JZAR JOURNAL OF ZOO AND AQUARIUM RESEARCH
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Evidence-based practice

Monitoring the behaviour and stress physiology of male gorillas *Gorilla gorilla gorilla* for one year following bachelor group formation

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Keywords: androgens, behaviour, glucocorticoids, non-invasive, primates, proximity, social introductions

Article history:
Received: 4 Jan 2021
Accepted: 12 Jan 2022
Published online: 31 Jan 2022

Abstract

Gorillas *Gorilla gorilla gorilla* are polygynous so zoos are challenged to provide lifelong socialisation for males not living in mixed-sex or breeding troops. One approach is to establish and manage all-male "bachelor" groups; however, there is little published information on the behavioural and physiological impacts that group formation may have on these individuals. Therefore, we monitored the physiology and sociality of four male gorillas who were between 5.5 and 9 years old during the formation of a bachelor group at Lincoln Park Zoo (Chicago, IL, USA). Our objectives were to monitor negative behaviours (abnormal and agonistic), proximal inter-individual distance and faecal glucocorticoid (FGM) and androgen metabolites (FAM) during group formation. Data were collected in two six-month periods: immediately following the introduction (Period 1) and the subsequent six months (Period 2). The percentage of time spent engaging in agonistic and abnormal behaviours was low (less than 3%) for all males during both Period 1 and Period 2. Proximity (i.e. inter-individual distances) within each possible dyad of males did not differ across periods, except for between two individuals, where their average inter-individual distance increased from Period 1 to 2. From Period 1 to Period 2, mean FGM (ng/g wet faeces) decreased significantly for two of the four males, but there was no change for the other two males. In Period 2, FAM differed significantly (increased) for only one male. Relatively low levels of behavioural and physiological stress indicators during the study were desired outcomes for this bachelor group formation.

Background

Whenever possible, zoos aim to replicate species-typical social groupings for animals in their care. In the wild, most lowland gorillas *Gorilla gorilla gorilla* live within polygynous social groups composed of mature females, their offspring and one breeding silverback male (Gatti et al. 2004, Parnell 2002, Robbins et al. 2004). Male offspring typically leave their natal group when they are sub-adults (6–8 years old; Parnell 2002) and these males will then either live a solitary life or join an all-male group of three to twelve "bachelor" gorillas (Gatti et al. 2004, Harcourt 1988, Robbins et al. 2004) prior to acquiring a family group with sexually mature females. However, because gorillas are polygynous and are born in approximately equal sex ratios (Pullen 2005, Stoinski et al. 2004), zoos are challenged to provide lifelong socialisation for males not living in mixed-sex or breeding troops (Stoinski et al. 2001). It has therefore become increasingly common for adolescent and adult males to be housed in bachelor groups at institutions accredited by the Association of Zoos & Aquariums (AZA; Gartland et al. 2018a, Pullen 2005). At the time of writing in 2021, there are 168 male gorillas in AZA zoos, of which 74 are housed in 23 bachelor groups (Lukas et al. 2021). Such social groupings have been shown to be a viable management option (Stoinski et al. 2001, Stoinski et al. 2013).

The literature suggests that zoo-housed gorilla bachelor groups display increased species-typical behaviour (Leeds et al. 2015) and have lower urinary cortisol (Stoinski et al. 2002)

Table 1. The male gorilla study subjects involved in bachelor group formation at the Lincoln Park Zoo (LPZ; Chicago, IL, USA).

ID	Place of birth	Age at beginning of study (years)	Weight at beginning of study (kg)	Relevant rearing history
AZ	LPZ	9	114	Mother-reared in intergenerational family group
AM	LPZ	7	91	Mother-reared in small family group
UM	Cheyenne Mountain Zoo	6	62	Initially hand-reared by staff at place of birth and then transferred to surrogate gorilla mother at Columbus Zoo
MO	Little Rock Zoo	5.5	65	Mother-reared in family group of all adults without any similar-aged peers

compared to solitary-housed males, and that socially housing males together does not confer increased wounding rates (Leeds et al. 2015). However, little has been published about the process of forming such bachelor groups, and while inferences can be drawn from published information about the formation of mixed-sex groups (e.g. Huskisson and Chism 2018) or the manipulation of all-male groups (e.g. Gartland et al. 2021), the characteristics of all-male group formation are likely unique and demand study. Monitoring the group formation process specifically is important because the introduction of new gorillas can lead to changes in behaviour and physiology in all individuals (Gartland et al. 2018b, Hoff et al. 1996, Jacobs et al. 2014), especially directly after the introduction process (Burks et al. 2001). To assess the success of group formation it is important to measure both the changing relationships between group members and each individual's welfare during the process.

