Modes of transmission of Simian T-lymphotropic Virus Type 1 in semi-captive mandrills (*Mandrillus sphinx*)

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**A B S T R A C T**

Non-human primates (NHPs) often live in inaccessible areas, have cryptic behaviors, and are difficult to follow in the wild. Here, we present a study on the spread of the simian T-lymphotropic Virus Type 1 (STLV-1), the simian counterpart of the human T-lymphotropic virus type 1 (HTLV-1) in a semi-captive mandrill colony. This study combines 28 years of longitudinal monitoring, including behavioral data, with a dynamic mathematical model and Bayesian inference. Three transmission modes were suspected: aggressive, sexual and familial. Our results show that among males, STLV-1 transmission occurs preferentially via aggression. Because of their impressive aggressive behavior male mandrills can easily transmit the virus during fights. On the contrary, sexual activity seems to have little effect. Thus transmission appears to occur primarily via male–male and female–female contact. In addition, for young mandrills, familial transmission appears to play an important role in virus spread.

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1. **Introduction**

Most non-human primate (NHP) species are increasingly threatened by habitat destruction due to human population expansion, and commercial hunting. Diseases caused by microorganisms are also recognised as an additional major threat to these animal populations, for example, Ebola (Walsh et al., 2003) and bacterial/viral respiratory outbreaks (Köndgen et al., 2008). Thus, understanding the transmission and impact of microorganisms in NHP populations has recently become an urgent issue to be addressed for the conservation of biodiversity (Boesch 2008). However, NHPs often inhabit inaccessible areas, display cryptic behaviors, and are difficult to follow in the wild (Pandrea et al., 2006). Moreover, NHP species generally live in highly complex, hierarchical societies structured around elaborate social networks, which, in addition to placing them at unusually high risk from infectious diseases, increases the complexity of the mechanisms that have to be deciphered to get insights into NHP disease dynamics (Altizer et al., 2003).

Mandrills (*Mandrillus sphinx*) are endangered long-lived (15–20 years life expectancy) NHPs, endemic to the rain forests of West-Central Africa. Because they are extremely difficult to observe and follow in their densely forested wild habitat (Abernethy et al., 2002; Bret et al., 2013), like many NHPs, especially monkeys, mandrills are also poorly studied. The colony of mandrills housed at the International Centre for Medical Research in Franceville (CIRMF), Gabon, offers a unique opportunity to unravel a number of unexplored aspects of host-microbe interactions in NHPs in general, and in mandrills in particular (Fouchet et al., 2012; Bret et al., 2013; Roussel et al., 2015). This population lives in semi-captive conditions offering the possibility to monitor individuals throughout their lives while preserving a wild population dynamic. However, there are certainly differences given the limited surface of the forest enclosure and the fact that being semi-captive they do not need to actively search for food and are also less exposed to aggression or predation from other animals. Mandrills from this colony are naturally infected by a retrovirus, the simian T-lymphotropic virus type 1 subtype D (STLV-1 hereafter). As yet, very little is currently known about the epidemiology of the disease in this species.

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STLV-1 is the simian counterpart of the human T-lymphotropic virus type 1 (HTLV-1) discovered in 1982 in Japanese macaques (Macaca fuscata) (Miyoshi et al., 1982). The virus infects a wide range of NHPs in Asia and Africa including baboons, African green monkeys, guenons, mangabeys, orangutans, mandrills, chimpanzees and gorillas (Ishikawa et al., 1987; Saksena et al., 1994; Ibufi et al., 1997; Mahieux et al., 1997; Niphuis et al., 2003), and shares viral, immunological, molecular and pathological characteristics with HTLV-1 (Saksena et al., 1994; Gessain et al., 1996). Many phylogenetic studies argue that STLV-1 is the simian ancestor of HTLV-1, the latter resulting from multiple NHP transmissions to humans (Mahieux et al., 1998; Ettena et al., 2008; Kazanj et al., 2014). For instance, the mandrill STLV-1d is strongly suspected to be at the origin of the pygmy population's HTLV-1d infection in West-Central Africa (Mahieux et al., 1998). Although they remain largely asymptomatic, HTLV-1 and STLV-1 are responsible for severe diseases including adult T-cell leukemia of which cases have been observed in captive green monkeys, baboons and gorillas (Miyoshi et al., 1982; Voevodin et al., 1985). Up to now, no disease from STLV-1 has been reported for mandrills (George-Courbot et al., 1996; Kenriet et al., 1998; Souquier et al., 2009), except in individuals co-infected with SIVmnd-1 (Souquier et al., 2014).

