

Predictors of dominance rank and agonistic interactions in captive Livingstone's fruit bats

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Abstract

Male dominance hierarchies have been studied in many animals but rarely in bats (Chiroptera). The dominance rank of social animals may dictate access to resources and mates; therefore, it has important implications for an individual's fitness and is crucial for successful captive management. Between January and December 2018, at both Bristol Zoo Gardens (Bristol, UK) and Jersey Zoo (Jersey, British Isles), we observed 19 male Livingstone's fruit bats *Pteropus livingstonii* using focal follows for 345 h overall, noting the outcome of all agonistic interactions. We recorded instigators of interactions, along with winners and losers, and analyzed these data using the R-package "EloRating" to create Elo-rating temporal plots of dominance ranks. We used generalized linear mixed models and multiple linear regression to analyze interaction data and test hypotheses regarding predictors of dominance rank, frequency of agonistic interaction, and choice of interaction partner. Age was positively correlated with dominance rank up to around year 9, when an asymptote was attained. Highly ranked bats instigated the most agonistic interactions, and largely directed these interactions at bats with much lower rankings than themselves. Hierarchies were extremely stable throughout the data collection period at both sites. We conclude that Livingstone's fruit bats have a stable linear dominance hierarchy, with high-ranking, typically older males instigating the most interactions with lowest ranking males to secure dominance rank. This study adds to the limited discourse on *Pteropus* social behaviors, indicating that some bat species may have social systems similar in complexity to some nonhuman primates.

Key words: bats, Chiroptera, captive, Elo-rating, social, hierarchy.

Dominance hierarchies in social animals regulate intraspecific relationships, with rankings established through competitive interactions (Ratcliffe et al. 2007). By establishing clear rankings rapidly, the frequency of high-intensity interactions is reduced, which is beneficial to all individuals in a social group (Clutton-Brock et al. 1982). In primates, for example, animals with high dominance ranks gain a range of benefits including increased reproductive success (Ellis 1995), higher infant survival (Majolo et al. 2012), and priority of access to food (Whitten 1983). However, maintaining high ranks can be costly, causing immunosuppression and limiting reproductive function (Muehlenbein and Watts 2010), as well as increasing energetic expenditure and basal metabolic rate (Buchanan et al. 2001).

The establishment of dominance ranks may be influenced by several factors. For example, in several species of cercopithecine primates and the spotted hyena *Crocuta crocuta*, maternal rank correlates strongly with offspring rank and is "inherited" either through heritable genetic rank-related traits or via observational learning (Frank 1986; Holecamp and Smale 1991). Inheritance of maternal rank is additionally seen in juvenile macaques *Macaca fuscata* of both sexes; however, physical strength and age are also important

in determining their ranks (Koyama 1967). Hormones may be linked to dominance rank, as seen in talapoin monkeys *Miopithecus talapoin* (Eberhart et al. 1980) and bearded capuchin monkeys *Sapajus libidinosus* (Mendonça-Furtado et al. 2014), where plasma testosterone levels were positively correlated with dominance rank. In male fallow deer *Dama dama*, rut dominance rank is strongly and positively related to body mass (McElligott et al. 2001) and dominance ranks are the highest in males with the greatest age-related muscle mass that possess optimal age-related fighting ability (Jennings et al. 2010; Machanda and Rosati 2020).

Dominance hierarchies may be largely stable and high-ranking animals may maintain their status for much of their life, with periods of disruption within groups caused by the removal or death of dominant animals (Tibbetts et al. 2022). Dominant animals may maintain their rank through punishments and threats toward lower ranking animals, or through honest signals of dominance, such as large body size, and via individual recognition (Tibbetts et al. 2022). The majority and most intense aggressive interactions will sometimes occur between males of a similar rank as they jostle for position, because subordinate males may have the opportunity to win the interaction and outcomes may still be uncertain (Wright

et al. 2019). However, alternative hypotheses for dominance hierarchy maintenance, such as the suppression hypothesis, suggest that low-ranking animals may be targeted more frequently by dominant individuals to condition them to avoid or lose future conflicts (Forkman and Haskell 2004).

Flying foxes (*Pteropus* spp.) are large-bodied frugivorous bats, which exhibit complex and intricate social behaviors (Kunz et al. 1994; Hayes et al. 1996; Menge et al. 2013; Welch et al. 2020). However, there are comparatively fewer studies on social dominance in this genus than in other social mammals, such as primates (Whitten 1983; Ellis 1995; Muehlenbein and Watts 2010; Majolo et al. 2012), due largely to their nocturnal lifestyles. One such species, Livingstone's fruit bat *Pteropus livingstonii*, is endemic to 2 islands in the Comoros in the Western Indian Ocean (Bronwen et al. 2016). This species has a mean body mass of 576 g (males) and 171 g (females) in the wild (Smith and Leslie 2006), and a mean adult body mass of 855 g (males) and 850 g (females) (Bell et al. 2019) in captivity. Due to anthropogenic and natural threats, *P. livingstonii* is categorized as Critically Endangered (Sewall et al. 2016). Between 1990 and 1995, conservationists collected 17 bats from the wild to establish a captive breeding program at Jersey Zoo as an attempt to safeguard the species from extinction (Sewall et al. 2007). Jersey Zoo later expanded the captive breeding program to include Bristol Zoo Gardens, allowing the transfer of animals between sites to attempt to reduce inbreeding and retain genetic diversity, informed by a European Studbook (Sewall et al. 2007). As of December 2021, 87 bats exist in captivity across 3 sites; 9 at Bristol Zoo Gardens, 73 at Jersey Zoo, and a bachelor group of 3 bats at Biotropica, France (not included in this study).

