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FEATURED STUDENT RESEARCH PAPER

Interrelationship among spatial cohesion, aggression rate, counter-aggression and female dominance in three lemur species

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Abstract

How social and ecological factors are associated with variation in dominance style across species of animals has been studied frequently, but the underlying processes are often not addressed. Theoretical research indicates that stronger spatial cohesion among individuals in a group causes a higher frequency of fighting and, thus, through the self-reinforcing effects of winning and losing fights, a stronger differentiation of the dominance hierarchy and dominance of females over more males. Our aim in the present paper is to study whether the same interrelationship among processes may underlie differences in dominance style among three species of lemur that differ in their degree of despotism: *Lemur catta*, *Propithecus verreauxi* and *Eulemur rufifrons*. We investigated their agonistic interactions and spatial cohesion based on 2752 h of observational data of 20 wild groups of these three species. We determined dominance style using the proportion of counter-aggression, with a lower proportion indicating a more despotic dominance style. We found that stronger spatial cohesion among individuals is associated with a higher rate of aggression, stronger despotism and dominance of females over more males. The results of our study emphasise the general importance of spatial cohesion in determining dominance style.

Significance statement

Theoretical studies have shown that the spatial configuration of individuals in a group influences the dominance style. In an agent-based model, DomWorld, individuals are guided by simple rules of grouping and fighting and emergent patterns of behaviour switch between resembling those of despotic or egalitarian primates depending on the degree of cohesion in groups. Yet this link has seldom been studied empirically. We, therefore, examine the relevance of spatial cohesion on patterns of behaviour of individuals in groups of three species of lemur. We confirm the predictions from the model and show that stronger spatial cohesion results in more frequent aggression, a more despotic dominance style and stronger female dominance over males. In light of this, we urge future research of animal dominance to include measures of cohesion.

Keywords Dominance style · Female dominance · Lemurs · Social structure · Counter-aggression · Winner-loser effect

Introduction

Group living in animals is associated with advantages such as enhanced detection of predators, defence of resources and transmission of information (Krause and Ruxton 2002). However, as the number of individuals in a group increases, so does competition over access to limited resources. Dominance relationships formed through repeated agonistic interactions among individuals represent a widespread adaptation to prevent costly conflicts because individuals are unlikely to attack if they think they will lose (Jackson 1991; Hemelrijk 1999a). The dominance style in a particular hierarchy can be classified on a continuum from despotic to egalitarian (Vehrencamp 1983),

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reflecting the degree of power asymmetry between individuals (Flack and de Waal 2004). In despotic societies, some individuals are much more socially powerful than others and can exclude others from resources, whereas in more egalitarian societies, group members have similar agonistic power and seldom exclude others from resources (Vehrencamp 1983). The drivers of this interspecific variation remain poorly known, however.

The identity of the winner of a fight is thought to result from prior attributes, self-organisation or both. The prior attribute hypothesis relates dominance to biological traits such as body size, where larger individuals are more likely to win than smaller ones (Chase and Seitz 2011). Yet, sometimes, smaller females are dominant over larger males in sexually dimorphic species, leading to variable patterns of intersexual dominance (Hemelrijk et al. 2008, 2020; Izar et al. 2021; Kappeler et al. 2022). The self-organisation hypothesis attributes this outcome to the winner-loser effect, which implies that following a conflict, winners are more likely to win their subsequent fight and vice versa for losers (Hsu et al. 2006; Chase and Seitz 2011). This effect has been demonstrated throughout the animal kingdom, including insects, crustaceans, fishes, amphibians, reptiles and primates (Hsu et al. 2006; Franz et al. 2015), and has also been shown to influence intersexual dominance (Hemelrijk et al. 2008, 2020; Izar et al. 2021).

Variation in dominance styles among groups and species has also been related to variation in the distribution and abundance of food and the resulting type of competition individuals experience for it (e.g. scramble vs contest). The underlying socioecological model was originally developed for non-human primates (Wrangham 1980), and subsequently extended to include risks of predation and infanticide (van Schaik 1989; Sterck et al. 1997). More recently, the extended model has also been tested in non-primates, such as coatis and ungulates (de la O et al. 2019; Szemán et al. 2021). Yet critiques of this model have suggested that a one-size-fits-all approach may not be suitable (Thierry 2008, 2021).

