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Rank changes in female chimpanzees in Taï National Park

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Photo 18: Kinshasa with Kayo in peaceful times. c/o Liran Samuni

Anecdote

In February 2015, we had to leave the field site for a couple of days. When we were able to return, Kinshasa's 4-year-old daughter, Kayo, had disappeared without a trace. Before, Kinshasa had mostly associated with other females, especially Sumatra, who had an infant of the same age. After Kayo's death, she became less central in the community, vocalizing and interacting less, and associating more with the males, especially her brother Kuba and the subadult males, Oscar and Ravel. Based on her behaviour and the pant grunts between females, we had always seen her as the fourth-ranking female. However, after her daughter disappeared, two younger females, Mbeli and Uapaca, would regularly approach her swaggering, leading her to pant grunt to them. It seemed we were witnessing a female losing not only her infant, but also her social status.

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18.1 Introduction

In most animal species that see individuals repeatedly interact with conspecifics, dominance hierarchies are an important response to resource competition, allowing individuals to reduce the danger of costly injuries during aggression (Kaufmann, 1983). If hierarchies are clearly defined, it is not necessary to establish priority of access to resources with each new conflict (Clutton-Brock & Huchard, 2013). The type of hierarchical system, its stability and flexibility, depends on the ecological and social environment of a species, such as the availability of resources or the permanence of association (Isbell, 1991). Most primate species, with relatively stable associations of at least one sex over the lifespan, show largely linear hierarchies (Sterck et al., 1997).

In most species, there are clear fitness benefits for higher-ranking individuals of both sexes (Majolo et al., 2012), but rank acquisition and maintenance differ between species and sexes (Clutton-Brock & Huchard, 2013). Changes in established hierarchies are mainly driven by two forces (Foerster et al., 2016): demographics (individuals appearing and disappearing over time) resulting in a system where individuals queue for rank, or challenges to the existing hierarchy by lower-ranking individuals, indicating higher resource competition within the system. The possibility for the second mechanism introduces an element of instability and complexity into a hierarchical system because ranks become less predictable over the long term.

Many female Old World primates have very stable hierarchies, often based on matrilineal kin relationships (Sterck et al., 1997). Female chimpanzees differ from these species by dispersing before adulthood, arriving in a new community with limited kin and having to compete for their own dominance rank and social relationships (Langergraber et al., 2009). Because female chimpanzees, especially of the Eastern subspecies, are less gregarious than males, it has long been difficult to gather sufficient data to create reliable dominance hierarchies and test their properties (Pusey & Schroepfer-Walker, 2013). Association avoidance often seems to be a better strategy for females than submitting to a hierarchy (Miller et al., 2014). In the Ngogo community, females associate at high levels, but with a small clique of non-kin females to avoid competition (Wakefield, 2008; Langergraber et al., 2009). Research in recent decades has shown, however, that female chimpanzees do possess linear ranks (Wittig & Boesch, 2003; Foerster et al., 2016), and that there are clear rank-related benefits for higher-ranking individuals, with such individuals having better core territories (Williams et al., 2002; Murray et al., 2007) and higher reproductive success (Pusey et al., 1997).

Using the long-term female pant–grunt data from the Kasekela community in Gombe National Park, Foerster et al. (2016) established that while male community members competed through direct challenges, female individuals ‘queued’ for rank, only changing rank through demographic changes in the group. Rank is therefore very strongly correlated with age (Foerster et al., 2016). However, females at the Gombe research site are relatively solitary (Wrangham & Smuts, 1980), inhabiting clearly circumscribed core areas with little overlap (Williams et al., 2002).

Little is still known about how more gregarious female chimpanzees acquire and defend their ranks. The factor driving gregariousness (clumped resources) is also predicted to drive contest competition (Wittig & Boesch, 2003) and contest competition appears to be rare in females in East African field sites (Murray et al., 2006; Wakefield, 2008). If permanent association between females, as seen in Taï (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2005; Riedel et al., 2011; Wittiger & Boesch, 2013), increases the likelihood of conflict over resources and reduces the viability of avoidance as a strategy, a more pronounced dominance hierarchy could reduce the potential for conflicts between females. In Taï chimpanzees, predation by leopards increases the need to associate with other group members, in contrast to Eastern chimpanzees, where predators have been mainly eradicated (Boesch, 1991). Thus, avoidance is likely more costly than increased competition that arises from high rates of association. This might promote competition within female dominance ranks, such that benefits outweigh the costs of fighting rather than queuing for high dominance positions.