The captive populations of Livingstone's fruit bats provide a rare opportunity to investigate dominance hierarchies in this species, which are difficult to observe in the wild. For example, although little is known in the wild regarding social structure, Courts' (1996) captive study defined the mating system of *P. livingstonii* as harem-defense polygyny, with males competing in agonistic interactions for dominance rank and access to both territory and resources. Through the improvement of our understanding of these Critically Endangered animals, we can provide the best captive care and potentially improve conservation efforts. The IUCN Conservation Action Plan for Livingstone's flying fox (Sewall et al. 2007) encourages the undertaking of behavioral research on captive *P. livingstonii* for these reasons. By understanding how male dominance rank is established and maintained, we can further unravel the implications of dominance on social and physiological traits, such as muscle wastage in less-mobile dominant animals (Wormell et al. 2018) and cardiomyopathy (Segura-Cortijos et al. 2022), enabling effective mitigation strategies to be developed.

In this study, we examine the predictors of dominance rank and agonistic interactions in male Livingstone's fruit bats *P. livingstonii* by observing agonistic interactions between males, then using outcomes to quantify individual dominance rank. Our 3 main hypotheses were as follows: First, that Elo-rating, our proxy for dominance rank, would be positively correlated with both the age of male bats and their body mass. Second, we predicted that the frequency of agonistic interactions instigated would increase as dominance rank increases. Finally, we predicted that agonistic interactions would occur most commonly between bats of similar ranks, with dyads of large rank disparity interacting less.

Materials and Methods

Study sites and subjects

We collected data from 2 sites housing captive breeding populations of Livingstone's fruit bat, Bristol Zoo Gardens (5 males, 5 females) (Bristol, UK) and Jersey Zoo (27 males, 21 females) (Jersey, British Isles). As weaning occurs around 8 months of age and male territorial aggression rises after 6 months of age, we only selected males for observation if they were fully mature. In this study, we selected males of at least 2 years of age as a conservative estimate of sexual maturity (Courts 1998; Trewhella et al. 1995). We provide full details of males observed in this study in [Supplementary Material S1](#).

Bristol Zoo Gardens' bat enclosure has an area of approximately 250 m³ (6.3 m × 9.0 m × 4.4 m). It has a bark-chip substrate, rope suspended throughout, drip water bottles, food provided in troughs or on kebab skewers, brick walls, and seasonal access throughout the summer if ambient temperatures rise above 10 °C. Jersey Zoo's bat enclosure is approximately 1800 m³ (16 m × 38 m × 3 m). It has AstroTurf substrate lining the perimeter, soil and planting throughout the middle of the enclosure, netting lining the polytunnel walls, rope suspended around the perimeter only, water provided in suspended cups, and food provided in both suspended cups and troughs (photographs in [Supplementary Material S2 and S3](#)).

Data collection

We collected data between November 2017 and December 2018. Due to constraints of travel and time at each site, data collection schedules at our 2 sites varied. At Bristol Zoo Gardens, we collected data up to 3 times a week, with longer and more intense periods of data collection every day for up to 2 weeks at Jersey Zoo every other month.

All data collection occurred between 08:00 and 17:00. As social behavior occurs throughout diurnal periods in other *Pteropus* species such as Indian flying foxes *Pteropus giganteus* (Roy et al. 2020) and gray-headed flying foxes *Pteropus poliocephalus* (Connell et al. 2006), we chose to only assess diurnal social interactions. In total, we recorded 366.5 h of behavioral observations at Jersey Zoo and 112.5 h of behavioral observations at Bristol Zoo Gardens, due to the larger number of focal males that we observed at Jersey Zoo ($N = 14$) compared with Bristol Zoo Gardens ($N = 5$).