HTLV-1 transmission modes are well established and can occur through direct blood contact (transfusion, intravenous drug use), sex (mostly man-to-woman) (Schreiber et al., 1997) and from mother-to-infant, mainly through breast-feeding (Nyambi et al., 1996). In contrast to the human situation, little is known about STLV-1 transmission modes in natural populations of NHPs (Niphuis et al., 2003; d’Offay et al., 2007). In captive and wild chimpanzees (Pan troglodytes verus), most transmissions appear to result from social conflicts leading to blood to blood contacts (Niphuis et al., 2003). Mother-to-infant (Niphuis et al., 2003; Leendertz et al., 2004) and sexual transmission (Leendertz et al., 2004) appear to be uncommon. In mandrills, it has been suggested that STLV-1 is mainly transmitted among males, probably during fights, while sexual transmission is rare (George-Courbot et al., 1996; Kenriet et al., 1998). Female-to-female transmission has been reported to be as important in captive baboons (Papio anubis), but female-to-infant transmission also occurs (d’Offay et al., 2007). Mothe-to-infant transmission has also been observed in captive rhesus macaques (Macaca mulatta) (Parrish et al., 2004). Behavioral differences among NHP species are expected to lead to different patterns of STLV-1 circulation in their populations (Bahi-Jaber et al., 2008; Souquier et al., 2009).

Until now, in order to understand how STLV-1 is transmitted, epidemiological studies have been based on analyses of surveillance prevalence, neglecting the dynamical aspect of the STLV-1 transmission process. This aspect is particularly important to determine the transmission mode of agents since it allows statistical links between infection of individuals and their congeners of different age and sex class that potentially have infected them to be established, rather than deducing the information from a static view of the age and sex prevalence data. In the present paper, we propose to combine the long-term longitudinal monitoring of the CIRMF semi-captive mandrill colony conducted over the past 28 years, using the method of Fouquet et al. (2012) i.e., a dynamic mathematical model representing a variety of transmission routes (sexual, aggressive, familial) to evaluate the relative weight of the different suspected STLV-1 transmission modes based on Bayesian inference.

2. Methods

2.1. Study population

Mandrills live in large, highly structured social groups of several hundreds of individuals composed of females and their dependent offspring. Submature and mature males join the groups only during the breeding season, from June to October (Abernethy et al., 2002). Outside the breeding season, most submature and mature males emigrate from the groups and live a solitary, nomadic life (Abernethy et al., 2002; Setchell et al., 2002). Mandrills have the highest level of sexual dimorphism of all NHPs (Setchell et al., 2005a) with males being three times heavier than females and displaying spectacular secondary sexual characters such as long canine teeth that serve as weapons (Setchell et al., 2005b).

Most of mandrill studies derive from the CIRMF semi-captive mandrill colony in Gabon. This colony was founded in 1983 when 15 unrelated mandrills (8 females and 7 males), originating from the wild, were released into a 6.5 ha natural rain-forest enclosure (E1). Subsequent increase in group size has been due to natural reproduction of the founder animals. In 1994, due to several mandrills being infected by simian immunodeficiency virus type 1 (SIVmnd-1), the CIRMF created a second enclosed area (E2) of 3.5 ha where all SIVmnd-1-infected mandrills and their families (offspring and other relatives) were put. A total of 17 individuals, corresponding to four matrilineals were transferred into the new E2 enclosure. Over the years, individuals from the E1 enclosure that were SIVmnd-1 – or STLV-1-positive were transferred to E2 so that E1 contained only SIVmnd-1- or STLV-1-negative individuals. This was instigated in 2005, when new infections began to be identified following incidents in which adult males crossed the fence between the two enclosures in search of mates. These voluntary intrusions and transfers of adult males from one enclosure to another are reminiscent of the natural patterns of seasonal male immigration into social groups during breeding periods (Abernethy et al., 2002).