Based on this, the question we address here is whether the more gregarious female chimpanzees in Taï show the same pattern of queuing, or if their ranks show evidence of change due to competition. Taï females exhibit linear hierarchies with competition over clumped food sources (Wittig & Boesch, 2003). Females form long-term social relationships with other females and males (Gomes & Boesch, 2009; Gomes et al., 2009; Lehmann & Boesch, 2009; Foerster et al., 2015; Surbeck et al., 2017), which lead to differentiated patterns of cooperation (Gomes & Boesch, 2009, 2011; Mielke et al., 2018). Females are involved in hunts (Boesch & Boesch, 1989) and group defence (Samuni et al., 2017), offer post-conflict bystander affiliations to their friends (Wittig & Boesch, 2010) and do not show the pattern of exclusive core areas seen in Gombe (Riedel et al., 2011). They therefore spend a lot of their time around other females, competing for resources. In times of food scarcity, high-ranking females can maintain a higher level of gregariousness, potentially protecting them from predators (Riedel et al., 2011). We implemented and improved on the method developed by Foerster et al. to determine if rank changes between females occur, how frequent they are and whether specific events, like the loss of offspring or rank changes between males, mediate them.

18.2 Methods

18.2.1 Data set

To test the stability of rank relationships in female chimpanzees in the Taï Forest, we used data for two communities where sufficient pant–grunt vocalizations were available in the Taï long-term database, collected by trained field assistants using all-day continuous focal animal sampling (Altmann, 1974). We supplemented this with data from researchers who worked with the two communities at different points in time (Wittig & Boesch, 2003; Mielke et al., 2017; Samuni et al., 2017; Wittiger & Boesch, 2013). In contrast to previous studies (Newton-Fisher, 2017), we exclusively used pant–grunt vocalizations and no aggressions to establish the rank order. Aggressions in chimpanzees regularly go against the hierarchy, while pant grunts are generally accepted to be unidirectional signals of submission, given strictly by low-ranking individuals towards higher-ranking individuals (Bygott, 1979; Laporte & Zuberbühler, 2010). Additionally, rank is often used as a variable in studies of aggression, making it important to calculate the hierarchy independent of aggressions.

Individuals were included if they were present for at least 2 years after reaching 12 years of age or immigrating, and had more than 10 recorded pant–grunts as sender or receiver within their own sex. While this led to the exclusion of a number of females, especially those who were only part of the communities in the first years of data collection, it prevents false rank assignments based on insufficient data. The Taï North Community has been habituated since 1984 (Boesch & Boesch-Achermann, 2000) and long-term data were available since 1995. We extracted 330 pant–grunts between 14 adult females of 22 adult females who lived in this community over the years. For the Taï South Community, long-term data have been collected since 1999, allowing us to extract 580 pant–grunts between 19 females of 36 total females in this community.

18.2.2 Dominance hierarchy

The Elo rating system to measure rank has been successfully applied to animal social systems (Albers & de Vries, 2001; Neumann et al., 2011). It calculates the winning likelihood of one individual over another by dynamically incorporating every interaction of interest (here, pant–grunts) of the dyad. Originally, each dyad starts with a likelihood set by the researcher (‘start value’). Each win by an individual increases their winning likelihood depending on the gain factor (k) and their previous winning likelihood, with expected outcomes changing the winning likelihood less than unexpected ones.