We recorded interactions between male bats using continuous focal sampling in person and by naked eye, as agonistic interactions are event behaviors which occur suddenly and unexpectedly for short durations (Altmann 1974) and so can be missed through other data collection methods. By naked eye, it was possible to individually identify males at distance due to conspicuous ear shapes, pelage marking, and scar damage; however, these markings were not conspicuous enough for identification in video recordings. Additionally, as the captive environments are large and complex, and as this species can move quickly over large distances by flight, direct observation was the most suitable method of data collection. The captive populations of *P. livingstonii* have become strongly habituated to human presence over the 30 years that the captive breeding program has existed, allowing direct observation without disruption. For additional confirmation of identity, a noninvasive Trovan ARE-H5 microchip scanner, with a range of up to 15 cm (AEG ID 2022),

was available when needed. Only males were observed, as they are the only sex involved in territory-related agonistic dyadic encounters in this species (Courts 1996). Therefore, the welfare concerns arising from territorial behaviors are found only in males, such as cardiomyopathy (Segura-Cortijos et al. 2022) and muscle wastage (Wormell et al. 2018), providing justification for focusing observations on males. We assigned a number to each bat at the start of this study and used a random number generator (Haahr 2021) each day to decide the order of focal sampling, to avoid preferential bias, and each male was observed focally for 30 min. We decided the winners of agonistic interactions by displacement, with winners remaining stationary or advancing and losers retreating away from contending male. When receiving males did not retreat from contending males and neither male was displaced, we coded the interaction as a draw. If retaliatory behavior was observed within 30 s of the initial interaction, this information was used to update the outcome of the initial interaction. If retaliatory behavior occurred after 30 s of the initial interaction, the new interaction was coded separately.

We developed an ethogram of social behaviors, from Courts' (1996) original ethogram on *P. livingstonii* and Newton-Fisher's work on chimpanzees *Pan troglodytes* (2017) and recorded the agonistic behaviors described in Table 1. During focal sampling, we entered these behaviors into a time-recording and programmable Android "Tap Log" on a Samsung Galaxy Tab E T560, with customized buttons that we added for each behavior to improve the speed and accuracy of data collection (Tap Log 2015).

Table 1 Agonistic interactions recorded during this study, with intensity of interaction represented by *k*-value

Categorization of aggression	<i>k</i>
Threat/static/vocalize	50
Threat/static/gesture (wing clap/cuff/open mouth)	50
Threat/static/gesture (wing clap/cuff/open mouth) and vocalize	50
Threat/approach/vocalize	100
Threat/approach/gesture (wing clap/cuff/open mouth)	100
Threat/approach/gesture (wing clap/cuff/open mouth) and vocalize	100
Chase	150
Chase and vocalize	150
Attack/strike in passing (wing cuff)	200
Attack/strike in passing (bite)	200
Attack/< 5-s duration (wing cuff)	250
Attack/< 5-s duration (bite)	250
Attack/> 5-s (grapple)	300
Attack/serious injury	300
Attack/> 30-s duration (not observed)	350
Attack/> 5-min duration and/or fatal (not observed)	400

The higher the *k*-value, the more intense the level of aggression—behaviors and attributed *K*-value are modeled on Newton-Fisher (2017).

Elo-rating

Many methods of quantifying dominance rank have been developed over the decades, each with its own strengths and suitability (Bayly et al. 2006). Although originally developed by Arpad Elo in the 1950s for use in chess competitions (Glickman and Jones 1999), Elo-ratings are now widely used in animal dominance studies (Franz et al. 2015; Foerster et al. 2016; Wooddell et al. 2017). Elo-rating assigns points after competitions between two individuals based on both interacting competitor's prior rankings and probability of winning (Glickman and Jones 1999), with higher Elo-ratings equating to more dominant individuals. This method permits temporal plotting of ranks, it is independent of demographic changes, and it has no requirement of a minimum number of individuals to establish ranks (Neumann et al. 2011). This last requirement is particularly useful in studies on captive and Critically Endangered species, where sample sizes are often restricted. Courts (1997) previously defined the dominance hierarchy present in *P. livingstonii* as plastic, which would validate our choice of Elo-rating as an index of dominance (Neumann et al. 2011).

We conducted all statistical analyses in R (R Core Team 2021). We used the R-package "EloRating" (Neumann and Kulik 2020) to create Elo-ratings of male adult bats, derived from winners and losers of agonistic interactions using the function "elo.seq" and the following formulas (taken directly from Neumann et al. 2011):

Higher rated individual wins:

$$\text{Winner Rating}_{\text{new}} = \text{Winner Rating}_{\text{old}} + (1 - p) \times k$$

$$\text{Loser Rating}_{\text{new}} = \text{Loser Rating}_{\text{old}} - (1 - p) \times k$$

Lower rated individual wins (against the expectation):

$$\text{Winner Rating}_{\text{new}} = \text{Winner Rating}_{\text{old}} + p \times k$$

$$\text{Loser Rating}_{\text{new}} = \text{Loser Rating}_{\text{old}} - p \times k$$

where *p* is the likelihood of an individual winning an interaction and *k* is the number of points available to gain or lose. We chose a variable *k*-value for this study that depended on the intensity of observed aggression, modeled from Newton-Fisher's work on chimpanzee hierarchies (2017) (Table 1).

As Elo-ratings benefit from a "burn-in" period to establish an accurate initial rank (Newton-Fisher 2017), we included data from September 2017 to December 2018; however, rank was determined with data taken only from January 2018 onward, once ranks of individuals had stabilized.

