



Disease avoidance, and breeding group age and size condition the dispersal patterns of western lowland gorilla females

Alice Baudouin, Sylvain Gatti, Florence Levréro, Céline Genton, Romane H Cristescu, Vincent Billy, Peggy Motsch, Jean-Sébastien Pierre, P. Le Gouar, Nelly Ménard

► To cite this version:

Alice Baudouin, Sylvain Gatti, Florence Levréro, Céline Genton, Romane H Cristescu, et al.. Disease avoidance, and breeding group age and size condition the dispersal patterns of western lowland gorilla females. *Ecology*, 2019, 100 (9), pp.e02786. 10.1002/ecy.2786 . hal-02178868

HAL Id: hal-02178868

<https://univ-rennes.hal.science/hal-02178868>

Submitted on 17 Sep 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Running head: Disease avoidance and dispersal in apes

Disease avoidance, and breeding group age and size condition the dispersal patterns of western lowland gorilla females

Alice Baudouin¹, Sylvain Gatti¹, Florence Levréro², Céline Genton¹, Romane H. Cristescu³, Vincent Billy⁴, Peggy Motsch⁴, Jean-Sébastien Pierre⁵, Pascaline Le Gouar^{1*}, Nelly Ménard^{1*}

¹ UMR 6553, ECOBIO: Ecosystems, Biodiversity, Evolution, CNRS/University of Rennes 1, Biological Station of Paimpont, Paimpont, France,

² Université de Saint-Etienne/Lyon, Equipe de Neuro-Ethologie Sensorielle, Neuro-PSI, CNRS UMR 9197, Saint-Etienne, France,

³ GeneCology, Faculty of Science, Health, Education and Engineering, University of the Sunshine Coast, Sippy Downs, QLD, Australia,

⁴ Odzala-Kokoua National Park, African Parks Network, Mbomo, Republic of Congo

⁵ UMR 6553, ECOBIO: Ecosystems, Biodiversity, Evolution, CNRS/University of Rennes 1, Rennes, France,

Corresponding author: Nelly Ménard: nelly.menard@univ-rennes1.fr

Abstract

Social dispersal is an important feature of population dynamics. When female mammals occur in polygynous groups, their dispersal decisions are conditioned by various female-, male-, and group-related factors. Among them, the influence of disease often remains difficult to assess. To address this challenge, we used long-term monitoring data from two gorilla populations (*Gorilla gorilla gorilla*) affected by infectious skin disease lesions. After controlling for other potentially influential factors, we investigated to which extent disease avoidance drives the dispersal decisions of gorilla females. We showed that the infection of a silverback of a breeding group by the skin disease increased the probability of adult females to emigrate. Moreover, adult females avoided breeding groups with a high prevalence of skin disease by emigrating from them and immigrating into healthier ones. Age of the breeding group was also an important factor. Adult females left older groups, near the end of a male tenure, to join younger ones led by younger fully-grown silverbacks that could be of high reproductive and protective value. Our study highlights that, while females select for high quality males, disease avoidance is a critical driver of their dispersion decision.

Keywords: skin disease, social dispersal, female emigration and immigration, breeding male quality, social environment, polygynous mammal, gorillas

Introduction

Male-biased dispersal and philopatry of females are the most common patterns in social mammal species (Greenwood 1980). However, in polygynous species structured in multi-female groups defended by one male [e.g. most social equids, several tropical bats, several primate species, (Clutton-Brock and Lukas 2012)], adult females can disperse several times throughout their lifetime (Lawson Handley and Perrin 2007). The social dispersal of a group-living female involves a change of social partners and mates (Clutton-Brock and Lukas 2012). Social dispersal, similarly to locational dispersal, plays a major role in individual fitness as well as in the genetics and dynamics of the overall population (Greenwood 1980, Clobert et al. 2001).

Proximal forces influencing social dispersal are intrinsically linked to the major risks and benefits of group living. The major proximal forces described as potential drivers of female social dispersal are inbreeding avoidance, reduction of predation risk, reduction of feeding and intra-sexual competition, selection of a higher-quality male (Sterck et al. 2005, Clutton-Brock and Lukas 2012), and reduction of pathogen transmission through behavioral avoidance of diseased conspecifics (Curtis 2014, Sarabian and MacIntosh 2015, Poirotte et al. 2017). Social dispersal implies first that females decide whether to remain in a social group or leave it, and then that they choose the target group into which to immigrate (Isbell and VanVuren 1996, Debeffe et al. 2015). These decisions require gathering information on other social groups and suggest a social and fitness cost-benefit analysis (Isbell and VanVuren 1996, Clobert et al. 2009). Studies on wildlife and humans show that individuals attempt to avoid disease transmission using external signs of disease on conspecifics such as behavioral changes (Croft et al. 2011), chemical cues (Behringer et al. 2006, Kavaliers and Choleris 2018), or visual sickness symptoms (Axelsson et al. 2018). In group-living species, females

may choose smaller social groups despite increased predation risks (Côté and Poulin 1995) and choose healthy mates (Altizer et al. 2003, Tybur and Gangestad 2011) to limit the risk of inter-individual disease transmission. However, among the range of behaviors reducing the risk of disease transmission [for review see e.g. (Hart 1990)], the extent to which disease avoidance conditions the choice of social and/or mating partners and promotes dispersal has remained poorly investigated in social species (Behringer et al. 2006, Debeffe et al. 2014, Kavaliers and Choleris 2018).