In the colony, life expectancy is much lower in males (14 years) than in females (>22 years) (Setchell et al., 2005a). Juvenile males often play between themselves and have little interaction with adults and become adolescent at about 3–4 years old. Adolescent and adult males are aggressive with each other and also with females. Their aggression towards females might be one of the factors influencing their expulsion from the group (Charpentier et al., 2004). The mating system is polygynous. Females reach sexual maturity at 3–4 years old whereas males reach it at around 9–10 (Setchell et al., 2005b). Sexual selection is stronger in males than in females by the fact that males fight for access to fertile females while females choose their partners by avoiding male relatives (Setchell et al., 2005b). Dominant males mate-guard fertile females and sire most offspring of the social group (Setchell et al., 2005a).

In order to study STLV-1 transmission modes, we used the 28-year period of CIRMF monitoring (1983–2011) focusing on the E1 mandrills prior to 1994 and those of E2 - i.e., the STLV-1- and SIVmnd-1-infected mandrills and their matrilineals transferred from E1 to E2 - from 1994 to 2011.

2.2. Behavioral data

The observations regarding the mandrills’ physical state and their genealogy were taken from Fouquet et al. (2012). Observations on their physical state were collected every day during feeding. Annual captures for blood tests gave information about their serological status. Otherwise, part of the colony’s genealogy was established according to observations of maternal behavior during the young mandrills’ first six months of life. In addition, paternity tests were systematically performed based on microsatellite markers until 2002 (Charpentier et al., 2006). Further information is available in the Supplementary Material, File S1.

2.3. Serological status of mandrills

High genetic similarity between STLV-1 and HTLV-1 allowed the use of HTLV-1 diagnostic criteria in humans for STLV-1 in
mandrills. As previously described (Mahieux et al. 1997), STLV-1 serologies were performed using a commercial HTLV-1 ELISA test (Vironostica, bioMérieux, Marcy l’Étoile, France). STLV-1 infection was confirmed by Western blot (HTLV blot 2.4, Genelabs Diagnostics Pte Ltd., Science Park Drive, Singapore). Mandrills were considered STLV-1-seropositive if a complete Western blot profile was obtained (Souquière et al. 2009).

Young mandrills are breastfed for almost a year, and consequently, if the mother is infected, maternal antibodies will be found in her infant during this period and a few months later, even if it is not infected (Nyambi et al. 1996). It was important to take this information into account in order not to detect false positives.

2.4. Modeling

To quantify the contribution of STLV-1 transmission modes, we used a model developed by Fouchet et al. (2012), which is a $SI$ type model with two compartments: susceptible ($S$) and infected ($I$). It is a discrete-time, stochastic, age- and gender-structured model. The use of a discrete-time model was appropriate given the low rate of STLV-1 spread and the fact that it greatly simplified the calculations given the data structure (a quasi-exhaustive census each year). The model only focuses on the contamination of individuals without taking into account demographic events (births, deaths).

We did not expect to find the same age distribution of cases for each transmission mode. According to the age and the gender of infected individuals at time $t$, each transmission mode predicted different cases at time $t+1$ (in terms of age and gender). Different transmission modes led to different epidemiological stories. Conversely, individual epidemiological stories allowed us to assess the weight of the different transmission modes.

The likelihood of the model is based on the epidemiological stories. The probability that an individual $k$ remains susceptible to STLV-1 in the lapse of time between its first and last STLV-1-negative observation, respectively $FS$ and $LS$, is $e^{-\sum_{t=0}^{n-1} \lambda_k(t)}$. The probability that it becomes infectious between $LS$ and the first year it was observed infected ($FI$) is $1 - e^{-\sum_{t=0}^{n-1} \lambda_k(t)}$. The term $\lambda_k(t)$ represents the infection rate of the individual $k$, depending on its gender, its age and the population state (number of infected mandrills by age and gender at time $t$). The global likelihood ($L$) is the product of all individual likelihoods:

$$L = \prod_{k \in \Omega_T} e^{-\sum_{t=0}^{n-1} \lambda_k(t)} \prod_{k \in \Omega_L} 1 - e^{-\sum_{t=0}^{n-1} \lambda_k(t)}$$

where $\Omega_T$ is the set of all individuals and $\Omega_L$ is the set of infected individuals. As mentioned above, over the years STLV-1-infected mandrills were transferred from E1 to E2 after they had been detected as being seropositive. We did not consider these infections in the likelihood calculation because their contamination occurred outside the study area (i.e., E2 after 1994).