Elo-ratings were extracted from R-package "EloRating" (Neumann and Kulik 2020) and plotted manually using R-package "ggplot2" (Wickham 2016), allowing for direct plotting of results using the function "geom_line" and smoothed plots of results using the function "geom_smooth." Reliability of Elo-rating was checked by comparison with David's scores, an alternative method for quantifying dominance rank (David 1987), which were calculated using function "DS" within the "EloRating" package (Neumann and Kulik 2020). A 2-sample *t*-test was used to compare averaged Elo-rating scores and David's scores, both of which were transformed to a standardized *z*-score between 0 and 1 (0—lowest rank, 1—highest rank), using R functions "t.test" and "scale," respectively.

Generalized linear mixed models and multiple linear regression

Age, body mass, and dominance rank

We evaluated our first prediction of age and body mass correlating positively with dominance rank using a generalized linear mixed model (GLMM) with the “glmmTMB” function of the glmmTMB R-package (Brooks et al. 2017), as our response variable followed a Gaussian distribution. We extracted age and Elo-rating data on days that body mass was recorded for individual animals, and body mass data from the Species 360 Zoo Information Management System (2021), and Elo-rating scores were extracted using the R-package EloRating, function “extract_elo” (Neumann and Kulik 2020). Elo-rating was set as the response variable, age and body mass as predictor variables, individual ID was set as a random effect, and location was set as a control effect. Each weighing occurrence created a data point ($N = 69$). Eighteen out of 19 males were weighed at least once throughout 2018 and so were included in this analysis. We standardized both age and body mass to a mean of 0 and standard deviation of 1 by transforming them to z -scores using R-function “scale.”

Number of agonistic interactions instigated per male

Our second prediction investigated the relationship between the frequency of agonistic interactions instigated per male and their average rank, age, and average body mass. We used a multiple linear regression using function “lm” of the core “stats” package of R (R Core Team 2021), to evaluate if higher average dominance rank, age, or body mass predicts higher number of agonistic interactions instigated. The model had 1 data point per male ($N = 19$) and the response variable was the number of male–male agonistic interactions that each male initiated, summed to 1 data point. Our test predictors were each male’s average dominance rank and age and body mass at the time of dominance rank extraction.

Frequency of interactions between dyads

Our third prediction was that males with similar average dominance ranks would interact more frequently and we evaluated that using a GLMM with Poisson error structure and log link function. We created this GLMM using the function “glmer” of the “lme4” R-package (Bates et al. 2015). This GLMM had 1 data point per aggressor within a dyad ($N = 106$), where we summed all interactions between the dyads. The response was the number of agonistic interactions occurring between each pair, with the aggressor and recipient indicated. We included the number of focal samples as an offset term (log-transformed) to control for different-sized data sets (39 focal samples at Bristol Zoo Gardens per male, 36 focal samples at Jersey Zoo per male). Our test predictors were dyad differences in age and average rank. To assess whether similarly matched dyads in age and dominance rank experienced more interactions, we also included the square of these terms. The test predictors of differences in age and average rank were transformed to z -scores to align them on similar scales, with a mean of 0 and a standard deviation of 1 using R-function “scale.” Our control variable was location, and our random effects were the aggressor ID, dyad ID, and recipient ID.

Hierarchy stability

We calculated hierarchy stability using the “stab.elo” function within the “Elo-rating” R-package, grouping dates into months to assess potential seasonal variability in hierarchy stability. Stability index values range from 1 to 0, where a value of 1 indicates that a hierarchy is stable with no rank changes in the allotted time, and a value of 0 indicates that the hierarchy is completely unstable, with high numbers of rank change in the allotted time.

Results

Overall, we recorded 356 agonistic interactions at Bristol Zoo Gardens and 299 at Jersey Zoo, during 366.5 and 112.5 focal hours, respectively. This equated to 3.17 agonistic interactions per hour at Bristol Zoo Gardens and 0.81 agonistic interactions per hour at Jersey Zoo. A summary of all interactions between January 2018 and December 2018, categorized by individual and outcome, is presented in [Supplementary Material S4](#). There was no significant difference between an animal’s average rank across Elo-rating and David’s scores ($t = 0.19$, $df = 36$, $P = 0.850$).

[Figure 1](#) shows the Elo-ratings of all male bats present over 2 years old within the Bristol Zoo Gardens and Jersey Zoo main colonies throughout 2018, created from all agonistic interaction outcomes. As “Ishaka” and “Enzo” died, and as “Hombo” was transferred to a hospital colony at Jersey Zoo, away from the main group early into 2018, these 3 animals featured for less than 10% of the data collection period and so we excluded them from further analysis.

Age was significantly positively correlated with Elo-rating in the 2 locations (glmmTMB, estimate \pm SE: 85.81 ± 39.39 , $Z = 2.178$, $P = 0.029$), with older bats holding higher rankings up to around 9 years of age when rankings become stable with further increasing age ([Figure 2](#)). Body mass was not significantly correlated with Elo-rating (glmmTMB, estimate \pm SE: 26.12 ± 38.55 , $Z = 0.677$, $P = 0.498$). We included both age and body mass as independent variables in subsequent analysis as they showed a low variance inflation factor (VIF) of a maximum of 2.94, removing potential concerns regarding collinearity.