Indeed, in macaques, ecological differences cannot so far explain the interspecific variation in dominance style (Thierry 2021). Rather, selection may have only acted on one or two ‘pacemaker’ traits (e.g. intensity of aggression and degree of nepotism), which cause a shift in a suite of behavioural traits concerning agonism and affiliation that co-vary with one another (Thierry et al. 2004). For instance, more despotic (intolerant) species of macaque exhibit higher intensity of aggression, stronger nepotism, more uni-directionality of aggression and less reconciliation than more egalitarian species (Thierry 2000; but see Balasubramaniam et al. 2012, 2018). Moreover, since those macaque species that are more similar in their dominance style are also sometimes more strongly related, phylogenetic distances may influence interspecific variation in aspects of dominance style as well (e.g. Balasubramaniam et al. 2018).

An agent-based model, DomWorld (Hemelrijk et al. 2017), demonstrated a causal relationship among agonistic and affiliative traits. In this model, each individual is guided to group with others and fight nearby individuals. After losing a fight, the loser is more likely to lose again, and after winning, the victorious individual is more likely to win again, representing the winner-loser effect (Hsu et al. 2006). Even though all individuals of one sex start with the same fighting capacity, represented by their Dom-Value, over time a hierarchy differentiates due to these self-reinforcing effects (Chase et al. 1994). Emergent patterns of behaviour switch from resembling despotic species to egalitarian ones by changing a single trait: the intensity of aggression. When intensity of aggression is high rather than low, outcomes of fights have a strong impact on the hierarchy, causing it to differentiate strongly, which leads to aggression being more uni-directional, reconciliation and consolation occurring less often and grooming being mainly directed up the hierarchy (Puga-Gonzalez et al. 2009, 2014).

In the primate radiation of lemurs, group living evolved twice independently (Kappeler and Pozzi 2019) and species range from clearly despotic to much more egalitarian. It remains unknown what underlies differences in dominance styles and whether patterns of behaviour co-vary in species of lemur. Unlike macaques, lemurs supposedly do not differ in their intensity of aggression (Kappeler 1993). Moreover, phylogenetic closeness seemingly cannot explain differences in dominance style among species either, as more distantly related species are more similar in dominance style than more closely related species (e.g. *Eulemur macaco* and *Lemur catta* are more despotic than *Eulemur fulvus* (Kappeler 1993; Roeder et al. 2002)).

An alternative mechanism that may underlie differences in dominance style in lemurs is again suggested by DomWorld, which relates dominance style also to the degree of group cohesion (Hemelrijk et al. 2017). Specifically, the model shows that when individuals in a group are closer together, they have higher rates of aggression because they are more often close to potential interaction partners. This higher rate of aggression causes the hierarchy to differentiate more through the winner-loser effect, causing a more despotic hierarchy and the associated patterns of behaviour (Hemelrijk 1999b, 2003). However, empirical studies on the association between the frequency of aggression and dominance style are missing.

In DomWorld, a further side effect of stronger group cohesion is an increase of dominance of females over males. This occurs because individuals interact more often, which results in a more differentiated dominance hierarchy of males and females, and as a consequence, some females become dominant over some males. Yet, this effect has only been demonstrated when males are larger than females and, thus, are equipped with a higher initial dominance and intensity of aggression. In the present study, we examine how cohesion, and thus frequency of aggression, influences intersexual dominance in lemurs, where males and females do not differ in body size, and female dominance over males is common but differs in its degree among species (Eichmueller et al. 2013; Rina Evasoa et al. 2019; Kappeler et al. 2022).

In this study, we want to unravel whether, as predicted by DomWorld, the degree of spatial cohesion underlies variation in dominance style and the degree of intersexual dominance in three species of lemur. These are, ranging from most to least despotic, as follows: ring-tailed lemurs (*Lemur catta*), Verreaux's sifakas (*Propithecus verreauxi*) and red-fronted lemurs (*Eulemur rufifrons*) (Kappeler 1999; Norscia and Palagi 2015). We studied several groups of each species to determine in particular whether individuals in groups with stronger cohesion fight more often (prediction 1), whether a more despotic dominance style is associated with a higher rate of aggression initiated (prediction 2) and whether stronger cohesion underlies a higher degree of female dominance over males in lemurs (prediction 3).