While this process allows for the identification of changes in the dominance hierarchy over time and the winning likelihood allows for more differentiated hierarchies than ordinal ranks (Albers & de Vries, 2001), a k-value must be assigned by the researcher a priori, which can influence the resulting hierarchy. Identifying the correct k-value is important, as underestimating it would result in ignored rank changes, while overestimating it would result in apparent rank changes between individuals that are not supported by the data. Similarly, the assumption that all individuals start with the same value is not met in permanent animal social groups, and creates a burn-in phase in which the hierarchy is unreliable (Neumann et al., 2011). Foerster et al. modified the original formula to optimize the start value and k-value, thus removing the need for a data-intensive burn-in phase and allowing for the k-value to be 0, thereby removing apparent rank changes that do not correspond with empiric rank changes. This posits an important advantage for animal researchers.

Applying this method, we noticed that it performed strongly with a data set consisting of large amounts of data and regular interactions between all dyads (as we see in most male chimpanzee data sets). However, if the data points were fewer and further between, and some dyads did not update their value regularly (as we see in chimpanzee females), the optimization algorithm would converge on a k-factor of 0 even in cases where rank changes were observed empirically, thus ignoring potentially important information. This is due to a fundamental difference between the original Elo measure, which is used to represent contest situations where two individuals have a relative strength that can be captured as a winning likelihood of one over the other (as we see in primate aggressions), and the meaning of a pant–grunt, which is never a contest that can be won but a signal of submission by the lower-ranking individual. Thus, the winning likelihood of one individual over any lower-ranking group member is by definition 1, until there is a rank change, after which it is 0. The winning likelihood values provided by the Elo method, when used on pant–grunts, therefore have no direct interpretation, as they have for contest situations.

The method itself can still offer valuable information about rank changes over time. Instead of only optimizing the winning likelihood, we modified the script provided by Foerster et al. to additionally optimize a second parameter, the number of correct classifications provided by the optimized k-value and start values. Correct classifications are situations where the winner of the pant–grunt (the recipient) had a higher Elo value before the interaction than the loser (the sender).

In a perfect representation of the hierarchy, there are only two situations in which the assumedly higher-ranking individual pant–grunts towards the lower-ranking individual: first, if there are errors in the data collection, which given the size of the data set is always possible, but should not have an extreme effect on the rank order; and second, if a rank change takes place, in which case the contender should overtake the former dominant individual after the interaction. If the optimization algorithm only considers the winning likelihood and data are sparse, a third option appears: if there are not enough interactions after a rank change, the optimal k-value and start values can be such that a rank change is simply ignored. However, a property of the optimization algorithm can be exploited to achieve a high winning likelihood while also increasing the number of correct classifications: with each iteration of the optimization algorithm used by Foerster et al., the winning likelihood increases, and so does the number of correct classifications. However, the two parameters do not necessarily reach their optimum at the same time, and the number of correct classifications at times reaches a maximum before the winning likelihood does, to then drop again as the start value and k-value get fixed. Note that this is only the case for sparse data sets: if enough data are available, the optimal winning likelihood also has the maximum number of correct classifications.

To make use of this property, we repeatedly ran the optimization as provided by Foerster et al., with different numbers of iterations for the ‘optim’ function (between 10 and 200) (R Core Team, 2017), selecting the one that had the maximum number of correct classifications and using it to calculate our final Elo rank measure for the respective group. This way, we calculated the dominance hierarchy for the females of the Taï North and South Communities. The goal was to test whether we would observe the same pattern seen in the Gombe community, with females showing no rank changes over time. If the method indicated rank changes, we extracted the pant–grunt history of the two individuals to determine whether an actual rank change could be confirmed. We only considered rank changes as having occurred if at least one pant–grunt in the original direction (A to B) was recorded, and multiple pant–grunts in the new direction (B to A) followed. We dismissed apparent rank changes due to single pant–grunts to remove possible impact of data collection errors. Additionally, we tried to determine what could cause rank changes between females, by analysing whether they followed the loss or birth of offspring. We do not assume that the winning likelihood provided by the Elo measure can be meaningfully interpreted for pant–grunts, and we thus present only ordinal ranks, standardized between 0 and 1.