The average rank of males correlated positively with the number of agonistic interactions they instigated (lm, estimate \pm SE: 83.285 ± 32.524 , t -value = 2.561, $P = 0.021$), indicating that higher ranking males instigated significantly more agonistic interactions than lower ranking males ([Figure 3](#)). Average age and body mass of males had no relationship with the number of interactions instigated. VIF values showed a maximum of 1.78, indicating that collinearity was not a concern.

Unexpectedly, the relationship between average rank difference and number of interactions is curvilinear and shows a “U-shaped” curve, where the closer males are in rank, the less they interact (GLMM, estimate \pm SE: 0.203 ± 0.084 , $Z = 2.401$, $P = 0.016$) ([Figure 4](#)). VIF levels were maximum 1.14 between differences in age and average dominance rank, showing acceptably low levels of collinearity. At Bristol Zoo Gardens, the most common agonistic dyadic interaction was between the highest ranking male “Stefan” and the lowest ranking male “Finn,” which accounted for over 33% of all agonistic interactions at this site ($N = 102$). At Jersey Zoo, the most common agonistic dyadic interaction was between the highest ranking male “Bathory” and the third lowest ranking

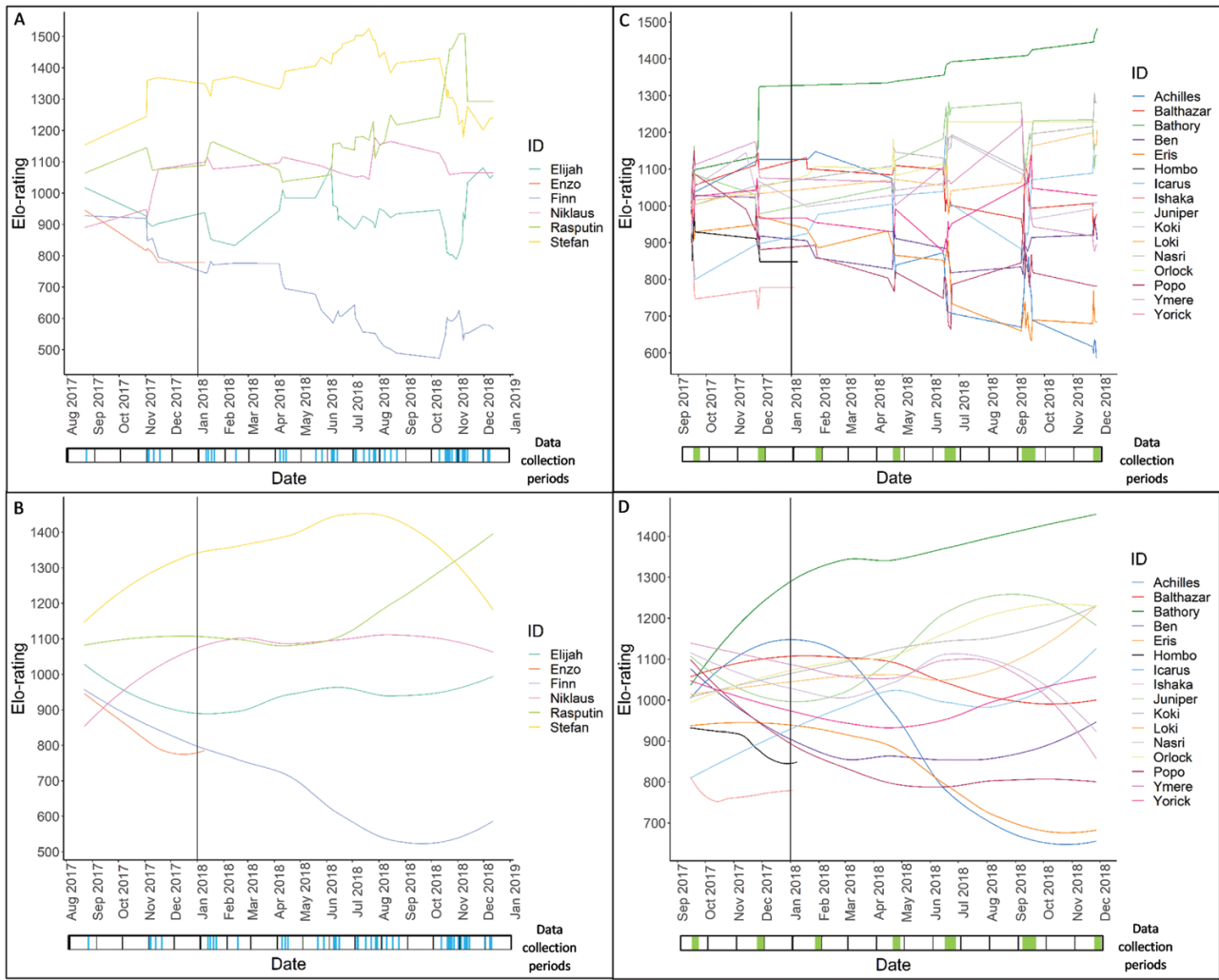