Methods

Study species, site and groups

Ring-tailed lemurs (RTLs), Verreaux's sifakas (VS) and red-fronted lemurs (RFLs) live in multi-male multi-female groups and are endemic to Madagascar. Adult ring-tailed lemurs weigh around 2 kg and form groups of individuals ranging from 9 to 16 individuals. We studied them at Berenty Reserve, where they feed mostly on *Tamarindus indica* (Simmen et al. 2006). We studied Verreaux's sifakas, who have a body size of 3.6 kg and an average group size of six individuals in Kirindy Forest (Kappeler and Fichtel 2012). They are highly folivorous and feed mostly on mature leaves and flowers (Koch et al. 2017). Red-fronted lemurs weigh 2.2 kg and occur in dry-deciduous forests in western Madagascar but also in rain forests in south-eastern Madagascar. Their group sizes vary between 4 and 18 individuals, with an average of nine individuals. The diet of red-fronted lemurs is diverse, including different plant items and insects, with leaves making 52% of their diet in the dry season in Kirindy Forest (de Winter et al. 2013).

Five groups of ring-tailed lemur (C1, C12, C2A, T2, YF) were studied in Berenty Reserve in southern Madagascar (Jolly 2012). Individuals were identified by natural markings on their face and fur. Nine groups of Verreaux's sifakas (C, E, F, F1, G, G1, H, J, L) and six groups of red-fronted lemurs (A, A1, B, B1, F, J) were studied in Kirindy Forest in western Madagascar, (Kappeler and Fichtel 2012). Groups of Verreaux's sifakas and red-fronted lemurs were tracked by radio collars that were worn by a single individual in each group. Individual group members were identified by collars of different colour combinations (Kappeler and Fichtel 2012).

Data collection and analyses

Data collected before 2018 were collected by conducting continuous focal observations of adult individuals. In 2018, we performed all-occurrence observations of agonism of adults in groups, as well as scan-sampling every 10 min to record the location of individuals (Table 1). Here, a focal individual was selected to follow and the location of all individuals relative to it was recorded to quantify group cohesion. An effort was made to ensure each individual in a group was observed for a similar amount of time by preselecting the observation of individuals via a rotation system. Three hours of focal observation of individuals from a group were recorded in the morning and in the afternoon. Focal observations per individual per day lasted 30 min, except for some groups of sifaka (C, E, F, F1, G, H, J, L)

Table 1 Details of data collection per species: observation period, field site, number and size of groups and number of hours observed and scans per group

Species	Observation period	Field site	Groups	Average number of adults (mean + range)	Total observation (# hours)	# of scans
Ring-tailed lemur	Sept–Oct 2011	Berenty Reserve	C1	10	895	
	May–July 2012		C2A, YF	8.5 (8–9)		
	May–June 2018		C12[a], T2[a]	9.5 (9–10)		141
Verreaux's sifaka	March 2012–March 2013	Kirindy Forest	C, E, F, F1, G, H, J, L	3.6 (2–4)	1,460.5	
	March–May 2018		G1[a]	5		105
Red-fronted lemur	March–August 2011	Kirindy Forest	A, B, F, J	8 (3–11)	397	
	March–May 2018		A1[a], B1[a]	5 (5)		142

= number

[a] Groups where spatial scans of individuals were collected

which lasted 1 h. During observations, all agonistic interactions were recorded, including the identity and behaviour of the interaction partner. Some data had already been collected as part of previous projects (e.g. Koch et al. 2017; Fichtel et al. 2018). It was not possible to record data blind because our study involved focal animals in the field.

Agonistic interactions were defined by the exchange of either aggression or submission or both. Aggressive behaviours included chase, grab, lunge, bite and displace while submissive behaviours included submissive vocalisations (‘spat call’ in ring-tailed lemurs and ‘chatter’ in Verreaux’s sifakas) or fleeing in all three species. Agonistic interactions were classified as ‘decided’ (AS) if only one of the opponents exhibited submissive behaviour to the other. Spontaneous submission (OS) was characterised by submissive behaviour that was not prompted by an aggressive act, with the loser being the individual that submitted. Following other studies in lemurs, we considered spontaneous submission as a decided agonistic interaction (Pereira and Kappeler 1997). Interactions were classified as undecided when there was no clear winner, meaning that submission from either opponent was absent. In these cases, aggression was either met with counter-aggression (AA) or a neutral behaviour (AO), such as doing nothing or turning but remaining on the same location. For a full ethogram and definitions, see Pereira and Kappeler (1997) and Kraus et al. (1999).