Disease avoidance behavior may be difficult to identify because individual dispersal decisions likely result from compromises involving other (and potentially confounding) factors such as body condition and reproductive status, food or sexual competition, predation and infanticide risks, or availability of a high-quality male (Clobert et al. 2001, Curtis 2014). For instance, being in a good condition (e.g. high body fat, no injury or disease) allows an individual to disperse since it is better equipped to bear dispersal costs (Debeffe et al. 2012), whereas diseased or parasitized individuals may be too weak for this task (Debeffe et al. 2014). Alternatively, heavily diseased or parasitized individuals might be more prone to disperse in a ‘leave-it’ strategy as a last chance attempt to improve their situation (Isbell and VanVuren 1996, Debeffe et al. 2014). Pregnancy, lactation, or the presence of unweaned thus dependent offspring can reduce the likelihood of female dispersal (Sterck et al. 2005, Robbins and Robbins 2015, Sicotte et al. 2017). Consequently, nulliparous adult females (*i.e.* that have not yet reproduced) may have more opportunities to disperse than parous females and may disperse several times before their first pregnancy (Linklater and Cameron 2009, Robbins et al. 2009). In addition, females may disperse from large groups to smaller ones (Clutton-Brock and Lukas 2012, Marjamaeki et al. 2013), thereby limiting food or intra-sexual competition (Stokes et al. 2003, Sicotte et al. 2017).

We examined the extent to which disease avoidance is involved in the dispersal decisions of western lowland gorilla adult females, after controlling the potential influence of other factors such as the reproductive status of females, intra-group competition, and adult male reproductive and protective value. We used a long-term dataset on the immigration to and emigration from known social groups of individually identified gorillas some bearing yaws-like skin lesions. Yaws is a disease caused by a *Treponema* species described in humans (Mitjà et al. 2013) and in non-human primates (Cousins 2007, Giacani and Lukehart 2014). The consequences of yaws can be debilitating, the worst cases lead to deformities and severe handicaps (Levréro et al. 2007, Mitjà et al. 2013). Early stages of the disease are regarded as infectious and can be determined visually according to presence of red, ulcerative, puritic granulomatous papillomas (Engelkens et al. 1991, Antal et al. 2002). This disease spreads mainly through skin contact between individuals (Engelkens et al. 1991, Giacani and Lukehart 2014). Lesions are apparent and mostly facial, and therefore may serve as visible cues to avoid diseased conspecifics.

Gorillas are polygynous; their breeding groups are composed of a dominant adult male called a silverback and several adult females with their offspring. Less than 60% of silverbacks lead breeding groups, while the others are unmated males (Gatti et al. 2004). The reproductive and protective abilities of the leader silverback are believed to decline at the end of his breeding-group tenure, which lasts up to 12 years (Breuer et al. 2010). A previous study on one western lowland gorilla population showed that females with an unweaned infant avoided emigration, possibly to limit infanticide risks from silverbacks (Stokes et al. 2003). Moreover, after their natal dispersal, females experienced up to three secondary dispersal events in their life and preferred transferring into smaller groups (Stokes et al. 2003). We focused our study on secondary dispersal, excluding cases of natal emigration that are predominantly linked to incest avoidance.

We tested three hypotheses of potential influences of disease avoidance in female dispersal at emigration and immigration steps of their dispersal process, encompassing relevant factors of the socio-sexual environment of females and their disease status. First, females should leave diseased silverbacks for silverbacks in good health. Second, females should emigrate from, and avoid immigrating into, breeding groups with numerous diseased individuals. Finally, diseased females should disperse less than healthy ones. Simultaneously, we controlled for the possible influence of 1) the presence of an unweaned infant and the females' reproductive status; 2) intra-group competition, using group size as a proxy; 3) silverbacks' reproductive and protective abilities, using group composition, e.g. the number of offspring of several age-classes as a proxy of silverback age. The presence of only the infant age-class indeed indicates early breeding-group tenure by a young fully mature silverback that is assumed to provide better protection against infanticide and predation than an older male at the end of his tenure.

Materials and methods

Study sites and populations

We collected demographic data from two different gorilla populations [Lokoué, (00°54'23''N, 15°10'33''E) and Romani (00°41'28"N; 14°53'31"E)] in the Odzala-Kokoua National Park (Republic of Congo). We monitored the Lokoué population from 2001 to 2003 and the Romani population over 11 years (2005-2015). Each gorilla was identified and its sex and age-class were determined according to physical characteristics and behavior with the help of a database of photographs and videos (for details on study periods and observation methods see Appendix S1 : Table S1). We differentiated nulliparous females, who have never been observed with an infant and have non-elongated nipples and undeveloped breasts, from

parous females. We distinguished individuals that displayed “severe” skin lesions from the others according to the presence of red, ulcerative and/or granulomatous papillomas characteristic of yaws’ infectious stages and irreversible lesions such as tissue necrosis and bone deformations (Engelkens et al. 1991, Giacani and Lukehart 2014). Among the 593 individuals identified, the overall prevalence was around 22% while 13.3% were categorized as “severely diseased” (*i.e.* showing severe skin lesions, for description of the disease and prevalence *per* population and year, see Appendix S2: Fig. S1, Table S1). We identified each of the 109 different gorilla units (59 breeding groups; 50 unmated units; for details on samples *per* population and year, see Appendix S3: Table S1) and we recorded its composition. According to the “ageing” process of breeding groups (BG) subsequently to their formation (Appendix S4), we classified them into four stages : young BG [one silverback + adult females with infants (≤ 4 years old)]; juvenile BG [one silverback + adult females and offspring up to juveniles (4-7.5 years old)], mature BG [one silverback + adult females and offspring up to sub-adults (7.5-10 years old for females, 7.5-11 years old for males)], senescent BG [one silverback, adult females and several cohorts of offspring from infants to blackbacks (11-14 years old)].