18.3 Results

Applying our modified Elo rank rating to the female pant–grunt data of the Taï North and South Communities revealed that both showed rank changes. The parameters (see Table 18.1) showed that, in the North Group, the optimal rank solution was reached with k = 110, leaving us with 302 of 330 pant–grunts (91.5%) yielding correct classifications (i.e. lower-ranking individual pant–grunting to the higher-ranking individual). Of the 28 incorrect classifications, 11 incorrect classifications concerned the first pant–grunt of the dyad, potentially indicating that the start value of both individuals was based on their interactions with others and needed time to adjust. Although these might indicate rank changes (especially new females joining and advancing in rank), we cannot rule out that this is an artefact of the method. Of the remaining 17 incongruent pant–grunts, nine were not followed by further pant–grunts from either individual. A further two potential rank changes were followed by pant–grunts congruent with the original rank direction, making it possible that the incongruent pant–grunt was an observation error. One of the remaining incongruent cases was represented twice, leaving us with five unique possible rank changes. Three females pant–grunted multiple times towards a previously lower-ranking female without ever receiving another pant–grunt from them, indicating a complete rank change (see Table 18.2). Of those, two were connected, with one female (Mystère) losing two rank positions in the same time period in 2014. In a further two dyads, we recorded multiple pant–grunts in both directions over multiple years, which could be either due to recurring data collection errors, or could indicate a lack of a clear linear hierarchy between the involved females. See Figure 18.1 for a graphic representation of the hierarchy.

In the South Group, the optimal k was k = 56, with 563 of 580 pant–grunts (97.1%) being correct classifications. Of the 17 incorrect classifications, seven concerned the first interaction of the dyad. Of the remaining ones, a further four were not followed by pant–grunts in either direction, and one was followed by pant–grunts congruent with the original dominance hierarchy. Three dyads showed multiple pant–grunts in both directions over the years, indicating unclear or changing hierarchies, or multiple collection errors. The female Wapi seemed to overtake multiple other females for a short period of time, just to fall back behind them after a few

Table 18.1 **Data set and result of Elo optimization for females in the Taï North and South Communities. 'Congruent pant–grunts' are vocalizations that were in line with the previous established dominance hierarchy.**

Community	# Females	# Pant–grunts	Optimal k	# Congruent pant–grunts	% Congruent pant–grunts
North	14	330	110	303	91.5
South	19	580	56	563	97.1

Table 18.2 **Rank changes between females in the Taï North and South Groups, with the date of the first reversed pant–grunt, number of offspring lost by the previously dominant female in the year before, the number of infants born by the subdominant in the year before and the number of sons above 9 years of the dominant/subdominant female. In bold, permanent rank changes; in italics, dyads that showed pant–grunts in both directions over multiple years.**

Group	Original dominant	Original subdominant	Date rank change	Lost offspring dominant	Births subdominant	Subadult male sons present
North	Goma	Ricci	20 April 1997	0	0	0/1
North	Mystère	Narcisse	16 July 2014	2	0	0/1
North	Mystère	Belle	1 December 2014	2	1	0/1
North	*Perla*	*Castor*	–	–	–	–
North	*Goma*	*Venus*	–	–	–	–
South	Isha	Julia	19 December 2013	0	1	1/1
South	Kinshasa	Mbeli	4 March 2015	1	0	0/0
South	*Wapi*	*Isha*	–	–	–	–
South	*Isha*	*Olivia*	–	–	–	–
South	*Bienvenue*	*Atra*	–	–	–	–