To be included in our analyses, individuals had to have been engaged in at least one agonistic interaction (decided or undecided). Therefore, two males from group B1 and one female as well as one male from group B of red-fronted lemurs were omitted. We also excluded one male from group T2 of ring-tailed lemurs because he was in the process of immigrating into the group and was not yet socially integrated.

Dominance hierarchy

We derived the dominance hierarchy among adults of each group from decided agonistic interactions (AS + OS). For this, we used the Average Dominance Index (ADI). The average dominance index is the average proportion of winning by an individual from all of its opponents, excluding opponents with whom it did not interact. The degree of female dominance over males was measured by the Female Dominance Index (FDI; Hemelrijk et al. 2008). This is the average proportion of males in the group over which females are dominant. If males and females are equal in their dominance (ADI), we use the common procedure of ties (the tie counts for each of the pair members as 0.5).

To assess the dominance style in a group, we used the proportion of fights with counter-aggression, which has been suggested to be an appropriate measure of dominance style in macaques (Balasubramaniam et al. 2012; Thierry 2021). A higher proportion of counter-aggression indicates species to be more egalitarian. We use this over the common measure of steepness (Gammell et al. 2003; de Vries et al. 2006) since steepness is known to be highly influenced by a high proportion of unknown relationships and small group sizes (Klass and Cords 2011), which were common in our data. We calculated the proportion of counter-aggression as the number of counter-attacks (conflicts in which the receiver of aggression immediately aggresses back to an aggressor) divided by the total number of interactions per group (all agonistic interactions). The proportion of counter-aggression per group was strongly correlated with the average proportion of counter-aggression per interacting dyad, and per individual per group, and thus, it was little influenced by a single individual or dyad ($R = 0.99$, $p < 0.001$, Fig. S6). To understand how the proportion of counter-aggression relates to differences in fighting capability among individuals in a group, we tested per species whether interactions involving counter-aggression occurred more often between individuals of closer dominance rank than decided interactions did. We did this by comparing per species the rank difference (ADI of actor – ADI of receiver) when agonistic interactions were decided or involved counter-aggression.

Agonistic interactions

The rate of aggression per individual was calculated as the sum of the number of decided and undecided agonistic interactions (not including spontaneous submissions) it initiated per hour. We combine rates of aggression calculated by focal and all-occurrence collection methods since these did not significantly differ within the same species (Table S9, S10). Intensity of aggression was recorded on a scale from 1 to 5 according to Kappeler (1993), with level 1 for displacements; level 2 for aggression without physical contact, such as using signals or threatening another individual; level 3 for physical contact, such as wrestling or hitting; level 4 for intense physical aggression such as biting; and level 5 for chasing. Agonistic interactions with aggression were scored based on the most intense aggression displayed by the initiator, meaning that for example if an interaction included a chase as well as a signal, it would be scored as 5. The intensity of aggression was averaged over all fights initiated per individual. Spontaneous submissions were not included in the rate of aggression or intensity of aggression because in this case neither partner performed an aggressive act.

Cohesion

Data regarding cohesion were measured for fewer groups than for agonism (5 groups vs 20 groups, respectively). This is because focal observations collected during previous projects did not collect data on group cohesion. Data on cohesion were collected specifically for the present study between March and July 2018. Data were collected using Animal Observer App for iPad (Caillaud 2018). Here, an individual was chosen and followed for 30 min. Every 10 min, a scan of the group was taken, and the location of all other individuals relative to the focal individual was recorded on a map. Scans were conducted in 2D. Per scan, the heading of the front of the group was taken as the direction of movement of the whole group (and considered ‘north’ in the map interface). As a proxy of cohesion, we calculated per individual per scan the number of individuals within 3 m.

Statistical analyses

Data processing and statistical tests were conducted in R (version 4.0.3) (R Core Team 2020) and RStudio (RStudio Team 2020). Graphs were created in RStudio with *ggplot2* (Wickham 2016) and *ggpubr* (Kassambara 2020). General and linear models were fitted using *stats* package from R (R Core Team 2020), *glmmTMB* package (Brooks et al. 2017) and *lme4* (Bates et al. 2015). Goodness of fit was measured through statistics based on simulated residuals from the package *DHARMa* (Hartig 2022) and dfbetas and variation inflation factor using the *car* package (Fox and Weisberg 2019). For some models, significant outliers were found and they were removed from the dataset and the model was conducted again. If the results were qualitatively the same (same direction and similar magnitude of the estimate and degree of significance), we report results from the full dataset (see supplementary material for details).