Typically, behavioural measures are used to monitor group cohesion and affiliation. However, during introductions, gorillas do not tend to display affiliative behaviours nor begin to form strong social bonds (Burks et al. 2001), therefore measuring inter-individual distance is a useful alternative measure of social tolerance, affiliation and conflict resolution both in the wild (Stokes 2004) and in captive settings (Mallavarapu et al. 2006, Ross et al. 2009, 2010, 2011a, Stoinski et al. 2001).

To assess welfare, it is useful to take both behavioural and physiological measures. Behavioural measures of agonistic interactions and displays of abnormal behaviour can provide information regarding group cohesion and individual welfare (e.g. Bastian et al. 2020). In addition to behavioural monitoring, changes in endocrinology can be used to indicate changes in welfare. Previous studies have used faecal hormone metabolites and behaviour to non-invasively monitor changes in management and group composition in captive lowland gorillas (Jacobs et al. 2014, Peel et al. 2005). Repeated or chronic physiological stress can have detrimental implications, such as suppression of the immune system and reduced fertility (Sapolsky et al. 2000) and can be measured as glucocorticoid (e.g. cortisol) production. Additionally, androgen (e.g. testosterone) concentrations have links to fertility, maturation and social status in gorillas (Stoinski et al. 2002). Primates, particularly polygynous non-seasonal breeding species like gorillas, have higher production of androgens during times of conflict and increased aggression (Muller 2017) and following introduction of conspecifics (Jacobs et al. 2014). However, this has not been investigated during the initial period of bachelor group formation.

Our goal was to monitor the effects on behaviour and physiology immediately following the creation of a bachelor gorilla group through the first year of the group's formation. Our objectives were to monitor negative behavioural indicators of welfare (abnormal and agonistic behaviours), the social relationships (measured via inter-individual distance), and glucocorticoid and androgen metabolite concentrations. We measured all of these indicators for one year post-introduction, comparing the first half of that year to the second half. Our overall purpose was to provide this report on group formation so that managers may be better equipped when they plan future introductions.

Actions

This group formation involved extensive planning and consultation with the AZA Gorilla Species Survival Plan (SSP) Gorilla Behavior Advisory Group (GBAG). The demographic composition of the bachelor group met several of the recommendations by Stoinski et al. (2004): a group size of four immature males with diverse rearing histories housed in a state-of-the-art facility with the ability to house individuals separately if needed (Coe et al. 2009).

Subjects and housing

Four immature male western lowland gorillas were the focal subjects of our study: AZ, AM, UM and MO (Table 1). All four gorillas were housed at the Regenstein Center for African Apes at Lincoln Park Zoo (LPZ) in Chicago, Illinois, USA in an expansive indoor/outdoor (1932 m^2) enclosure with climbing structures, deep-mulch bedding and an off-exhibit holding area. The exhibit was designed to house a bachelor group, but also had accommodations for an individual gorilla to be housed alone for short periods, a feature that was used during the introduction process prior to the start of our study. The gorillas were given access to the outdoor yard when temperatures were at least 10ºC. The gorillas' daily diet consisted of multiple meals of fresh vegetables and primate biscuits, with water available ad libitum.