Regarding the transmission modes, sexual and aggressive interactions are the commonly suspected routes in STLV-1 transmission. However, Fouchet et al. (2012) recently reported that in this colony that saliva and blood exchanges between closely

![Fig. 1. Spread of STLV-1 within the CRMF semi-captive mandrill population. (a) Number of STLV-1d infected individuals present within the study population each year (black line, males; grey line, females). (b) Age at first infection in males (black squares) and females (grey circles). Each symbol represents an individual. (c) Distribution of age at first infection in E2 (black bars, males; grey bars, females). (d) Kinship relation with infected individuals according to the first infectious observation for males (black squares) and females (grey circles). Each symbol represents an individual.](image-url)
related individuals represent a potentially significant mode of SIVmnd-1 transmission. As saliva and blood exchanges are also suspected to transmit STLV-1, we decided to assess whether familial interactions – the route by which virus is transmitted from an infected female to a related individual of either gender – play an important role in STLV-1 transmission.

STLV-1 has a priori both horizontal and vertical transmission. Since in our data set only one potential case of vertical transmission was identified (an individual born from a seropositive mother, who was detected as being seropositive when first captured at less than one year old, and who was still seropositive when recaptured during the following years), we chose to focus only on horizontal transmission. The suspected case of vertical transmission was thus discarded from the data.

The transmission rate \( \lambda_k \) can be divided into three terms corresponding to the three possible transmission routes:

\[
\lambda_k = \lambda_k^A + \lambda_k^S + \lambda_k^F
\]

where \( A \) stands for the aggressive route, \( S \) for the sexual route and \( F \) for the familial route. The weight of each mode of transmission was quantified by Bayesian inference. We chose non-informative prior and posterior distributions, simply derived from the Bayes formula.

To test the kinship effect we calculated the statistic \( s \) as being the sum of the family links between all possible pairs of infected individuals and their potentially infecting counterparts. The distribution of \( s \) under the H0 hypothesis – "maternal kinship does not affect STLV-1 transmission" – was estimated by randomly permuting the new infections observed each year while keeping the set of already infected individuals non-permutted. See Fouchet et al. (2012) for additional information on the three transmission rates, the method of estimation using Bayesian inference and on the use of the statistic \( s \).

3. Results

3.1. Behavioral study

From 1983 to 2011 174 births were recorded. Females and males reached sexual maturity at, respectively, 4 and 9 years old. The dominant males made the contribution to the colony's increase in terms of sired offspring. Regarding injuries, males have mainly severe injuries (deep wounds) at the beginning of the breeding season, when they need to assert their dominance to mate. Females and male adolescents mostly have a few minor injuries (superficial wounds; further information is given in the Supplementary Material, File S1).

3.2. STLV-1 epidemic

Globally there were 53 cases of STLV-1-infected mandrills until 2011: 33 males and 20 females. STLV-1 was introduced by a seropositive male when the colony was initiated in 1983, increased gradually until 2007, then rose rapidly until 2011. In females STLV-1 appeared later - in 2000 - and rapidly increased to almost equal the number of infected males. In 2011 there were 17 males and 15 females infected (Fig. 1a), the prevalences, i.e., the ratio of the number of infected individuals to the total number of individuals at a given time, reached 34% and 45% in males and females, respectively.

![Fig. 2. Contributions of the different STLV-1d transmission routes within (a) male and (b) female mandrill populations. Marginal posterior probability distributions of the three transmission parameters: aggressive \( c^A \) (long dash dot dot line), sexual \( c^S \) (solid line) and familial \( c^F \) (dash line).](image-url)
The age of first infection in males was usually around 9–12 years old with several infection cases at about 2–3 years old (15% of STLV-1 infections affected juvenile males). For females, infections were mostly between 4 and 11 years old with a few cases between 16 and 20 years old (Fig. 1b and 1c).

3.3. Quantification of the differential contribution of STLV-1 transmission modes

A Bayesian framework was used to quantify the contribution of the three potential transmission modes: aggressive \( I_{2} \), sexual \( I_{3} \) and familial \( I_{4} \), with G standing for the gender (M for males and F for females). For males (Fig. 2a) the dominant transmission mode was the aggressive route (for \( I_{4M} \) median = 0.72, 95% CI [0.47–0.91]) before the familial route (for \( I_{4M} \) median = 0.17, 95% CI [0.04–0.38]). Sexual transmission was little supported by the data (for \( I_{3M} \) median = 0.05, 95% CI [0–0.21]). For females (Fig. 2b) the main transmission modes were aggressive and familial (for \( I_{4F} \) median = 0.42, 95% CI [0.14–0.74], for \( I_{4F} \) median = 0.39, 95% CI [0.08–0.71]). Sexual transmission was also little supported by the data (for \( I_{3F} \) median = 0.12, 95% CI [0–0.37]). Parameter values are listed in Table 1.