We confirmed whether species differed in their intensity of aggression or not using a linear mixed model (LMM) with average intensity per individual as the response variable and species as the predictor variable with group as a random effect.

We investigated whether individuals that had more neighbours within 3 m also had a higher rate of aggression (prediction 1). We conducted a negative binomial regression with a log link to examine whether the rate of aggression (number of aggressive acts initiated per individual) was predicted by the average number group members within 3 m. We include group size and species as control factors, group identity as a random factor and the number of observational hours as an offset.

To investigate whether a higher rate of aggression is related to a more despotic dominance style (prediction 2), we performed a binomial GLM with a logit link. We used the proportion of counter-aggression per group as the response variable (inputted as the number of interactions involving counter-aggression per group as ‘successes’ and the number of decided fights per group as ‘failures’ using the cbind function), and the average rate of aggression per group as predictor. We included species and group size as control factors.

Finally, to study whether in more cohesive groups, females were dominant over relatively more males (prediction 3); we compared whether species that had stronger female dominance over males also had a stronger group cohesion. Variation in female dominance was compared across species by fitting a binomial regression with group size as a control factor. Due to the complete separation in the logistic regression of the Female Dominance Index (all FDI of Verreaux’s sifaka = 1), we applied the brglm fitting method (Kosmidis and Firth 2021). Differences in the average degree of cohesion (number of individuals within 3 m) per individual were compared among species using an LMM with group as a random effect. We did not directly correlate group cohesion and FDI because of the low number of datapoints for group cohesion ($n = 5$).

We tested per species whether the rate of aggression initiated differed between the sexes using negative binomial GLMM with log link, using group as random effect and the number of observation hours as an offset.

For comparisons among species, we report likelihood ratio tests (LRTs) between full and null models (just control factors and random effects). If significant, we conducted post hoc pairwise comparisons using the *emmeans* package (Lenth 2021) to compare the estimate marginal means. We corrected p-values for multiple comparisons using the Tukey method.

Results

In line with previous findings, intensity of aggression of fights was on average intermediate and did not differ significantly among species (mean ± SE RTL: 2.26 ± 0.20; VS: 2.40 ± 0.27; RFL: 2.48 ± 0.23; LRT: $X^2 = 0.86$; df = 2; $p = 0.65$; Table S1, S2, Fig. S1). We also demonstrate that counter-aggression occurred more often between individuals of a similar dominance rank (ADI) than decided fights, especially in ring-tailed lemurs and red-fronted lemurs (RTL: $W = 29{,}601.5$, $n_1 = 3118$, $n_2 = 12$, $p < 0.001$; VS: W = 338, $n_1 = 368$, $n_2 = 1$, $p = 0.15$; RFL: $W = 1318.5$, $n_1 = 86$, $n_2 = 23$, $p < 0.01$, Table S8, Fig. S7).

In line with prediction 1 (stronger cohesion results in a higher rate of aggression), individuals in groups aggressed others at a higher rate when they had more neighbours ($\beta = 1.17$, se = 0.42, $z = 2.80$, $p = 0.005$, $n = 34$ individuals, Fig. 1A, S4, Table S3, S4). This result was robust even when cohesion was measured as the number of individuals within different distances around the focal individual (Fig. S5, Table S7). In support of prediction 2 (higher rate of aggression, more despotic dominance style), groups with a higher average rate of aggression had a lower proportion