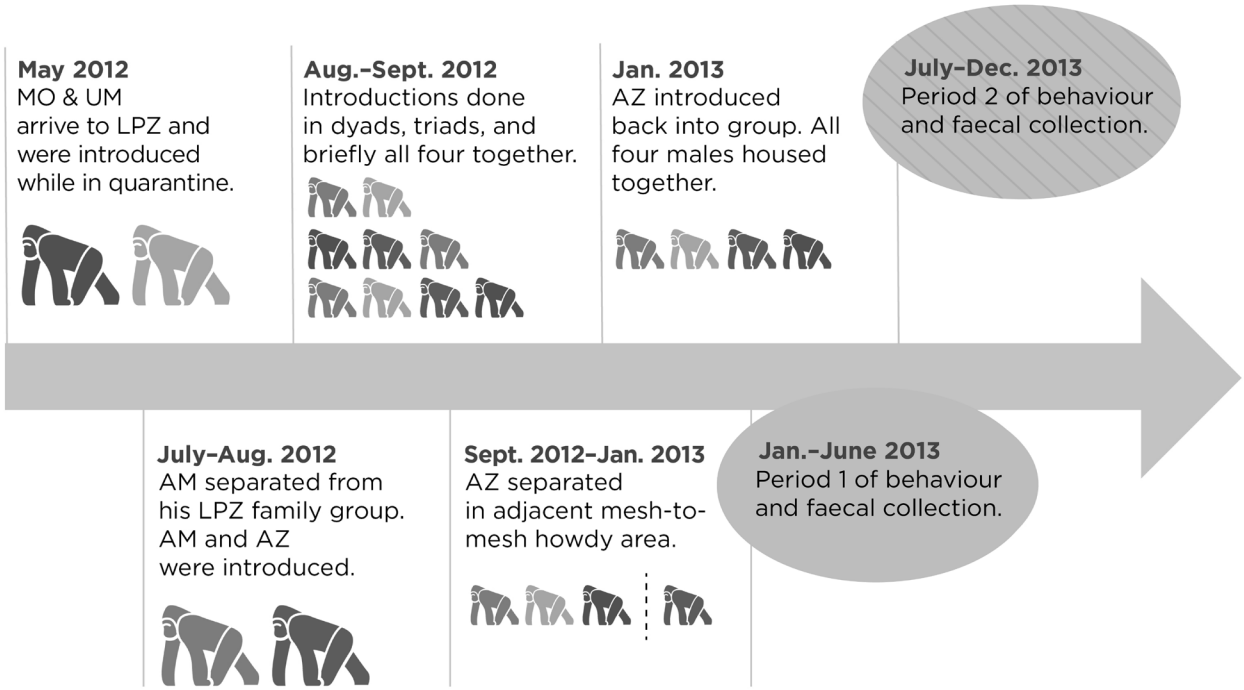

Figure 1. Timeline of introduction events, beginning in May 2012, for four male gorillas (AM, AZ, MO and UM) housed at Lincoln Park Zoo (Chicago, USA) and the study period (January to December 2013).

Group formation timeline

The introduction process commenced in May 2012 (Figure 1) and beginning in September 2012, all four males were slowly introduced to one another, in dyads and triads, until eventually all four were housed together. While the gorillas were being introduced, it was not possible to routinely collect behavioural data and faecal samples because of quarantine restrictions and the fluid housing situation. As soon as all four gorillas were housed together in the same habitat, in January 2013, data collection began and continued for one year.

Before the males were introduced there was a "howdy" period through mesh to allow visual, tactile and olfactory experience. Part of their husbandry involved cooperative training sessions and enrichment to encourage close proximity. Importantly, animal care staff were flexible in the daily management of the gorillas and responsive to the short- and long-term needs of each individual and to the sustainable maintenance of the group. Care staff distributed additional unscheduled browse, food items and enrichment to preoccupy the gorillas during this introduction. Because of this management strategy, it is not possible to accurately compare the amount of time during which the gorillas participated in positive indicators of welfare, such as time spent foraging, resting and engaging with enrichment.

Behavioural and proximity data collection

The collection of behavioural data was overseen as part of a long-term monitoring program. Data were collected by 13 trained researchers having passed reliability testing of at least 85% (Ross et al. 2011b). Briefly, the observers recorded the gorillas' behaviour from 10 am to 5 pm, five days a week across all social, environmental and management conditions when the gorillas were visible in their public-viewing shared space. Abnormal and agonistic behaviours, the selected behavioural welfare indicators (Table 2), were recorded as part of a larger ethogram using 10-min focal follows and a 30-second inter-sample interval on a tablet computer running Noldus Observer®. The ethogram is used at LPZ as part of the zoo's long-term behavioural monitoring of gorilla and chimpanzee *Pan troglodytes* behaviour (Bonnie et al. 2016, Jacobs et al. 2014, Kurtycz et al. 2014, Ross et al. 2011b). In total, 329 hours of observational data were recorded: 88 hours for AZ, 70 hours for AM, 99 hours for UM and 72 hours for MO.