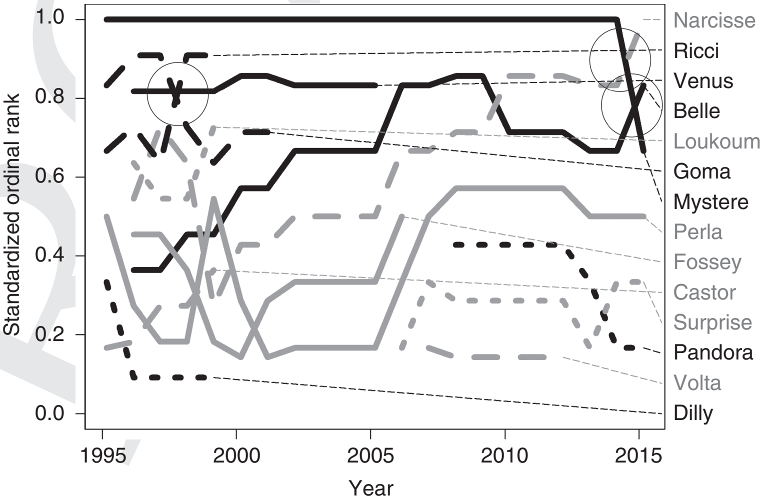

Figure 18.1 Rank trajectories of females in the Taï North Community. Ordinal rank standardized between 0 and 1. Circles mark confirmed rank changes. Apparent rank changes without circles had no preceding pant–grunts, were not followed by further pant–grunts in the dyad, or were followed by pant–grunts supporting the original hierarchy and thus cannot be confirmed with the existing data.

months and disappear subsequently. For the remaining two dyads, the algorithm indicated rank changes that where followed by multiple pant–grunts of the former dominant, indicating an actual change took place (Figure 18.2).

While no quantitative analysis is possible, and the long time between pant–grunts in a dyad (up to 14 years) makes it hard to pinpoint the exact point of rank change, we find evidence for multiple life events that could invite female rank changes (Table

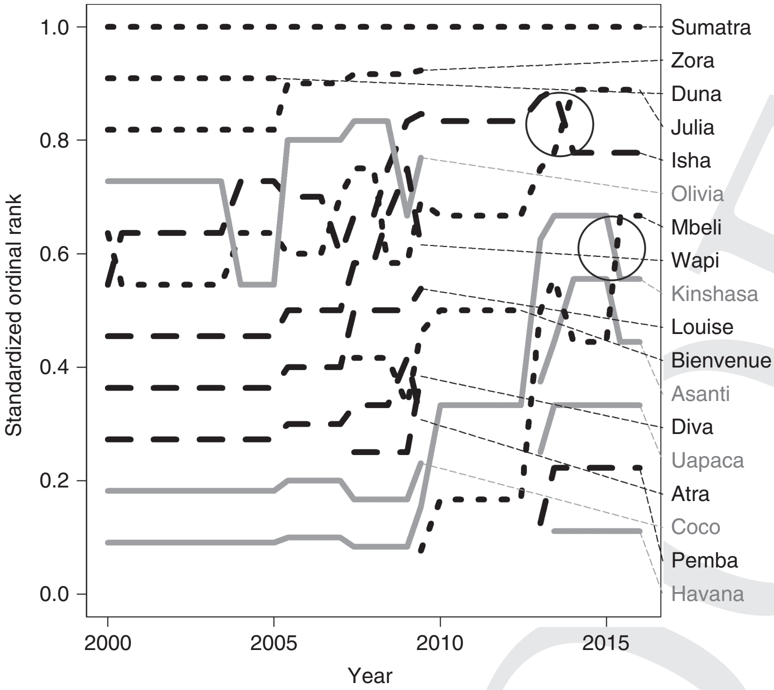

Figure 18.2 Rank trajectories of females in the Taï South Community. Ordinal rank standardized between 0 and 1. Circles mark confirmed rank changes. Apparent rank changes without circles had no preceding pant–grunts, were not followed by further pant–grunts in the dyad, or were followed by pant–grunts supporting the original hierarchy and can thus not be confirmed with the existing data.

18.2), but none of them explains all of the cases. In three of six cases of clear rank change, the previously dominant female lost offspring in the months preceding the first reversed pant–grunt (Kinshasa, Mystère). In three cases, the challenger had a subadult son on the verge of adulthood or entering the adult hierarchy, while the previously dominant female did not; however, in one case (Isha/Julia) both had teenage sons, but the challenger's son was higher-ranking. Goma developed a neurological disease in 1997 that made it hard for her to follow the group, which could explain the rank change with Ricci. One of the dyads with unclear rank relations seemed to temporarily change ranks due to the same event, with Goma pant–grunting to Venus for around 3 months before the rank was reversed again. The second dyad, Perla/Castor, seemed to take turns in pant–grunting over multiple years.