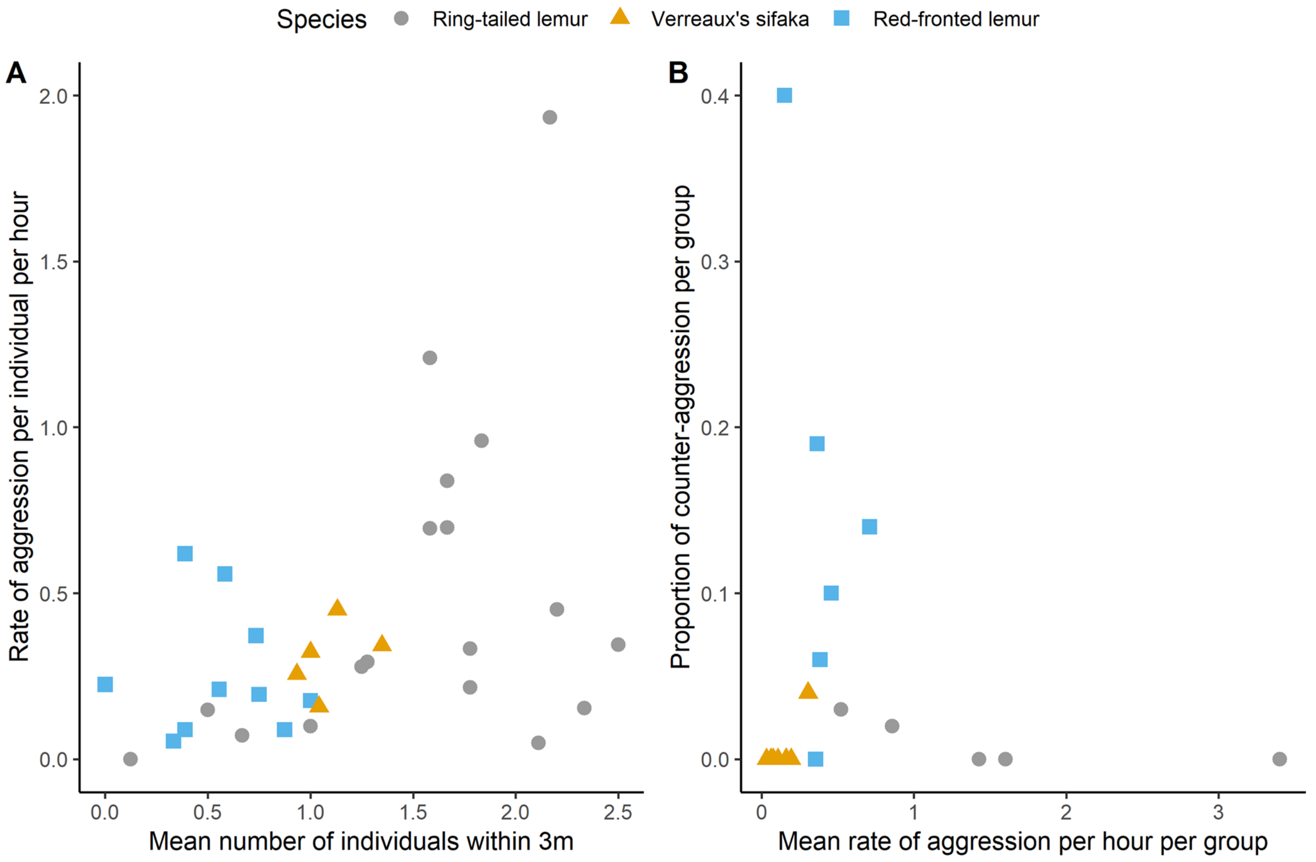

Fig. 1 **A** Average number of aggressive acts initiated per hour of observation per individual plotted against the average number of individuals within 3 m in several groups of ring-tailed lemurs, Verreaux's sifakas and red-fronted lemurs. One extreme value was omitted from the graph for visualisation purposes (ring-tailed lemurs: aggression rate = 4.2, mean number of individuals within 3 m = 1.7). (**B**) Proportion of fights with counter-aggression per group and average rate of aggression of several groups of ring-tailed lemurs, Verreaux's sifakas and red-fronted lemurs

of counter-aggression ($\beta = -1.45$, se = 0.51, $z = -2.84$, $p = 0.0045$, $n = 20$ groups, Fig. 1B, Fig. S10).

Regarding prediction 3 (stronger cohesion is associated with stronger female dominance), we show that groups of species that exhibited a stronger group cohesion also had a higher female dominance index (Fig. 2A, B, Table 2, S15–18). Note also that in groups of species where the Female Dominance Index was higher, females initiated a higher rate of aggression than males (Fig. 2C, ring-tailed lemur $\beta = -1.71$, SE = 0.23, $z = -7.57$, $p < 0.001$; Verreaux's sifaka $\beta = -1.46$, SE = 0.29, $z = -5.02$, $p < 0.001$; red-fronted lemur $\beta = 0.54$, SE = 0.31, $z = 1.74$, $p = 0.08$).

Discussion

In this study, we provide evidence indicating that the dominance style of three species of lemur depended on the degree of cohesion, but not on the intensity of aggression. Firstly, we confirmed that individuals that had more group members nearby initiated more fights (prediction 1). Secondly, we demonstrated that a higher rate of aggression correlated with a more despotic dominance style in lemurs (prediction 2). Thirdly, we showed that stronger cohesion may underlie a stronger degree of female dominance over males (prediction 3). We discuss these points in detail below.