Trained observers also recorded proximity data (i.e. inter-individual distances) using a map interface of the gorillas' exhibit displayed on a tablet computer to record the location of the gorillas in their exhibit (Bonnie et al. 2016). Observers used 60-second group scans for 30 minutes each weekday between the hours of 10 am and 5 pm for a total of 258.5 hours. As for the behavioural data, all 13 observers passed reliability testing of at least 85%. For each scan, the observers recorded the location of all group members within their enclosure and the custom software generated the inter-individual distance for each potential dyad.

Faecal sample collection and processing

Care staff collected faecal samples in the morning within four hours of defecation using gloved hands and spatula for an average of three times per week for each male, giving a total of 409 samples (108 for AZ, 100 for AM, 101 for UM, 100 for MO). All samples were stored at −20°C at LPZ until analysis. Samples were extracted by agitating 0.5 g of wet faeces in 90% ethanol, per Jacobs et al. (2014). The FGM concentrations were analysed using a cortisol enzyme immunoassay (EIA; polyclonal antiserum R4866 and cortisol horseradish peroxidase [HRP] provided by C.

Table 2. Ethogram of agonistic and abnormal behaviours for western lowland gorillas housed at Lincoln Park Zoo. Behaviours were recorded using 10-min focal follows with a 30-sec inter-sample interval for one year following bachelor group formation.

Behaviour category	Behaviour	Description
Agonism	Contact aggression	Focal directs aggressive behaviours to another individual that involve some physical contact between individuals.
Agonism	Receive contact aggression	Receiving any aggressive behaviours that involve some physical contact between individuals.
Agonism	Non-contact aggression	Focal directs aggressive behaviours to another individual that do not include any physical contact.
Agonism	Receive non-contact aggression	Receiving any non-physical contact, including lunging, rush and threats.
Agonism	Display	Focal engages in aggressive and attention-getting behaviour not directed at any one individual.
Agonism	Submission	Focal engages in crouching, bobbing, fleeing, avoiding fear grimacing, bared teeth screaming, pant grunting while in close proximity to conspecific partner.
Agonism	Receive submission	Focal receives submission behaviour from group mate, including crouching, bobbing, fleeing, avoiding fear grimacing, bared teeth screaming, pant grunting.
Abnormal	Coprophagy	Focal deliberately ingests faeces from the self or another individual.
Abnormal	Manipulate coprophagy	Focal paints, smears, manipulates (with hands or mouth) or otherwise investigates his own or another's faeces.
Abnormal	Regurgitation and re-ingestion	Focal deliberately regurgitates and re-consumes previously ingested material.
Abnormal	Urophagy	Focal deliberately ingests urine from the self or another individual.
Abnormal	Self-hair pluck	Focal pulls out own hair, frequently using a "flicking" motion of the wrist.
Abnormal	Abnormal body manipulation	Focal engages in repeated, sustained and purposeless manipulation of a specific area of own body.
Abnormal	Abnormal movement	Focal engages in repeated and sustained unusual and potentially purposeless full body movement with a definitive repetitive pattern, such as rocking.

Munro, UC Davis; Loeding et al. 2011). The FAM concentrations were measured at LPZ using testosterone EIA (polyclonal antiserum R156/7 and testosterone HRP provided by C. Munro, UC Davis; Loeding et al. 2011). These assays were biologically and biochemically validated for western lowland gorilla FGM and FAM by Jacobs et al. (2014). Assay sensitivity for cortisol was 3.9 pg/50 µL and for testosterone was 2.3 pg/50 µL. Inter-assay coefficient of variation was <15% and intra-assay coefficient of variation was <10% for standards, controls and samples. Loeding et al. (2011) describe complete cross-reactivities; in short, cortisol EIA has 0.1% cross-reactivity with testosterone, and testosterone EIA has 0.02% cross-reactivity with cortisol.