Dispersal status of adult females

At each observation of breeding groups we recorded changes, if any, in adult females. We then categorized each adult female according to her dispersal status in a given year as follows:

- i) resident female: an adult female that has remained in the same breeding group; ii) emigrating female: an adult female that has left her breeding group; iii) immigrating female: a new adult female in a group (for information on gorilla social organization and dispersal patterns see Appendix S5). No female was observed as immigrant and emigrant the same year. We used the term “transfer event” when we knew both the original and target groups of the dispersing female. Females not observed again after emigrating were considered as having

emigrated out of the population. We could not differentiate them from those who died, but none of them showed evidence of bad body conditions. Females not known within the population before they immigrated were considered to have immigrated from a neighboring population.

Analyses of dispersal patterns

To test our hypotheses on emigration and immigration patterns, we built two respective datasets (DataS1). We assumed no significant difference in habitat quality among gorilla units because they live in the same dense *Marantaceae* forest and their home ranges overlap (see Appendix S1). Since we had no a priori hypotheses on differences between the two populations, data were pooled. The emigration dataset included the female-related response variable (*i.e.* each female was either an emigrant or a resident *per* year, named “female-year” observation, with a binomial distribution weighted by the total number of adult females within the group), and 9 explanatory variables (*i.e.* the characteristics of the adult female and the characteristics of her breeding group, see details in Fig. 1). We recorded 513 female-year observations. Resident females made up 469 female-years while 44 emigration events occurred (for details *per* population and year, see Appendix S3: Table S1). The immigration dataset included the gorilla unit-related response variable (*i.e.* either chosen or not by the immigrant female, named “unit-year” observation), and the 8 explanatory variables (*i.e.*, the characteristics of the gorilla units, see details in Fig. 1). We analyzed immigration patterns with a demographic data set of 56 different breeding groups and 54 non-breeding units with unmated silverbacks (either solitary or living in non-breeding groups). Totals of 97 different silverbacks either solitary or breeding group leaders, were identified. We recorded 313 unit-year observations, out of which 68 unit-years had female immigration (for details on samples *per* population and year, see Appendix S3: Table S1).

We used a generalized linear mixed model [*GLMM*, binomial family, logit link, *glmer* function, lme4 R-package, (Bates et al. 2014)] that considered population, group or female identity and year as random factors, to analyze each of our two datasets. Redundant explanatory variables were detected using canonical coefficients and were not considered in the same model during the model selection procedure (Appendix S6, Table S1). We used a model selection with an information-theoretic framework and Akaike Information Criterion adjusted for small sample sizes [AICc, (Burnham and Anderson 2003)]. No interaction was tested in the selection model procedure. Marginal and conditional R² of the selected models ($\Delta\text{AICc} < 2$) were computed. We estimated standardized coefficients of the selected variables and their 95% confidence intervals using a conditional model averaging procedure. The significance of variables was determined when the 95% confidence interval did not include zero. Technical details on the statistical approach are described in Appendix S6: Tables S1-S4.

Concerning immigration patterns, our *GLMM* analysis was designed to reveal differences in female choice among unit characteristics. However, it did not account for differences in unit type availability. Therefore, to assess if the choice of unit made by immigrating females differed from a random choice, we used a Manly standardized selection ratio [*widesIII* function, adehabitatHS R package (Manly et al. 2002)]:

$$W_i = \frac{u_i}{\sum_{j=1}^n \pi_{ij} u_j}$$

Where W_i is the selection ratio for the population (n animals) for the i th resource category, u_i is the number of type i resource units used by all animals, π_{ij} is the known proportion of resources available to animal j that are in category i , u_j is the resource units used by the j th animal.

In our analysis, the individuals are identified and the use and availability of units are measured for each one. We tested the significance of the observed distribution of the probability under a null hypothesis of a random choice using the log-likelihood statistic (Manly et al. 2002) for each of the following resource categories: silverbacks' skin disease status, number of severely diseased individuals in breeding groups, gorilla unit category, breeding group size, the infant-to-adult female ratio. Finally, the differences in the characteristics of the two units involved in female transfers were tested with Wilcoxon paired and chi-squared tests.

Results

Factors influencing the female emigration probability

Three plausible models best explained the probability of female emigration (conditional R^2 ranging from 0.46 to 0.53, Appendix S6: Table S3). They indicate that the probability for a female to emigrate increased with the number of severely diseased individuals (0.33 [0.09 – 0.58] 95%CI, 2 on the 10 best models Appendix S6, Fig. 2a), with the presence of severe skin lesions on the silverback (1.53 [0.42 – 2.63] 95%CI, 4 on the 10 best models Appendix S6, Fig. 2b), and with the age of the breeding group, females leaving more senescent groups (1.62 [0.55 – 2.69] 95%CI, 4 on the 10 best models Appendix S6, Fig. 2c) than young ones. By contrast, the probability for a female to emigrate decreased with the presence of an unweaned infant (-2.89 [-4.10 – -1.67] 95%CI, 10 on the 10 best models Appendix S6, Fig. 2d, see Appendix S7 for complementary results). The skin disease status of females had non-significant impact on their probability to emigrate (-0.66 [-1.75 – 0.43] 95%CI, 3 on the 10 best models Appendix S6).