To further investigate competition between females, we analysed how many aggressions were directed against the hierarchy direction in each group. Over the entire time period, 84/269 (31%) of aggressions between females in the North Group and 67/259 (26%) of aggressions in the South Group were initiated by lower-ranking females against higher-ranking females.

18.4 Discussion

Our results show another aspect of difference between the lives of female chimpanzees in different communities: while the dominance hierarchies of both the North and South Groups were largely stable over time, we found evidence for a number of rank changes, in contrast to a recent study in the Kasekala community (Foerster et al., 2016).

Chimpanzee females in West Africa have been argued to be more gregarious than those in East Africa (Riedel et al., 2011). This could be driven by the presence of leopards as predators in West Africa (Boesch, 1991), or by different distributions of food

(Wittiger & Boesch, 2013). Once individuals spend more time together, competition over resources cannot be avoided, and a clear linear hierarchy can limit aggression (Clutton-Brock & Huchard, 2013). If the benefit of possessing a higher rank is thereby increased, females might invest in challenging others, introducing a level of instability into the hierarchy.

Modifying the Elo rank method introduced by Foerster et al. allowed us to identify at least five long-term rank changes between adult females, and five further cases where pant–grunts were exchanged in both directions over multiple years. Given the combined study period of 39 years over the two communities, this is not a large number. However, we used a conservative estimate: to achieve higher levels of accuracy, we restricted the data set to individuals involved in more than 10 pant–grunts with other females, using only 33 out of 58 adult females in those communities. We also excluded potential rank changes if no pant–grunt within the dyad occurred before or after the incongruent pant–grunt. In another 14 pant–grunts in the North and eight in the South, two individuals apparently changed rank, but we did not have pant–grunts before or after the rank change to rule out methodological errors. Both of these rules will disproportionally exclude rank changes involving females that have recently joined one of the communities, a time when challenges between females are expected. It is therefore likely that rank changes are somewhat more common than presented here. While rank challenges influence the hierarchy in this population, demography and maturation are still main driving forces behind rank acquisition, and ranks are generally very stable.

Analysing which life events might have instigated rank changes, we found that three of the five certain rank changes followed the death of the former dominant's offspring. In one case, Mystère lost two sons, aged 8 and 12, who could have potentially been supporters in competitive situations. Similarly, one case of uncertain rank change and one permanent rank change were related to a female, Goma, developing a neuronal disease that impeded her movements. This could mean that females use the vulnerability of a higher-ranking female, due to an offspring's death or being afflicted with disease, to challenge their rank. However, not every death of an offspring led to a rank change, and the cases described here concern the end of the data collection period, making it hard to evaluate whether ranks changed back after the previously dominant female gave birth again. Similarly, a son reaching adulthood or an adult son being present might facilitate rank challenges, but it was neither a necessary nor sufficient condition for the mother attaining higher rank. This raises the question of whether adult sons could be a resource for female chimpanzees. One question that remains is whether rank changes might be temporary, or ranks between females unresolved at times (Douglas et al., 2017). In our data set, one of two unclear rank relations seemed to be temporary, returning to their original state.

Around 30% of aggressions between females in this population were initiated by the lower-ranking of the two individuals. With aggressions being more likely in food patches than outside (Wittig & Boesch, 2003), this would indicate that, even with few rank changes, female chimpanzees challenge each other for resources. While we do not include information on who won the confrontation or its cause, this pattern of aggression would indicate that female chimpanzees are relatively egalitarian, with lower-ranking individuals able to hold themselves against high-ranking females. We know that in male chimpanzees, agonistic alliances allow low-ranking individuals to beat higher-ranking competitors (de Waal, 1982). Whether the same holds true for females needs further confirmation. Another indicator for the relatively egalitarian nature of female dominance hierarchies is the low level of pant–grunts seen here: while males pant–grunt regularly upon meeting a high-ranking individual, females seem to go long periods of time without reiterating their rank positions with each other.