Figure 1 Line graphs of individual bat Elo-rating over time. Black vertical line signifies the end of “burn-in” data and the start of data collection used in later analysis. Data collection periods indicated by bars under line graphs, where bars show period when data were collected. (A) Nontransformed line graph of Elo-ratings at Bristol Zoo Gardens, plotted using geom_line; (B) smoothed line graph of Elo-ratings at Bristol Zoo Gardens, plotted using geom_smooth; (C) nontransformed line graph of Elo-ratings at Jersey Zoo, plotted using geom_line; (D) smoothed line graph of Elo-ratings at Jersey Zoo, plotted using geom_smooth.

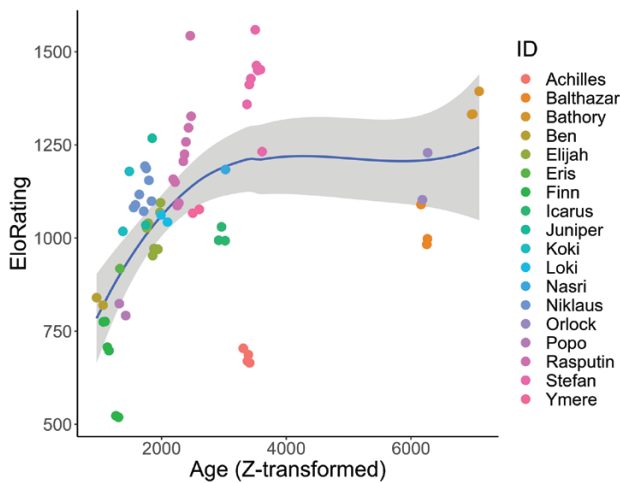


Figure 2 Relationship between age and Elo-rating. Each point refers to an age snapshot of each male and the related Elo-rating of the individual at that time ($N = 69$).

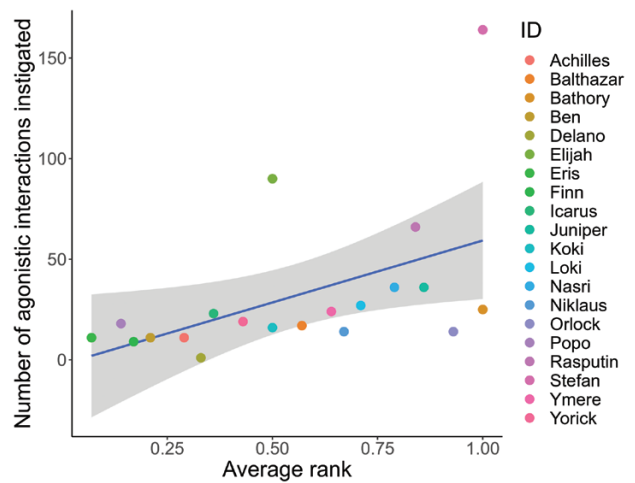


Figure 3 Relationship between average rank and the number of agonistic interactions each individual instigates. Each point refers to 1 male, with all interactions summed ($N = 19$).

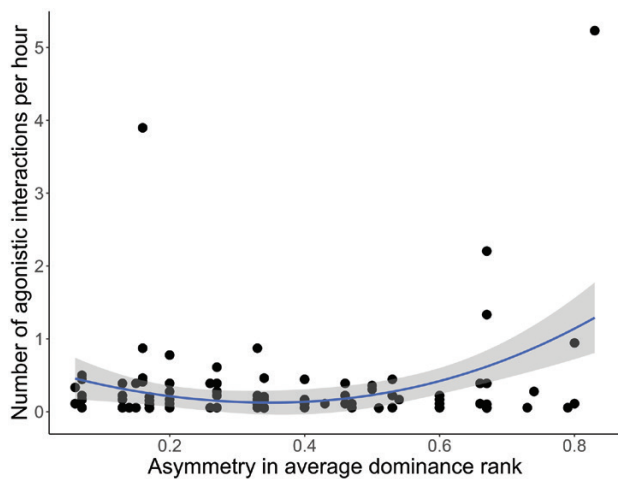


Figure 4 Relationship between asymmetry in dominance ranks of males and the number of agonistic interactions that occur between dyads ($N = 106$).

male “Popo,” which accounted for 7.5% of all agonistic interactions at this site ($N = 19$).

Stability in dominance hierarchies at both Bristol Zoo Gardens and Jersey Zoo groups was extremely high overall, with low levels of rank changes throughout the year and an average value of stability of 0.994 at Jersey Zoo and 0.997 at Bristol Zoo Gardens, where 1 indicates total hierarchy stability and 0 indicates complete hierarchy instability.