Factors influencing female immigration and target unit selection

We never observed a female immigrating with her infant. Among the 68 immigration events, 59 targeted breeding groups, nine females joined unmated silverbacks, mostly solitary males but one who was in a non-breeding group. The probabilities for a female to immigrate into a young group was ten times higher than the probability to join a solitary male (-3.60 [-5.60 – -1.62] 95%CI), or to immigrate into juvenile (-2.77 [-4.97 – -0.58] 95%CI) or senescent groups (-4.60 [-8.83 – -0.38] 95%CI), Fig. 3a). No female chose mature groups. The silverbacks' skin disease status had no effect on female immigration (0.08 [-1.69 – 1.95] 95%CI).

Concerning the influence of young breeding group characteristics (the most selected group category) on female immigration, two plausible models were selected amongst all possible ones (conditional R^2 respectively of 0.82 and 0.83, Appendix S6: Table S4). They indicate that the probability for females to immigrate into a young breeding group decreased with the presence of severely diseased individuals (-2.44 [-5.69 – -0.81] 95%CI, 3 on the 8 models Appendix S6, Fig. 3b), and with the size of the group (-0.43 [-0.72 – -0.14] 95%CI, 2 on the 8 models Appendix S6, Fig. 3c).

Manly's index analysis (Manly et al. 2002) strengthened the importance of the factors selected with *GLMM*. Most notably, females significantly avoided groups with more than two individuals showing severe signs of skin disease (Fig. 4a). In addition, females significantly selected young breeding groups whereas they avoided mature and senescent groups and non-breeding units; i.e. unmated silverbacks (Fig. 4b). They significantly selected groups composed of 2 to 4 individuals while they avoided groups composed of 9 and more individuals (Fig. 4c). Females preferred breeding groups without infants, which predominantly characterized young groups, to groups where all females had an unweaned infant (Fig. 4d).

This analysis confirmed that the silverback's skin disease had no significant effect on female choice.

Transfer characteristics

We recorded 16 transfer events concerning 15 females for which we knew both the original and target groups of the dispersing female. The number of severely infected individuals in the target groups was significantly lower than in the original groups (0.43 vs. 1.6, paired Wilcoxon's test, $P = 0.02$). This result remained relevant when correcting by group size (average ratio of infected individuals in original groups three times higher than in target groups ; 0.15 vs 0.05, paired Wilcoxon's test, $P = 0.06$). The original breeding groups of transferring females were on average larger than the size of their target groups (9.6 vs. 5.9, paired Wilcoxon's test, $P = 0.0171$). Most transfers (63%, $N = 16$) involved females emigrating from senescent or mature groups, and no female transferred into a target group older than their original group.

Discussion

We confirmed that the presence of an unweaned infant appears as a predominant constraint that limits females' secondary social dispersal in gorillas (Sicotte 2001, Stokes et al. 2003). Under normal conditions, delaying dispersal until their offspring is weaned is considered as a female strategy against infanticide risks (Robbins et al. 2013). On the contrary, the death of the leading silverback induces involuntary transfers of mother-infant pairs and increase the probability of infanticide (Robbins et al. 2013). However, in western lowland gorillas, infanticide is considered to be less common than in mountain gorillas (Yamagiwa et al. 2009, Robbins and Robbins 2015): in at least two different populations, mother-infant pairs involuntarily transferred into new social groups where the infants survived although the leader silverbacks were likely not their fathers (Stokes et al. 2003, Genton et al. 2012).

Influence of severe skin lesions

We found that silverbacks' disease status influenced emigration females' decision but not their immigration decision. A previous study showed that unmated males (*i.e.* solitaires and silverbacks in non-breeding units) suffered more from skin diseases than mated males (*i.e.* silverbacks in breeding groups) in the Lokoué population, suggesting that females avoided mating with diseased silverbacks (Levréro et al. 2007). Our results suggested that females leave infected silverbacks, leading silverback to lose their mating status. However, other factors such as silverback age and body size (Caillaud et al. 2008), previous interactions between the silverback and the female, or relatedness, are potentially involved in female choices. Further studies are needed to determine the role of these factors on females' mate choice in gorilla populations.

In gorillas, joining a new mated male means joining his breeding group. We found that the presence of skin disease in breeding groups determined the dispersal decision of females. Females showed a greater propensity to emigrate from breeding groups that contained numerous severely diseased individuals. Similarly, immigrating females avoided groups with more than two diseased individuals. Several studies conducted in captive conditions showed that primates, including gorillas, could have a relative numerosness judgment; e.g. gorillas are able to discriminate between two food quantities, selecting the larger one (Anderson et al. 2005). Therefore, these abilities may also be expressed in the wild when it is crucial to avoid disease. Severely diseased individuals are expected to increase the risk of contamination by inter-individual transmission (Giacani and Lukehart 2014). Hence, by avoiding contact with diseased individuals and leaving their group, female gorillas decrease the risk of being contaminated, as observed in other species (Kiesecker et al. 1999, Behringer et al. 2006, Vanpé et al. 2016). Other behavioral social avoidance of contagious individuals by healthy ones has rarely been found in the wild (Behringer et al. 2006, Poirotte et al. 2017). Mandrills

(*Mandrillus sphinx*) are able to socially exclude conspecifics infected by endoparasites by avoiding grooming with them (Poirotte et al. 2017). Grooming increased with a decreasing endoparasite load, revealing that healthy individuals avoided the risk of infection. By contrast, no disease avoidance has been found in other social species [*Mungos mungo*, (Fairbanks et al. 2015)]. Interestingly, these authors suggested that in this highly social species that lives in stable, long-term groups where group members frequently interact, individuals could hardly avoid diseased conspecifics. Therefore, this underlined the potential influence of the social systems on individuals' strategies to avoid pathogen contamination. In gorillas, although breeding groups may be stable all along the silverback tenure [up to 12 years, (Breuer et al. 2010)], females without an unweaned infant may prevent disease infection by conspecifics during this tenure by deciding to emigrate and choosing the unit they immigrate into.