Our results constitute yet another difference between females of the Eastern and Western chimpanzee subspecies: in contrast to females in Gombe (Foerster et al., 2016), who queue for rank and only rise in the hierarchy through demographic changes, females in both of the Taï communities studied here change ranks actively. While further research is needed into whether rank changes are precipitated by specific aggressive events, and whether females gain fitness benefits from challenging dominant individuals, this result indicates that rank position is more flexible in the more gregarious Taï females. As they are also more likely to participate in other cooperative behaviours such as grooming and form long-term social bonds with non-kin (Lehmann & Boesch, 2009), this flexibility could add a political dimension to female social life that is missing in females of more restricted social groups.

References

Albers, P. C. H. & de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour*, 61, 489–495. https://doi.org/10.1006/anbe.2000.1571

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–267. https://doi.org/10.1080/14794802.2011.585831

Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, 117, 220–241. https://doi.org/10.1163/156853991X00544

Boesch, C. & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, 78, 547–573. https://doi.org/10.1002/ajpa.1330780410

Boesch, C. & Boesch-Achermann, H. (2000). *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*. Oxford: Oxford University Press.

Bygott, J. D. (1979). Agonistic behaviour, dominance and social structure in wild chimpanzees of the Gombe National Park. In D. A. Hamburg & E. R. McCown (eds.), *The Great Apes* (pp. 405–427). Menlo Park: Benjamin/Cummings.

Clutton-Brock, T. H. & Huchard, E. (2013). Social competition and selection in males and females. *Philosophical Transactions of the Royal Society B*, 368(1631), 20130074–20130074. https://doi.org/10.1098/rstb.2013.0074

de Waal, F. B. M. (1982). *Chimpanzee Politics: Power and Sex Among Apes*. Baltimore: John Hopkins University Press.

Douglas, P. H., Ngomo Ngonga, A. C. & Hohmann, G. (2017). A novel approach for dominance assessment in gregarious species: ADAGIO. *Animal Behaviour*, 123, 21–32. https://doi.org/10.1016/J.ANBEHAV.2016.10.014

Foerster, S., Franz, M., Murray, C. M., Gilby, I. C., Feldblum, J. T., Walker, K. K., et al.(2016). Chimpanzee females queue but males compete for social status. *Scientific Reports*, 6, 1–11. https://doi.org/10.1038/srep35404

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., et al.(2015). Social bonds in the dispersing sex: Partner preferences among adult female chimpanzees. *Animal Behaviour*, 105, 139–152. https://doi.org/10.1016/j.anbehav.2015.04.012

Gomes, C. M. & Boesch, C. (2009). Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS ONE*, 4(4), e5116. https://doi.org/10.1371/journal.pone.0005116

Gomes, C. M. & Boesch, C. (2011). Reciprocity and trades in wild West African chimpanzees. *Behavioral Ecology and Sociobiology*, 65, 2183–2196. https://doi.org/10.1007/s00265-011–1227–x

Gomes, C. M., Mundry, R. & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B*, 276(1657), 699–706. https://doi.org/10.1098/rspb.2008.1324

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, 2, 143–155. https://doi.org/10.1093/beheco/2.2.143

Kaufmann, J. H. (1983). On the definitions and functions of dominance and territoriality. *Biological Reviews*, 58, 1–20. https://doi.org/10.1111/j.1469-185X.1983.tb00379.x

Langergraber, K. E., Mitani, J. & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 71, 840–851. https://doi.org/10.1002/ajp.20711

Laporte, M. N. C. & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour*, 80, 467–473. https://doi.org/10.1016/j.anbehav.2010.06.005

Lehmann, J. & Boesch, C. (2005). Bisexually bonded ranging in chimpanzees (*Pan troglodytes verus*). *Behavioral Ecology and Sociobiology*, 57, 525–535. https://doi.org/10.1007/s00265-004–0891–5

Lehmann, J. & Boesch, C. (2009). Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 77, 377–387. https://doi.org/10.1016/j.anbehav.2008.09.038

Majolo, B., Lehmann, J., de Bortoli Vizioli, A. & Schino, G. (2012). Fitness-related benefits of dominance in primates. *American Journal of Physical Anthropology*, 147, 652–660. https://doi.org/10.1002/ajpa.22031

Mielke, A., Preis, A., Samuni, L., Gogarten, J. F., Wittig, R. M. & Crockford, C. (2018). Flexible decision-making in grooming partner choice in sooty mangabeys and chimpanzees. *Royal Society Open Science*, 5, 172143.