Data analysis

Data were analysed in two six-month periods (Periods 1 and 2) to allow for comparison of the gorillas' behaviour and physiology over time once all four males were socially housed together, with Period 1 covering January–June 2013 and Period 2 covering July–December 2013 (Figure 1). Statistical analyses were performed using Sigma Plot (Systat Software, Inc., version 12) with a significance value set to 0.05. All values are reported as mean±standard error. Some assumptions may have been violated because there were multiple samples from each individual and

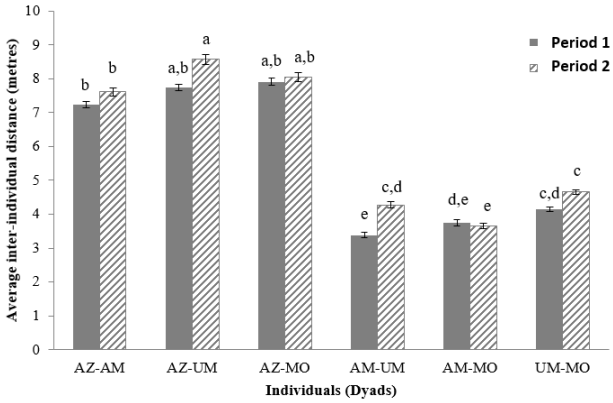

Figure 2. Means (±SE) of inter-individual distance (m) for each dyad of male gorillas housed at Lincoln Park Zoo for each period (Period 1: January–June 2013, Period 2: July–December 2013). Labels indicate differences (P<0.05) among each dyad and period.

samples may not be random since the gorillas were housed together and could possibly influence each other.

To analyse the percentage of time spent performing abnormal and agonistic behaviours, the data were normalised by arcsin square root transformation. The transformed data were analysed using two-way analysis of variance (ANOVA), with "Subject ID" and "Period" as model variables. Proximity data could not be transformed and were analysed using Kruskal-Wallis with post-hoc comparison using Dunn's method. The FGM and FAM concentrations were normalised via natural log-transformation and analysed using one-way ANOVA (Subject ID and Period combined into one variable) and Dunn's method for post-hoc analysis. FGM baseline concentrations were calculated iteratively (Moreira et al. 2001).

Consequences

Abnormal and agonistic behaviour

The percentage of time the gorillas spent engaging in agonistic behaviours was similar across the four individuals ($F_{3,3}$=1.658, P=0.344; AZ 0.22%±0.15; AM 0.07%±0.01; UM 0.06%±0.01; MO 0.02%±0.02) and across the two time periods ($F_{1,3}$=0.289, P=0.628; Period 1 0.13%±0.06; Period 2 5.38%±2.69). The percentage of time during which the males were observed engaging in abnormal behaviours was not significantly different ($F_{3,3}$=8.423, P=0.057; AZ 0.12%±0.05; AM 2.07%±0.88; UM 1.64%±1.14; MO 0.10%±0.05). Period did not influence the percentage of time for which the males demonstrated abnormal behaviours across the two study periods ($F_{1,3}$=5.784, P=0.095; Period 1 1.51%±0.75; Period 2 0.45%±0.23).

The gorillas' low rates of both agonistic and abnormal behaviours were comparable to those reported in previous studies regarding zoo-housed bachelor and mixed-sex groups (Gartland et al. 2018a b, Huskisson and Chism 2018, Leeds et al. 2015, Racevska and Hill 2017, Ross et al. 2011b). Of note, the males in this study were closely monitored by staff and trained volunteers throughout the day, which allowed for immediate identification of aggressive incidents, and although there were no instances of aggression that required substantive intervention by care staff during this study, care staff did sometimes increase the amount of enrichment provided to the group in response to potential group tension.