Chemical mechanisms can be involved in the detection of diseased conspecifics, with cues in the environment (Kiesecker et al. 1999, Behringer et al. 2006) or in the feces (Poirotte et al. 2017). In the case of skin disease in gorillas, we suppose that the intensity of skin lesions represented relevant visual cues of infection risks, similarly to humans who detect sick persons on the basis of visual symptoms (Axelsson et al. 2018). In particular, in humans as in gorillas, the face concentrates many traits used in inter-individual communication and is predominantly scanned by conspecifics as compared to the whole body (Kano et al. 2012). An abnormal aspect of the face can be used to appraise the health status of other individuals (Regenbogen et al. 2017). We suppose that in gorillas, behavioral signals, comparable to disgust in humans, can function as a disease-avoidance mechanism that could be acquired throughout individual development and into adulthood (Oaten et al. 2009, Curtis 2014). The use of social information on infection status of conspecifics plays an important role in disease avoidance (Kavaliers and Choleris 2018). Mechanisms of social cognition encompass assessing conspecifics disease status and decision on interaction or not with them (Kavaliers

and Choleris 2018). Gorillas could acquire, from other group members, a behavioral aversion towards individuals severely infected by skin diseases. In addition, owing to their long maturing period in social groups, they probably learn signals of disease risks from known diseased conspecifics by associating physical cues of infection and deleterious consequences (such as difficulty in breathing and eating due to tissue necrosis and perforation of the palate and nasal septum, difficulty in moving due to irreversible bone lesions).

Contrary to our hypothesis, the skin disease status of the females themselves did not influence their propensity to disperse. Dispersal is generally considered to induce energy and time costs, increase mortality risks, and reduce the advantage of being in a familiar social unit or habitat [loss of social rank or selection of a suboptimal environment (Bonte et al. 2012)]. Therefore, the individual body condition is a factor involved in the decision to disperse (Debeffe et al. 2012), although studies yielded contrasting results depending on the environmental context (Linklater and Cameron 2009, Loe et al. 2010, Le Galliard et al. 2012). The disease status of individuals is assumed to influence their body condition and thus their dispersal, but studies investigating the effects of disease on the dispersion probability remain scarce (Brown and Brown 1992, VanVuren 1996, Debeffe et al. 2014). Roe deer (*Capreolus capreolus*) highly parasitized by endoparasites delayed their natal dispersal to accumulate sufficient body condition to sustain locational dispersal (Debeffe et al. 2014). By contrast, yellow-bellied dispersing marmots (*Marmota flaviventris*) tended to host higher ectoparasite loads (VanVuren 1996), and similarly heavily parasitized cliff swallow (*Hirundo pyrrhonota*) nestlings dispersed more than slightly parasitized ones (Brown and Brown 1992). In our study, individual gorillas weakened by skin disease supported the cost of social dispersal because the impact on their body condition was not deleterious enough to prevent their dispersal. Alternatively, as in other dispersing primates, gorillas may take advantage of interunit encounters to switch groups without adding the cost of a risky solitary period (Isbell

and VanVuren 1996). In our studied populations, neither a potential influence of habitat quality nor an interaction with the level of infection in units on dispersal female decision could be evoked. This is because of i) the study sites are mostly covered by the dense *Marantaceae* forests providing ample staple foods (mainly *Haumania sp.*), and ii) the overlapping of all units' home ranges. The social environment may therefore be a more important driver of female dispersal decision than the ecological environment.

Females' preference for young mated males

Gorilla females showed a propensity to leave older breeding groups to preferentially immigrate into young breeding groups rather than join unmated silverbacks. These patterns underlie the formation and ageing processes of breeding groups (Parnell 2002). In most mammal species, young mature males are supposed to have reduced access to mates because of a reduced capacity to protect females (Clutton-Brock and McAuliffe 2009). For example, northern elephant seal (*Mirounga angustirostris*) females avoid mating with males that are unable to provide protection and call on older dominant males to get rid of the younger ones that harass them (McMahon and Bradshaw 2004). Comparatively, in our study, unmated silverbacks were possibly of less reproductive and protective value because they were either too young to form their own breeding group or old post-reproductive silverbacks. Females preferentially transferred toward younger breeding groups, *i.e.* with fully mature males at the peak of their physical abilities. Moreover, among those young groups, females preferred the smallest ones, possibly limiting competition for access to resources or to male proximity. By contrast, they avoided the mature or senescent breeding groups led by older silverbacks as compared to young breeding groups. Indeed, according to the classical group' life history, a silverback may form his breeding group once he is around 15-18 years old (*i.e.* a young breeding group), then he is aging during his subsequent tenure that can last up to 12 years while his group is maturing then becoming senescent (Breuer et al. 2010, Genton et al. 2012).

Females have a marked preference for breeding groups without any infant, therefore in the early phase of male tenure (*i.e.* no female having yet given birth). This preference reflects the strong attractiveness of those males, which is thought to result in fast female recruitment once a first female has joined a solitary silverback.