Mielke, A., Samuni, L., Preis, A., Gogarten, J. F., Crockford, C. & Wittig, R. M. (2017). Bystanders intervene to impede grooming in Western chimpanzees and sooty mangabeys. *Royal Society Open Science*, 4, 171296. https://doi.org/10.1098/rsos.171296

Miller, J. A., Pusey, A. E., Gilby, I. C., Schroepfer-Walker, K., Markham, A. C. & Murray, C. M. (2014). Competing for space: Female chimpanzees are more aggressive inside than outside their core areas. *Animal Behaviour*, 87(C), 147–152. https://doi.org/10.1016/j.anbehav.2013.10.023

Murray, C. M., Eberly, L. E. & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology*, 17, 1020–1028. https://doi.org/10.1093/beheco/arl042

Murray, C. M., Mane, S. V. & Pusey, A. E. (2007). Dominance rank influences female space use in wild chimpanzees, *Pan troglodytes*: Towards an ideal despotic distribution. *Animal Behaviour*, 74, 1795–1804. https://doi.org/10.1016/j.anbehav.2007.03.024

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., et al. (2011). Assessing dominance hierarchies: Validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, 82, 911–921. https://doi.org/10.1016/j.anbehav.2011.07.016

Newton-Fisher, N. E. (2017). Modeling social dominance: Elo-ratings, prior history, and the intensity of aggression. *International Journal of Primatology*, 38, 427–447. https://doi.org/10.1007/s10764-017–9952–2

Pusey, A. E. & Schroepfer-Walker, K. (2013). Female competition in chimpanzees. *Philosophical Transactions of the Royal Society B*, 368(1631), 20130077–20130077. https://doi.org/10.1098/rstb.2013.0077

Pusey, A. E., Williams, J. & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, 277(5327), 828–831. https://doi.org/10.1126/science.277.5327.828

R Core Team. (2017). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Riedel, J., Franz, M. & Boesch, C. (2011). How feeding competition determines female chimpanzee gregariousness and ranging in the Taï National Park, Côte d'Ivoire. *American Journal of Primatology*, 73, 305–313. https://doi.org/10.1002/ajp.20897

Samuni, L., Preis, A., Mundry, R., Deschner, T., Crockford, C. & Wittig, R .M. (2017). Oxytocin reactivity during intergroup conflict in wild chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 268–273. https://doi.org/10.1073/Proceedings of the National Academy of Sciences of the United States of America.1616812114

Sterck, E. H. M., Watts, D. P. & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291–309. https://doi.org/10.1007/s002650050390

Surbeck, M., Girard-Buttoz, C., Boesch, C., Crockford, C., Fruth, B., Hohmann, G., et al. (2017). Sex-specific association patterns in bonobos and chimpanzees reflect species differences in cooperation. *Royal Society Open Science*, 4(5), 1–20. https://doi.org/10.1098/rsos.161081

Wakefield, M. L. (2008). Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, 29, 907–929. https://doi.org/10.1007/s10764-008–9280–7

Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P. & Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour*, 63, 347–360. https://doi.org/10.1006/anbe.2001.1916

Wittig, R. M. & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology*, 24, 847–867. https://doi.org/10.1023/A:1024632923180

Wittig, R. M. & Boesch, C. (2010). Receiving post-conflict affiliation from the enemy's friend reconciles former opponents. *PLoS ONE*, 5(11), e13995. https://doi.org/10.1371/journal.pone.0013995

Wittiger, L. & Boesch, C. (2013). Female gregariousness in Western Chimpanzees (*Pan troglodytes verus*) is influenced by resource aggregation and the number of females in estrus. *Behavioral Ecology and Sociobiology*, 67, 1097–1111. https://doi.org/10.1007/s00265-013–1534–5

Wrangham, R. W. & Smuts, B. B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*, 28, 13–31.