Inter-individual proximity

Overall, the average proximity that males maintained to each other differed across the two time periods (H_{11}=2070.6, P<0.001). However, when considering each possible dyad within the group, only one pair of gorillas showed a significant difference in their average inter-individual distance across study periods: the average distance maintained within dyad AM-UM was significantly greater in Period 2 compared to Period 1 (Q=5.6, P<0.05). This is counter to our prediction that, with time, the gorillas would show increased cohesion (i.e. decreased inter-individual distances). However, given the low rates of agonism, this change in proximity between AM and UM might represent a tension-reduction strategy. AM and UM were the only two gorillas to show a change in inter-individual distance over time; the inter-individual distances within all other dyads did not differ across periods (P>0.05 for all; Figure 2).

Irrespective of time period, the inter-individual distance maintained between the three younger males and AZ was greater (P<0.05) than that among themselves (Figure 2). This pattern reflects a previous report by Stoinski et al. (2001) that showed that the silverback in an all-male group spent more time at distances of >5 metres from other group members than did the younger males. Indeed, the three younger gorillas in our study group maintained an average distance of >7 metres between themselves and the dominant male AZ during both periods. In contrast, the three younger males all maintained shorter average inter-individual distances (<5 metres) between each other during both periods. Specifically, the average distance maintained between AZ and the other three males was almost twice the distance that AM, UM and MO maintained between each other.

Table 3. Overall mean and baseline (±SE) faecal glucocorticoid metabolites (FGM; ng/g faeces) concentrations for the male lowland gorillas housed at Lincoln Park Zoo over the two periods of bachelor troop formation. Labels indicate differences (P<0.05) among each individual and period.

Male gorilla	Overall mean	Baseline	Period 1	Period 2
AZ	23.33±0.74	21.46±0.55	26.02±1.10^{c}	20.93±0.89^{d}
AM	26.41±2.75	19.57±0.59	28.19±5.51^{c,d}	24.84±1.81^{c,d}
UM	54.44±3.52	36.42±1.16	57.13±6.07^{a}	51.69±3.50^{a}
MO	32.95±1.59	20.68±0.34	37.10±2.61^{b}	29.26±1.77^{c}

Faecal hormone metabolites

The four males' FGM concentrations (ng/g faeces) varied (H_{7}=151.431, P<0.001) throughout the study (Figure 3, Table 3). Specifically, FGM concentrations decreased (P<0.05) for AZ and MO from Period 1 to Period 2, while FGM concentrations were similar (P>0.05) for AM and UM across both periods. In Period 2, AZ's FGM concentrations were lower (P<0.05) than those of the other males during the same period. Conversely, in both periods, FGM concentrations for UM were higher (P<0.05) than those of

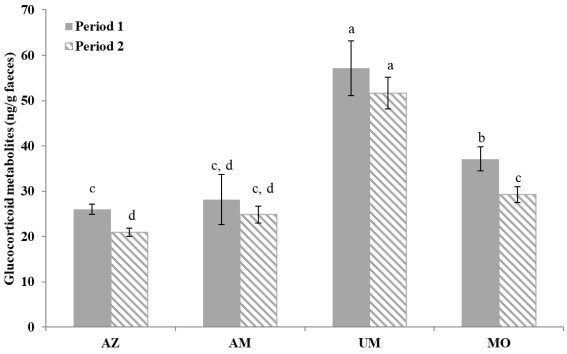

Figure 3. Means (±SE) of faecal glucocorticoid metabolite (FGM) concentrations for the four male gorillas housed at Lincoln Park Zoo for each period (Period 1: January–June 2013, Period 2: July–December 2013) during bachelor troop formation. Labels indicate differences (P<0.05) among each individual and period.

Table 4. Overall mean (±SE) faecal androgen metabolites (FAM; ng/g faeces) concentrations for the male lowland gorillas housed at Lincoln Park Zoo over the two periods of bachelor troop formation. Labels indicate differences (P<0.05) among each individual and period.

Male gorilla	Overall mean	Period 1	Period 2
AZ	117.77±6.54	136.54±15.56^{c}	107.43±5.00^{c}
AM	105.01±3.94	114.70±7.90^{c}	99.87±4.22^{c}
UM	287.31±17.84	231.97±28.02^{b}	318.43±21.95^{a}
MO	123.48±6.33	114.17±9.76^{c}	129.11±8.21^{c}

the other three males. MO's Period 1 FGM values were higher (P<0.05) than those of AZ and AM in both Period 1 and Period 2.