Conclusion & Perspectives

Dispersal of gorilla females results from a multifactorial decision based on the characteristics of females, silverbacks, and social groups. Our study highlights that the social environment of adult females, and in particular the presence of diseased individuals, determines their decision to disperse. The mechanisms of females' appraisal of their social environment and of the disease status of their conspecifics remain to be investigated.

Dispersal of individuals in a disease context is often linked to an increase of disease transmission and spread (Nunn et al. 2008). If infected individuals decide to immigrate into groups with low prevalence of the disease, and lacking resistance from social conspecifics against immigrants, they might increase the transmission rate, to the benefit of the spread of the pathogen. However, uninfected individuals may limit the risk of infection by avoiding groups with a large number of infected individuals, which will preserve host population viability. Disease avoidance behaviors by hosts influence disease dynamics and spread by reducing the intensity and duration of disease outbreaks and viral prevalence (Dolan et al. 2014). Integrating disease avoidance behaviors in epidemiological models would allow us to better understand host-pathogen co-evolutive dynamics.

Acknowledgments

We thank the team of the ECOFAC program (EU): C. Aveling, B. Djoni-Djimbi, P. Ngouembe, J-M. Froment, P. Marshall, P. Montuir, P. Mortier, P. Rickmounie, T. Smith, J. de Winter, and African Parks Networks: D. Zeller, L. Lamprecht, P. Darcis, and G. Le Flohic for

logistic assistance and permission to work in Odzala-Kokoua National Park. We are grateful to J-B. Lepale, S. Yaba Ngouma, D-J Ndebo, A. Lavandier, M. Douadi, D. Caillaud, C. Devos, M. Dewas, L. Bouquier, S. Navel, Q. Gautier, D-M. Paquet, P. Besnard, M. Boros for their assistance with data collection on site. This research work was funded by the ECOsystèmes FORestiers program (<http://www.gip-ecofor.org/>; Ministère de l'Ecologie et du Développement Durable France), the Espèces-Phares program (DG Environnement, UE), and the French agency for research via the ANR-11-JVS7-015 IDiPop project. We also thank A. Dazé and A. Buchwalter for editing English language. We are grateful to C. Wiegand and two anonymous reviewers for their constructive comments on the manuscript. P. Le Gouar and N. Ménard equally supervised this work.

References

- Altizer, S., C. L. Nunn, P. H. Thrall, J. L. Gittleman, J. Antonovics, A. A. Cunningham, A. P. Dobson, V. Ezenwa, K. E. Jones, A. B. Pedersen, M. Poss, and J. R. C. Pulliam. 2003. Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annual Review of Ecology Evolution and Systematics* 34:517-547.
- Anderson, U. S., T. S. Stoinski, M. A. Bloomsith, M. J. Marr, A. D. Smith, and T. L. Maple. 2005. Relative numerosness judgment and summation in young and old Western lowland gorillas. *Journal of Comparative Psychology* 119:285-295.
- Antal, G. M., S. A. Lukehart, and A. Z. Meheus. 2002. The endemic treponematoses. *Microbes and Infection* 4:83-94.
- Axelsson, J., T. Sundelin, M. J. Olsson, K. Sorjonen, C. Axelsson, J. Lasselin, and M. Lekander. 2018. Identification of acutely sick people and facial cues of sickness. *Proceedings of the Royal Society B* 285.

- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4.
- Behringer, D. C., M. J. Butler, and J. D. Shields. 2006. Avoidance of disease by social lobsters. *Nature* 441:421.
- Bonte, D., H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, E. Matthysen, K. Mustin, M. Saastamoinen, N. Schtickzelle, V. M. Stevens, S. Vandewoestijne, M. Baguette, K. Barton, T. G. Benton, A. Chaput-Bardy, J. Clobert, C. Dytham, T. Hovestadt, C. M. Meier, S. C. F. Palmer, C. Turlure, and J. M. J. Travis. 2012. Costs of dispersal. *Biological Reviews* 87:290-312.
- Breuer, T., A. M. Robbins, C. Olejniczak, R. J. Parnell, E. J. Stokes, and M. M. Robbins. 2010. Variance in the male reproductive success of western gorillas: acquiring females is just the beginning. *Behavioral Ecology and Sociobiology* 64:515-528.
- Brown, C. R., and M. B. Brown. 1992. Ectoparasitism as a cause of natal dispersal in cliff swallows. *Ecology* 73:1718-1723.
- Burnham, K. P., and D. R. Anderson. 2003. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, New York.
- Caillaud, D., F. Levréro, S. Gatti, N. Ménard, and M. Raymond. 2008. Influence of male morphology on male mating status and behavior during interunit encounters in western lowland gorillas. *American Journal of Physical Anthropology* 135:379-388.
- Clobert, J., E. Danchin, and A. A. Dhondt. 2001. Dispersal. Oxford University Press, Oxford, New York.
- Clobert, J., J.-F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* 12:197-209.