Cohesion, rate of aggression and dominance style

In groups of lemurs where individuals were surrounded by more neighbours, they initiated more aggression (prediction 1), particularly in ring-tailed lemurs and red-fronted lemurs. This higher rate of aggression was associated with a lower frequency of counter-aggression, and, thus, a more despotic dominance style (prediction 2). Hence, we offer support with our data in three species of lemurs for predictions made by the DomWorld model, suggesting that a higher rate of aggression from individuals resulting from their closer proximity causes stronger hierarchical differentiation through the winner-loser effect (Hemelrijk 2003; Hsu et al. 2006).

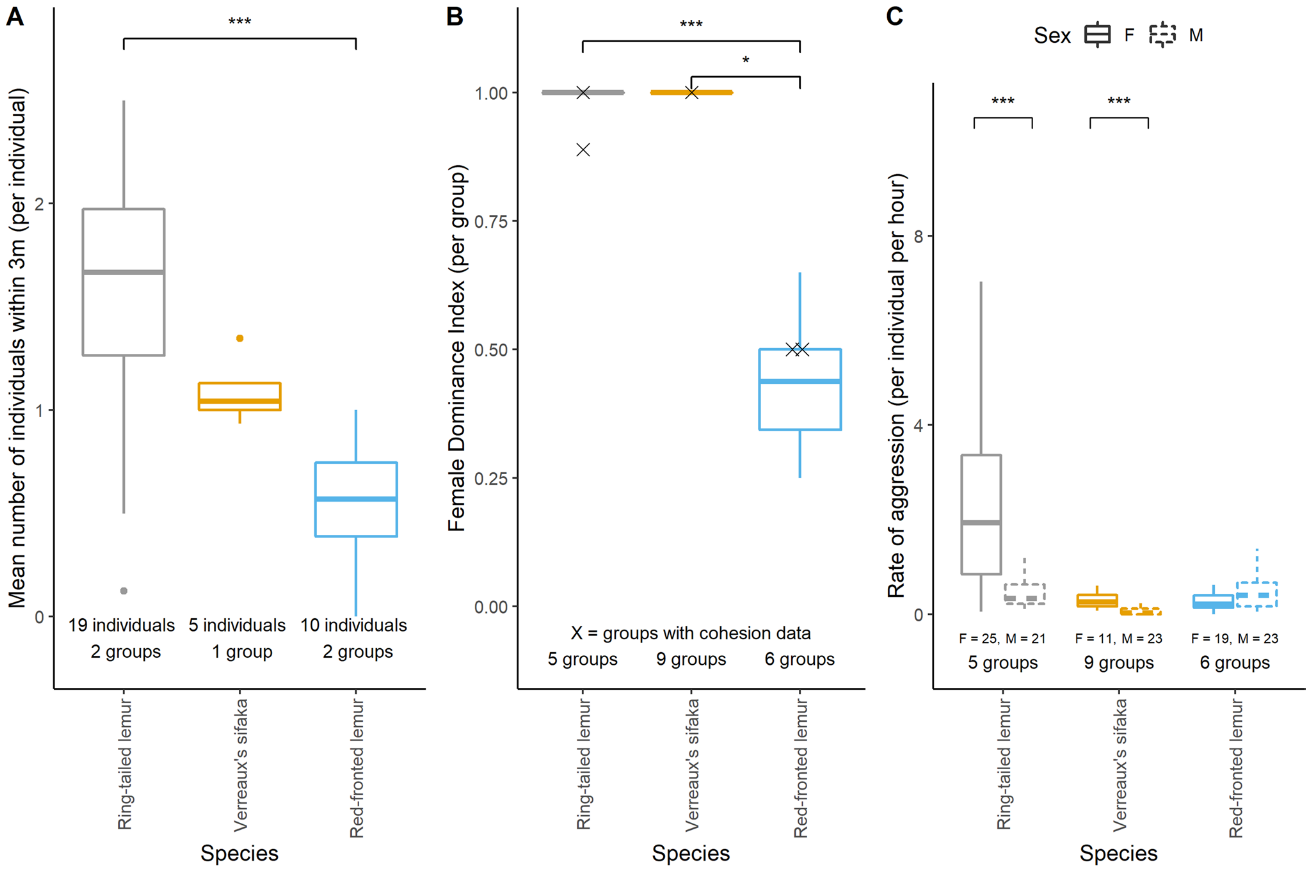

Fig. 2 Boxes indicate inter-quartile range with the central line depicting the median and whiskers extending to 1.5 times the inter-quartile range and dots indicate outliers. **A** Mean number of individuals within 3 m per individual per species **B** Female Dominance Index per group per species. Crosses indicate data points from groups collected in 2018 where cohesion data were also collected. **C** Rate of aggression initiated per individual per sex per species. $***p < 0.001$, $*p < 0.05$

Table 2 Likelihood ratio tests and post hoc tests comparing cohesion and Female Dominance Index (FDI) among species

	Likelihood ratio tests			Emmeans post hoc test	
Response variable	X^2	df	p	Comparison	p
Cohesion	20.43	2	< 0.001	RTL vs RFL	0.001
				RFL vs VS	0.16
				VS vs RTL	0.17
Female Dominance Index	86.6	2	0.001	RTL vs RFL	0.001
				RFL vs VS	0.001
				VS vs RTL	0.98

Despite our small dataset for group cohesion, our results are in line to those reported in other studies of wild lemurs (e.g. Hood and Jolly 1995; Cavigelli et al. 2003; Norscia and Palagi 2015). However, the underlying factors driving variation in group cohesion (and thus rate of aggression and dominance style) in lemurs are unclear. Here, we address three possible explanations according to the socio-ecological model (Wrangham 1980; van Schaik 1989; Sterck et al. 1997): (1) the distribution of food, (2) predation pressure and (3) group size. We limit ourselves to these three possible explanations that may underlie variation in cohesion, yet there may be other contributing factors; for instance, intergroup competition (Samuni et al. 2020), habitat fragmentation and seasonality (Irwin 2007) are also known to influence intragroup cohesion.