In comparing these results to a previous study at LPZ (Jacobs et al. 2014), the males' FGM values were similar to the adult male silverback that was being introduced to a new female in his troop (21 ng/g faeces). This silverback also showed an increase in FGM during the introduction phase to the new female, but then the post-introduction phase was significantly lower (mean 12 ng/g) and returned to FGM values similar to pre-introduction (mean 9 ng/g). The silverback studied by Jacobs et al. (2014) experienced an almost two-fold increase in FGM during the introduction phase compared to the post-introduction phase. Our study began immediately after the males were introduced as a group, but Period 1 FGM values were less than two-fold higher than Period 2 for all males.

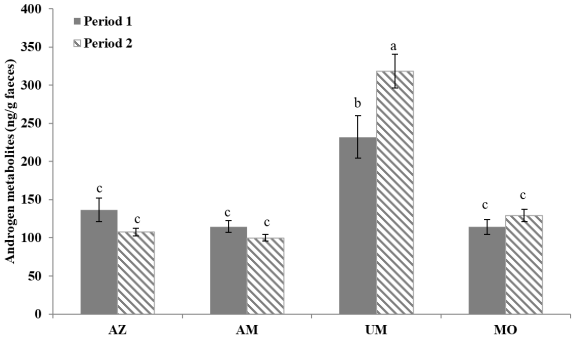

Figure 4. Means (±SE) of faecal androgen metabolite (FAM) concentrations for the four male gorillas housed at Lincoln Park Zoo for each period (Period 1: January–June 2013, Period 2: July–December 2013) during bachelor troop formation. Labels indicate differences (P<0.05) among each individual and period.

FAM concentrations increased between periods for UM (H_7=117.593, P<0.001), while the other males' FAM concentrations did not differ significantly across periods (P>0.05 for all) (Figure 4, Table 4). Additionally, UM's FAM values in Period 1 and Period 2 were higher (P<0.05) than the FAM values for the other three males, who had similar (P>0.05) FAM values to each other. Indeed, UM's FAM values were over two-fold higher than those recorded for an adult breeding silverback gorilla housed at the same zoo during an introduction to a female conspecific (Jacobs et al. 2014).

Conclusions

This case study is the first to assess both the behaviour (abnormal and aggressive behaviours, proximity) and physiology (FGM and FAM) of western lowland gorillas during the process of all-male bachelor group formation in a zoological setting. We used non-invasive methods to evaluate the males' adjustment to the new social group for the first year in which they were housed together at LPZ. In the first year after the group was fully formed, there were low rates of abnormal and agonistic behaviours, an increase in inter-individual distance between only two males, no increase in FGM and an increase in FAM in the hand-reared male UM.

As this study only provides information on formation of a single group, we encourage additional detailed behaviour and hormone monitoring during formation of other bachelor groups or changes to existing bachelor groups. By pooling data across groups and zoos, the methods and factors that facilitate successful introductions can be better understood. Given the variation across individuals in our study and our small sample size (one group, four gorillas), we encourage future documentation of the formation of all-male gorilla groups via positive and negative behavioural indicators of welfare. We also encourage research to explore other hormonal measures, such as oxytocin (Berg et al. 2019, Leeds et al. 2018), that could be used to evaluate relationships during group changes. Finally, as we lacked behaviour or hormone baseline data (i.e. data recorded before the start of the introduction), it would be especially informative if future work could also obtain and report such measures.

Acknowledgements

The authors would like to thank the Animal Care staff in the Regenstein Center for African Apes for their assistance with this project. The authors thank Marisa Shender, Kathy Wagner and the research interns in the Lester E. Fisher Center for the Study and Conservation of Apes for collecting these behavioural and proximity data. Also, the authors thank Michael Landeche, Emily Potratz and Stacy Rosenbaum for their assistance in organising and analysing faecal samples in the Endocrinology Laboratory. We would like to thank Joann Raia for the graphic design of Figure 1. Finally, the authors thank the Davee Foundation and the Leo S. Guthman Fund for supporting this research.

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