- Clutton-Brock, T., and K. McAuliffe. 2009. Female mate choice in mammals. *Quarterly Review of Biology* 84:3-27.
- Clutton-Brock, T. H., and D. Lukas. 2012. The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology* 21:472-492.
- Côté, I. M., and R. Poulin. 1995. Parasitism and group-size in social animals - A metanalysis. *Behavioral Ecology* 6:159-165.
- Cousins, D. 2007. Diseases and injuries in wild and captive gorillas: *Gorilla gorilla*. *International Zoo Yearbook* 12:211-218.
- Croft, D. P., M. Edenbrow, S. K. Darden, I. W. Ramnarine, C. van Oosterhout, and J. Cable. 2011. Effect of gyrodactylid ectoparasites on host behaviour and social network structure in guppies *Poecilia reticulata*. *Behavioral Ecology and Sociobiology* 65:2219-2227.
- Curtis, V. A. 2014. Infection-avoidance behaviour in humans and other animals. *Trends in Immunology* 35:457-464.
- Debeffe, L., N. Morellet, B. Cargnelutti, B. Lourtet, R. Bon, J.-M. Gaillard, and A. J. M. Hewison. 2012. Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. *Journal of Animal Ecology* 81:1327-1337.
- Debeffe, L., N. Morellet, H. Verheyden-Tixier, H. Hoste, J.-M. Gaillard, B. Cargnelutti, D. Picot, J. Sevila, and A. J. M. Hewison. 2014. Parasite abundance contributes to condition-dependent dispersal in a wild population of large herbivore. *Oikos* 123:1121-1125.
- Debeffe, L., E. Richard, S. A. Medill, J. N. Weisgerber, and P. D. McLoughlin. 2015. Costs of social dispersal in a polygynous mammal. *Behavioral Ecology* 26:1476-1485.
- Dolan, T. W., III, M. J. Butler, and J. D. Shields. 2014. Host behavior alters spiny lobster-viral disease dynamics: a simulation study. *Ecology* 95:2346-2361.

- Engelkens, H. J. H., J. Judanarso, A. P. Oranje, V. D. Vuzevski, P. L. A. Niemel, J. J. Vandersluis, and E. Stolz. 1991. Endemic treponematoses. part 1. Yaws. *International Journal of Dermatology* 30:77-83.
- Fairbanks, B. M., D. M. Hawley, and K. A. Alexander. 2015. No evidence for avoidance of visibly diseased conspecifics in the highly social banded mongoose (*Mungos mungo*). *Behavioral Ecology and Sociobiology* 69:371-381.
- Gatti, S., F. Levréro, N. Ménard, and H. A. Gautier. 2004. Population and group structure of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoué, Republic of Congo. *American Journal of Primatology* 63:111-123.
- Genton, C., R. Cristescu, S. Gatti, F. Levréro, E. Bigot, D. Caillaud, J. S. Pierre, and N. Ménard. 2012. Recovery potential of a Western lowland gorilla population following a major Ebola outbreak: results from a ten year study. *Plos One* 7:(e37106).
- Giacani, L., and S. A. Lukehart. 2014. The endemic treponematoses. *Clinical Microbiology Reviews* 27:89-115.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal behaviour* 28:1140-1162.
- Hart, B. L. 1990. Behavioral adaptations to pathogens and parasites - 5 strategies. *Neuroscience and Biobehavioral Reviews* 14:273-294.
- Isbell, L. A., and D. VanVuren. 1996. Differential costs of locational and social dispersal and their consequences for female group-living primates. *Behaviour* 133:1-36.
- Kano, F., J. Call, and M. Tomonaga. 2012. Face and eye scanning in gorillas (*Gorilla gorilla*), orangutans (*Pongo abelii*), and humans (*Homo sapiens*): unique eye-viewing patterns in humans among hominids. *Journal of Comparative Psychology* 126:388-398.

- Kavaliers, M., and E. Choleris. 2018. The role of social cognition in parasite and pathogen avoidance. *Philosophical Transactions of the Royal Society B* 373:(doi: 10.1098/rstb.2017.0206).
- Kiesecker, J. M., D. K. Skelly, K. H. Beard, and E. Preisser. 1999. Behavioral reduction of infection risk. *Proceedings of the National Academy of Sciences of the United States of America* 96:9165-9168.
- Lawson Handley, L. J., and N. Perrin. 2007. Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology* 16:1559-1578.
- Le Galliard, J.-F., A. Remy, R. A. Ims, and X. Lambin. 2012. Patterns and processes of dispersal behaviour in arvicoline rodents. *Molecular Ecology* 21:505-523.
- Levréro, F., S. Gatti, A. Gautier-Hion, and N. Ménard. 2007. Yaws disease in a wild gorilla population and its impact on the reproductive status of males. *American Journal of Physical Anthropology* 132:568-575.
- Linklater, W. L., and E. Z. Cameron. 2009. Social dispersal but with philopatry reveals incest avoidance in a polygynous ungulate. *Animal Behaviour* 77:1085-1093.
- Loe, L. E., A. Myrsterud, V. Veiberg, and R. Langvatn. 2010. No evidence of juvenile body mass affecting dispersal in male red deer. *Journal of Zoology* 280:84-91.
- Manly, B. B., L. McDonald, and D. Thomas. 2002. Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media, New York.
- Marjamaeki, P. H., A. L. Contasti, T. N. Coulson, and P. D. McLoughlin. 2013. Local density and group size interacts with age and sex to determine direction and rate of social dispersal in a polygynous mammal. *Ecology and Evolution* 3:3073-3082.
- McMahon, C. R., and C. J. A. Bradshaw. 2004. Harem choice and breeding experience of female southern elephant seals influence offspring survival. *Behavioral Ecology and Sociobiology* 55:349-362.

Mitjà, O., K. Asiedu, and D. Mabey. 2013. Yaws. *The Lancet* 381:763-773.

Nunn, C. L., P. H. Thrall, K. Stewart, and A. H. Harcourt. 2008. Emerging infectious diseases and animal social systems. *Evolutionary Ecology* 22:519-543.

Oaten, M., R. J. Stevenson, and T. I. Case. 2009. Disgust as a disease-avoidance mechanism. *Psychological Bulletin* 135:303-321.

Parnell, R. J. 2002. Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *American Journal of Primatology* 56:193-206.

