	2.03	2.48	15
Seed	0.85	1.07	15
Sap	0.68	0.53	15
Shoots	0.07	0.05	9
Liquid	0.07	0.02	4
Fungi	0.02	0.07	2
Bark	0.01	–	1
Invertebrate prey and associated parts	2.13	1.25	15
Vertebrate prey and associated parts	0.07	0.06	9
Supplementary food provided by observers	0.79	1.13	15
Not known	0.59	0.47	14

Anecdotal Feeding Behaviors

All chimpanzees ate insect matter (Table VI). Invertebrate prey included ants, sometimes with nest (soil), caterpillars, centipedes, grasshoppers, larvae of insects and wasps, wasps, weaver ant *Oecophylla longinpoda,* and termite *Macrotermes*. Chimpanzees also ate honey. Observers had previously shown chimpanzees how to crack *Elaeis guinnensis* (palm nut) with a wooden baton, and the subjects did so. The chimpanzees occasionally used tools such as leaf stems to extract insects, though we had not shown them how.

The chimpanzees hunted, and vertebrate prey included flying squirrel (*Anomaluridae*), pangolin (probably *Phataginus tricuspis*), potto (*Perodicticus potto*), birds, bird eggs, and tortoise (*Kinixys erosa*). On one occasion, a female chimpanzee smashed the shell of a tortoise several times against a tree trunk and then inserted twigs inside the shell in an attempt (unsuccessful) to access its torso. Chimpanzees also found prey opportunistically; we observed 1 female consuming the remains of a dead owl.

DISCUSSION

The released chimpanzees engaged in similar core activities that reflect, though not exactly replicate, the overall patterns in wild chimpanzee populations (Boesch and Boesch-Achermann, 2000; Doran, 1997; Fawcett, 2000; Teleki, 1981; Wrangham, 1975). Comparative data show variation between sites, multiple studies at the same site, and wild vs released populations, but one should not expect budgets to be directly comparable because they reflect adaptation to a particular ecological niche and environmental conditions. The low number of daily feeding hours in chimpanzees released in Gabon are explained by 30% of their diet being provisioned. If movements necessary to locate food are included then feeding time would increase to similar levels (Hladik, 1977). The data indicate that the chimpanzees adjusted their activity patterns to seasonal variations.

No consistent pattern of sex differences in activity budgets is reported in wild chimpanzees. Our female subjects spent more time feeding than males did, without any obvious reason. We found only 1 consistent discrepancy between the wild populations and the reintroduced chimpanzees: wild chimpanzees groomed socially more than the reintroduced chimpanzees did. The significance is unclear, but it may reflect the lack of bonds between them, or the need for them to spend more time foraging for food and performing other activities.

Like wild congeners, released chimpanzees had a broad fruit-dominated diet. As with activity budgets, there are differences, which may in part reflect variation in abundance and profitability of potential foods, and show that chimpanzees can obtain diets from a wide array of species in different habitats. Released chimpanzees spent >70% of their time feeding on a smaller number of species, and such specialization has also been observed in wild communities (Fawcett, 2000; Newton-Fisher, 1999; Tutin and Fernandez, 1993; Wrangham *et al*., 1996). Lack of consistent methodology made comparisons across different field sites problematic.

That released chimpanzees eat insects, use tools, and hunt further supports their nutritional and behavioral adjustment. Tool use and type vary among sites (Whiten *et al*., 1999), and evidence of tool use by wild chimpanzees in the area has yet to be identified. Wild chimpanzees in the Ituri Forest (DRC), in common with the reintroduced chimpanzees, use sticks to extract the contents of tortoise shells (J. Hart, personal communication, cited in McGrew, 1992). Despite the chimpanzees being captured from the wild at an ecologically naive age, clearly the pre-release environment provided adequate social and individual learning opportunities about potential foods.

Post-release monitoring costs *ca.* US$5,200 per chimpanzee per yr (Goossens *et al*., 2005), though costs could be reduced by use of a less intensive monitoring system. However, HELP attributes the high survival rates of the chimpanzees and overall success of the release program to careful planning and detailed post-release monitoring (Goossens *et al*., 2005). As with golden lion tamarin reintroduction, post-release monitoring has facilitated survival rates through the identification of sick and injured individuals requiring veterinary intervention. Further, the presence of observers has in some cases intercepted or interrupted aggressive encounters with wild congeners. These events cannot be predicted. If one purpose of post-release monitoring is to intervene as required to improve survivorship, then post-release monitoring must be as continuous as possible. If the monitoring is for other purposes, e.g., to study adjustment to the wild, or survival, monitoring need not be as intense.

The release of 13 chimpanzees in 2001 terminated the current phase of the HELP program and there is no plan to reintroduce more chimpanzees into CDNP. However, post-release monitoring is scheduled to continue for the next 5–10 yr to measure long-term ecological and behavioral adjustment and monitor female reproduction and males until they reach adult size and are able to defend themselves during aggressive encounters with wild chimpanzees (Goossens *et al*., 2005). However, defense is not just a matter of individual physical strength but also of group force. The released

community now comprises only 2 males and they will not be able to defend themselves against intercommunity aggression. Earlier concerns about releasing chimpanzees into areas where wild conspecifics live (Brewer, 1978) are clearly justifiable. Obviously HELP has a dilemma, either to continue intensive follows *ad infinitum* to afford protection, particularly for males that are more susceptible to intercommunity aggression, or to take a less interventionist, and undoubtedly more cost-effective approach. However, though the present intensive regimen appears costly, it has produced a unique body of field data, and many additional spinoffs accompany programs such as raising public awareness and promoting conservation (Farmer and Courage, in press; Cowlishaw and Dunbar, 2000; Tutin *et al*., 2001). The existence of the HELP project and its field staff contributes to the protection of the CDNP. Indeed there has been no sign of poaching or deforestation in the Triangle release zone, and this part of the reserve is in better condition now than it was in 1996 (Maisels and Onononga, 2000). Further, HELP, along with other stakeholders, were instrumental in highlighting the biological richness and uniqueness of the Conkouati Reserve which led to its classification as the Conkouati-Douli National Park in 1999 (Goossens *et al*., 2005). Studies such as this provide background information to assist sanctuaries to evaluate the costs and benefits of reintroduction, and highlight the importance of incorporating systematic data collection into post-release monitoring.

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