3.4. Suspected transmission modes of STLV-1

3.4.1. Infection and reproduction

For the first 15 years of the study, STLV-1 transmission was only male-to-male. However, an explosion of female cases followed the first case of an infected female. This suggests that female contamination occurred mainly via infected females. This aggregation of female cases at the end of the monitoring could be tested by a rank-sum test, which compared the infection year distribution in males and females. The test was significant with a type I error of 5% (SR = 2.03, p = 0.01), suggesting unsynchronized epidemics for males and females - which advocates for transmissions occurring within, rather than between, genders.

3.4.2. Infection and aggressiveness

According to the data, among the 33 STLV-1 infected males, 23 were observed to be wounded (70%) versus 31 among the 63 STLV-1 negative males (49%). Even if the association between STLV-1-infected and wounded males is not significant (Khi2 = 3.68, P = 0.055), it appears that STLV-1-infected males are more often wounded than STLV-1-negative males. In Supplementary Material, File S2, we provide a table that reports cases suspected to be caused by males' aggressiveness according to observation of fights. The aggressive route is well supported by the model, especially for males. Indeed, many cases can be attributed to this transmission due to the fact that males become infected around 9–12 years old, which is the period when they usually fight to assert their dominance to mate.

Table 1

<table>
<thead>
<tr>
<th>Gender</th>
<th>Parameters</th>
<th>Median</th>
<th>95% credibility intervals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>( I_{4M} )</td>
<td>0.72</td>
<td>[0.47–0.91]</td>
</tr>
<tr>
<td></td>
<td>( I_{3M} )</td>
<td>0.17</td>
<td>[0–0.38]</td>
</tr>
<tr>
<td></td>
<td>( I_{2M} )</td>
<td>0.05</td>
<td>[0–0.21]</td>
</tr>
<tr>
<td>Female</td>
<td>( I_{4F} )</td>
<td>0.42</td>
<td>[0.14–0.74]</td>
</tr>
<tr>
<td></td>
<td>( I_{3F} )</td>
<td>0.39</td>
<td>[0.08–0.71]</td>
</tr>
<tr>
<td></td>
<td>( I_{2F} )</td>
<td>0.12</td>
<td>[0–0.37]</td>
</tr>
</tbody>
</table>

3.4.3. Familial links between infected cases

Fig. 3 displays kin relationships and the associated distribution of STLV-1 cases within the matrilines of the mandrill population. For example, if we consider the kin relationships of the first female on the left we see that it has 10 offspring: 8 males, including 3 who were STLV-1-infected at 7, 11 and 10 years of age respectively, and 2 females including 1 STLV-1 infected at 18 years old. The infected female is represented with a red border meaning that it is a transferred individual (it was infected in E1, by males who had escaped from E2, and was then moved to E2 because of its STLV-1-positivity).

Among the 36 cases recorded, 23 (64%) occurred within the same matriline. The permutation test indicated a statistically significant kinship effect (p = 0.037). Infections by relatives are more suspected for females (71% of female infections) than males (20% of male infections, Fig. 1d). This is consistent with the results we found with the model, i.e. a high contribution of the family route for females but two times lower for males.

4. Discussion

STLV-1 infections are common in many different species of NHPs but the modes and timing of STLV transmission are largely unknown. In all studied NHP species, fighting, mother-to-infant and sexual contact transmissions are usually reported but their relative implication largely varies according to species (e.g., d’Offay et al. 2007). Studying a semi-captive colony of mandrills with a long-term follow-up including both epidemiological and behavioral monitoring, has provided us with a unique work opportunity to compare the relative importance of the different potential modes of STLV-1 transmission in both males and females: aggressive, sexual and familial.