Poirotte, C., F. Massol, A. Herbert, E. Willaume, P. M. Bomo, P. M. Kappeler, and M. J. E. Charpentier. 2017. Mandrills use olfaction to socially avoid parasitized conspecifics. *Science Advances* 3:e1601721. (doi:1601710.1601126/sciadv.1601721).

Regenbogen, C., J. Axelsson, J. Lasselin, D. K. Porada, T. Sundelin, M. G. Peter, M. Lekander, J. N. Lundstroem, and M. J. Olsson. 2017. Behavioral and neural correlates to multisensory detection of sick humans. *Proceedings of the National Academy of Sciences of the United States of America* 114:6400-6405.

Robbins, A. M., M. Gray, A. Basabose, P. Uwingeli, I. Mburanumwe, E. Kagoda, and M. M. Robbins. 2013. Impact of male infanticide on the social structure of mountain gorillas. *Plos One* 8:e78256.

Robbins, A. M., and M. M. Robbins. 2015. Dispersal patterns of females in the genus *Gorilla*. Pages 75-104 in T. Furuichi, J. Yamagiwa, and F. Aureli, editors. *Dispersing primate females - Life history and social strategies in male-philopatric species*. Springer, Tokyo.

Robbins, A. M., T. Stoinski, K. Fawcett, and M. M. Robbins. 2009. Leave or conceive: natal dispersal and philopatry of female mountain gorillas in the Virunga volcano region. *Animal Behaviour* 77:831-838.

- Sarabian, C., and A. J. J. MacIntosh. 2015. Hygienic tendencies correlate with low geohelminth infection in free-ranging macaques. *Biology Letters* 11:(doi: 10.1098/rsbl.2015.0757).
- Sicotte, P. 2001. Female mate choice in mountain gorillas. Pages 59–88 in M. M. Robbins, P. Sicotte, and K. J. Stewart, editors. *Mountain gorillas: three decades of research at Karisoke*. Cambridge studies in biological and evolutionary anthropology, Cambridge.
- Sicotte, P., J. A. Teichroeb, J. V. Vayro, S. A. Fox, I. Badescu, and E. C. Wikberg. 2017. The influence of male takeovers on female dispersal in *Colobus vellerosus*. *American Journal of Primatology* 79:e22436.
- Sterck, E. H. M., E. P. Willems, J. van Hooff, and S. A. Wich. 2005. Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). *Behaviour* 142:845-868.
- Stokes, E. J., R. J. Parnell, and C. Olejniczak. 2003. Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behavioral Ecology and Sociobiology* 54:329-339.
- Tybur, J. M., and S. W. Gangestad. 2011. Mate preferences and infectious disease: theoretical considerations and evidence in humans. *Philosophical Transactions of the Royal Society B* 366:3375-3388.
- Vanpé, C., L. Debeffe, M. Galan, A. J. M. Hewison, J.-M. Gaillard, E. Gilot-Fromont, N. Morellet, H. Verheyden, J.-F. Cosson, B. Cargnelutti, J. Merlet, and E. Quémère. 2016. Immune gene variability influences roe deer natal dispersal. *Oikos* 125:1790-1801.
- VanVuren, D. 1996. Ectoparasites, fitness, and social behaviour of yellow-bellied marmots. *Ethology* 102:686-694.
- Yamagiwa, J., J. Kahekwa, and A. K. Basabose. 2009. Infanticide and social flexibility in the genus *Gorilla*. *Primates* 50:293-303.

Figure legends

Figure 1. Illustration of the factors tested as explanatory variables of the dispersal decisions of adult females. Connector lines exemplify what types of choices dispersing females are expected to make. Each variable listed below is recalled in the figure with its corresponding letter, from a) to h). Adult females may stay in or emigrate their breeding group (BG) depending on a) their own disease (presence/absence of severe skin lesions) and reproductive status (nulliparous or multiparous, with or without an unweaned thus dependent infant), b) the presence of severe skin lesions on the leader silverback, c) the presence/absence and the number of severely diseased individuals in the BG, d) the BG ageing stage, e) the BG size, and f) the infant-to-adult-female ratio. Immigrant adult females may g) join an unmated silverback (solitary or in a non-breeding group) or immigrate into a BG, which is related to the silverback's mating status, b) avoid diseased silverbacks, or c) avoid BGs with severely infected gorillas (in terms of the presence or the number of severely diseased individuals); they choose their BG according to d) its ageing stage, e) its size, f) the infant-to-adult-female ratio, h) the number of adult females.

Figure 2. Predicted probability for adult females to emigrate from a breeding group related to a) the number of severely diseased individuals within breeding groups, b) the presence of severe skin lesions on the leader silverback, c) the age of breeding groups, d) the presence of an unweaned infant. Bars or dashed lines represent 95% confidence intervals.

Figure 3. Predicted probability for adult females to immigrate into a gorilla unit related to a) the type of gorilla unit, b) the presence of severely diseased individuals and c) young breeding group size. Bars or dashed lines represent 95% confidence intervals.

Figure 4. Manly's selection indices testing the preferences of immigrating females for different units, depending on (a) the number of individuals severely suffering from skin lesions (three categories), (b) the gorilla unit category (from young to senescent breeding groups and non-breeding units; *i.e.* unmated silverbacks), (c) the breeding group size (four categories), (d) the infant/adult female ratio (four categories from 0 to 1, *i.e.* all females had an unweaned infant); indices above 1 indicated preference, whereas indices below 1 indicated avoidance, 95% confidence intervals are represented.