Discussion

Our results revealed that older male bats held the highest dominance ranks and instigated the most agonistic interactions, the majority of which they directed at bats with considerably lower rankings than themselves. Although we predicted that body mass would be correlated with dominance rank, our results did not support this hypothesis. This was unexpected as there are many studies indicating that large body size confers advantages such as high dominance rank in several different species including mountain gorilla *Gorilla beringei beringei* (Wright et al. 2019); Asian elephants *Elephas maximus* (Chelliah and Sukumar 2013); sockeye salmon *Oncorhynchus nerka* (Quinn and Foote 1994); great Himalayan leaf-nosed bats *Hipposideros armiger* (Sun et al. 2021); and fallow deer *Dama dama* (McElligott et al. 2001). Body mass may not be a useful proxy for body size in *P. livingstonii* as it may show considerable seasonal variation, such as in gray-headed flying fox *P. poliocephalus* (Welbergen 2011), or it may just not be related at all, as with female vampire bats (*Desmodus rotundus*) (Crisp et al. 2021). Therefore, perhaps forearm or body length would be more effective measures of body size and relate more closely to dominance rank, as seen in Asian particolored bats *Vespertilio sinensis* (Liu et al. 2020). As these captive colonies of *P. livingstonii* are managed as noninvasively as possible; however, this additional data collection was not possible. Age was correlated with dominance rank, indicating that the older an animal is, the higher rank it tends to acquire. This is in line with studies on other mammalian species that exhibit dominance hierarchies such as bighorn sheep *Ovis canadensis* (Favre et al. 2008); African elephants *Loxodonta africana* (Archie et

al. 2006); and American bison cows *Bison bison* (Rutberg 1986).

This relationship between age and rank is not a perfect fit, however, which suggests that there are other factors influencing dominance rank. The relationship between age and dominance rank appears to level off as animals reach around 9 years of age. We would expect that if males senesced, their dominance rank would plateau and later decline, as seen in Japanese macaques (Takahashi 2002). However, this pattern of decline is not seen in the older Livingstone’s fruit bats probably because, as older animals accrue more health concerns, they are moved into a separate colony for more intense medical treatment at Jersey Zoo. For example, throughout this study, 3 of the older males (“Hombo”—D.O.B 05/05/03, “Otto”—D.O.B 12/11/99, “Orpheus”—D.O.B 25/01/98) were relocated out of the main colony for data collection for various health-related reasons. Without this health and age-related intervention in captivity and in the wild, we would expect to see a similar eventual decline in dominance rank in male *P. livingstonii*, as males become less capable at competing in agonistic interactions or at holding resources (Takahashi 2002).

As predicted, high-ranking males instigated significantly more agonistic interactions than low-ranking males. As dominant animals maintain their ranks using threats and punishments toward lower ranking animals (Tibbetts et al. 2022), it is likely that the frequency of aggressive interactions from high-ranking animals is an attempt to subdue conspecifics and prevent rank loss. Also known as the suppression hypothesis, winning agonistic interactions provide a positive feedback loop and increase the willingness of successful animals to engage in escalating contests (Hsu et al. 2006), whilst simultaneously conditioning low-ranking animals to avoid interactions (Otter 2007). The suppression hypothesis occurs across taxa such as domestic chickens *Gallus gallus domesticus* (Forkman and Haskell 2004), copperhead snakes *Agkistrodon contortrix* (Schuett 1997), and mice (Ginsberg and Allee 1942). Additionally, as agonistic interactions are inherently costly, males with high resource-holding potential and motivation are most likely to engage in more frequent and aggressive interactions, to attain higher dominance ranks and access to resources (Tibbetts et al. 2022).

We expected that males with similarly matched dominance ranks would interact most, as predicted by the continuous assessment model of dominance (Forkman and Haskell 2004), but our results did not support this prediction. Interactions between males with asymmetries in dominance ranks were more frequent than interactions between males of similar dominance rank. Escalations in agonistic interactions can be costly to the animals involved, causing serious injury or even death (Clutton-Brock et al. 1979), as seen in common loons *Gavia immer* (Piper et al. 2008), white-handed gibbon *Hylobates lar* (Palombit 1993), and chimpanzees (*Pan troglodytes*) (Mitani et al. 2010). To avoid such issues, high-ranking male Livingstone’s fruit bats are instigating aggressive interactions with low-ranking recipient males that they will easily outcompete, preventing escalation to more violent encounters. Consequently, we saw no examples of the most serious possible aggressive interactions (long duration or fatal physical attacks) and no physical injuries throughout our data collection. This increased the frequency of agonism toward considerably lower ranking males could also be a form of punishment from high-ranking males, whose fitness may

be threatened by their presence (Clutton-Brock and Parker 1995). This result again supports the suppression hypothesis of dominance hierarchy maintenance, where dominant individuals continuously attack low-ranking animals to condition them to lose or avoid conflict in future (Forkman and Haskell 2004). Low-ranking males are conditioned to avoid conflict with high-ranking animals through punishment, while the infrequent aggressive interactions from low-ranking bats toward high-ranking animals may be an attempt to check a conspecific's rank (Clutton-Brock and Parker 1995). An alternative suggestion could be that the disproportionately high number of aggressive interactions from the most dominant male "Stefan" toward the most subordinate and youngest male "Finn," which accounted for 33% of all agonistic interactions at Bristol Zoo Gardens, was due to limited territory and avoidance space. This is seen in rhesus macaques *Macaca mulatta*, which show increases in mild aggressive behaviors when forced into crowded conditions, with agonistic behavior most commonly being directed toward infants (Judge and de Waal 1993).