From the longitudinal data of the entire mandrill colony over three decades, it is clear that male-to-female sexual transmission of this virus is rare. First, as can be shown in Fig. 2b, females’ contamination through sexual contact is poorly consistent with the observed virus spread (low weight in the model). This result is reinforced by the finding that, before 2000, when STLV was only spreading in males, the virus did not pass to females despite the fact that most reproducing males were seropositive (90% of offspring born before 2000 originated from infected males; see Setchell et al. (2005a) for paternity analyses). This is all the more surprising since females usually mate with multiple males during their estrus period and males can mate up to 100 times with each female (Georges-Courbot et al. 1996; Nerrienet et al. 1998), leading to multiple opportunities of male-female transmission of the virus. The first case of infection in females may have resulted from an (unlikely) sexual transmission event or alternately from an aggressive interaction with males. It is noteworthy that it has been reported in mandrills that females can form coalitions to expulse an immigrant male, which exceptionally can lead to violent attacks including biting (Setchell et al. 2006). Following this transmission many females became infected, suggesting an important role of infected females in the contamination of new females.

In our colony, the data argue for a significant difference in the way STLV-1 spreads within males and within females. In males, transmission of STLV-1 was predominantly a result of male--male aggressive contacts, and secondarily as a result of familial transmission. This picture contrasts with that of females, for which aggressive transmissions are estimated to be twice less important than in males and equally weighted with familial transmission according to the mathematical model. Epidemiological differences observed between males and females are consistent with the known behavioral differences between sexes. The majority of transmission events in the males most probably occur.
during aggressive contacts when males compete for high dominance rank and reproductive access to a group of sexually attractive females (Nerrienet et al. 1998). Females in our colony live in stable inherited dominance relationships (Setchell et al. 2002). Although not yet studied, it is highly probable that dominant females assert their rank over lower-ranking females by aggressive behaviors such as biting, as reported for example in captive baboons (Papio Anubis), which exhibit the same social organization of females ruled by a dominance hierarchy (d’Offay et al. 2007).

As with SIVmnd-1 (Fouchet et al. 2012) the familial link between observed cases of STLV-1 was found to be significant (p = 0.037), but to a lesser extent. Similarly to SIVmnd-1, specific behavioral interactions among maternal kin and/or genetic susceptibility could be at the origin of this observed familial effect. For example, allogrooming and wound care (Nunn and Altizer, 2006) may facilitate saliva and blood exchanges between closely related individuals and thus, represent a potentially efficient mode of STLV-1 transmission. Infant play behavior (Charpentier et al. 2004) could be another route of at risk contact. Further behavioral studies and analyses of body fluids for STLV-1 detection should be implemented to investigate the plausibility of the familial transmission mode. Genetic susceptibility among the infected matrilineal lines could also be questioned. No information about genetic susceptibility to STLV-1 or HTLV-1 has been reported, as far as we know, contrary to SIV (Evans et al. 1999) and HIV (Pereyra et al. 2010) where studies showed differences of disease progression between individuals suggesting that genetic differences impact the propagation of SIV and HIV within individuals. Detailed analyses will be required to identify the factors underlying such potential susceptibility to infection by retroviruses (SIVmnd-1 and STLV-1) in this mandrill population.

STLV-1 transmission modes vary greatly between species. For example sexual transmission is preponderant in vervets [Cercopithecus aethiops, (Dracopoli et al. 1986)] while the aggressive mode of virus transmission is predominant in captive baboons (d’Offay et al. 2007) and mandrills (Nerrienet et al. 1998; this study). These different patterns of transmission modes can be interpreted with regard to the social organization of populations (Bahi-Jaber et al. 2008). For example, baboons and mandrills exhibit a similar multilevel social structure defined by dominance hierarchies in both males and females, and share the same aggressive mode of transmission for STLV-1 (d’Offay et al. 2007, this study). These divergences in transmission modes between species may reflect the fact that differences in the social organization of the species may impose different selection pressures on the virus. The inefficiency of sexual transmission coupled with the ability of the virus to be transmitted between females or from male-to-male aggressive contacts suggest different roles for both genders in the spread and persistence of STLV-1 in mandrills. Aggressive male-to-male transmission could be an efficient means for virus dispersal (males are the main dispersing individuals and upon arrival in a new group they suffer aggressive behavior from the rest of the group), whereas transmission between females, which represent the core of the social group in mandrills, could promote the local persistence of the virus.

5. Conclusion

In conclusion, our data on mandrills support the hypothesis that natural transmission of STLV-1 involves saliva to blood contamination via bites. Furthermore, these epidemiological results shed light on potentially important behavioral characteristics in mandrills (female coalitions against males, aggressive competition
over females for dominance rank) that deserve further investigation in the field.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.vetmic.2015.06.010.

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