Identification of a conspecific's dominance rank and decisions to initiate agonistic interactions may be occurring at distance through encoded information within social vocalizations, as seen in Asian particolored bats *Vespertillo sinensis* (Luo et al. 2017), or by conspecifics eavesdropping on agonistic interactions, as seen in Seba's fruit bat *Cariollia perspicillata* (Fernandez et al. 2014). Decisions to become involved in agonistic interactions may also be led by an animal's resource-holding potential and ability to self-assess this value, as observed in Great Himalayan leaf-nosed bats *Hipposideros armiger* (Sun et al. 2019). Additionally, kinship may influence the initiation of agonistic interactions between conspecifics, as in brown capuchin monkeys *Cebus Sapajus apella*, where animals are less likely to be aggressive towards kin (Gazes et al. 2022). *Pteropus livingstonii* exhibits several different social vocalizations relating to agonistic interactions (Courts 1996); however, further research is needed to investigate whether information regarding dominance rank is encoded within this species' social vocalizations. Further research should also be conducted to assess whether *P. livingstonii* are able to self-assess their resource-holding potential and are able to recognize kin, evaluating whether this contributes to the frequency and intensity of agonistic interactions between males.

The greater rate of agonistic interactions per hour observed at Bristol Zoo Gardens compared to Jersey Zoo is likely related to the smaller available space and higher density of male bats at Bristol Zoo Gardens, a trend predicted by the social subordination hypothesis (Gaines and McClenaghan 1980). However, more research is required on this topic as there are other variables to consider, such as differences in feeding regime and husbandry between sites. Regardless of the rate of interaction, both Bristol Zoo Gardens and Jersey Zoo colonies of bats showed extremely well-established linear dominance hierarchies, with almost complete stability across both sites and little transfer of ranks between males. In social primates with dominance hierarchies, rank changes can occur infrequently, remaining unchanged for 15–25 years in gorillas *G. beringei beringei*, with most rank transfers occurring with changes in group composition (Robbins et al. 2005). The year 2018 was a particularly stable one for colonies at both Bristol Zoo Gardens and Jersey Zoo, with no adult males transferring in or out of either location or dying after January, which may have contributed to the stability of the dominance

hierarchies. Additionally, all males observed during this study were adults and so their ranks were likely already established before the study began, with much of the instability and rank switching occurring during juvenile development, as observed in other social mammals (Holecamp and Smale 1991). Due to the potentially long durations of established dominance ranks, for example, in ring-tailed lemurs *Lemur catta* where alpha male rank changes on average every 2.2 years (Koyama et al. 2005), it is possible that 1 year of data collection was not enough to capture significant alterations to dominance rank structure.

Our findings suggest a straightforward model of dominance hierarchy in male captive Livingstone's fruit bats, with age playing a crucial role in determining an individual's dominance rank but with the frequency of aggressive interactions driven both by personal rank, and by the difference from the recipient male's rank. It appears that the methods of maintaining dominance rank within this species are highly effective, as hierarchy stability was extremely high throughout the data collection period. Further work is suggested to establish if body size is a reliable indicator of dominance rank, and if available territory size is affecting the number of aggressive interactions between males. Understanding the structure, mechanisms of establishment and maintenance of male dominance hierarchies in *P. livingstonii* provide several benefits for captive animal welfare and conservation. By understanding that dominant males instigate the most agonistic interactions, and that these are directed largely toward the lowest ranking animals, we would suggest that the lowest ranking animals are monitored closely within captive groups. In receiving more displacements and directed aggression, low-ranking males have a higher chance of injury and malnourishment from competition over food resources than higher ranked males. To aid *ex-situ* conservation further, newly established groups of *P. livingstonii* should include males of similar ages, to reduce excess male agonistic interactions. As dominant, territory-holding males are also more likely to be sedentary, rarely flying, losing muscle condition (Wormell et al. 2018) and at the highest risk of cardiomyopathy (Segura-Cortijos et al. 2022), we would also suggest that diets for high-ranking males are adjusted to accommodate reduced energy expenditure. This research adds to the discourse on *Pteropus* social systems, indicating that bats in this genus have some social structures similar in complexity to nonhuman primates.

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Conflict of Interest

All coauthors have declared that they have no conflicts of interest.

Ethics Statement

All research methodology reported here adhere to ethical requirements of the University of Bristol (UIN reference UB/16/064), Bristol Zoological Society and Durrell Wildlife Conservation Trust.

Author Contributions

Behavioral data collection, data analysis, and manuscript preparation completed by SR. Supervisory input and manuscript editing provided by GM and GJ. Assistance with project design, facilitation of data collection, and manuscript review provided by EP and DW.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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