Firstly, we hypothesise that stronger cohesion may be related to a patchier distribution of food. In support of this, ring-tailed lemurs, which exhibited the strongest group cohesion, have previously been reported to experience contest competition and to feed often within 3 m of their nearest group member (Sauther 1993; Gemmill and Gould 2008). In contrast, the less cohesive red-fronted lemurs are capable of switching their diet from fruit to other items during periods of scarcity (Erhart et al. 2018). Thus, they may group more sparsely at a food source and thus have fewer conflicts. In a controlled feeding experiment, red-fronted lemurs also exhibited more social tolerance towards conspecifics than ring-tailed lemurs (Fichtel et al. 2018). Indeed, nearest neighbour distance in primates has been shown to be larger when individuals are feeding on leaves than on fruits (Bryer et al. 2013; Le Flohic et al. 2015). Also, in other species of lemurs, the rate of aggression was lower in the folivorous *Hapalemur griseus*, than in the frugivorous *Eulemur macaco* (Digby and Stevens 2007), which may be a consequence of cohesion.

Because Verreaux's sifakas are highly folivorous (Koch et al. 2017), we expected individuals to be more spread out and to exhibit fewer conflicts. Instead, individuals had a relatively high number of neighbours nearby, but fought infrequently. Originally, it has been suggested that folivorous species do not fight over food because leaves are abundant (Isbell 1991). However, more recent studies revealed that this concept may be outdated because intense feeding competition has also been observed in folivorous species (Koenig 2002; Snaith and Chapman 2007). Unexpectedly, Verreaux's sifaka's dominance style appeared to be highly despotic (almost no counter-aggression) despite their rate of aggression being low. In general, the dominance style of Verreaux's sifaka was difficult to assess because of their low interaction rates. Note that dominance style in Verreaux's sifaka has been reported to be variable and difficult to determine elsewhere too, even when aggression matrices were more complete (Palagi et al. 2008; Norscia and Palagi 2015).

Secondly, cohesion may relate to risk of predation. Groups that experience stronger predation have stronger cohesion, because cohesion increases protection against predators (Sogard and Olla 1997; Schreier and Swedell 2012). However, this does not explain the differences in cohesion among our three study species. Ring-tailed lemurs were highly cohesive, but were studied in Berenty where they suffer less predation pressure than Verreaux's sifaka and red-fronted lemurs in Kirindy Forest (Fichtel and Kappeler 2011). Moreover in Kirindy Forest, red-fronted lemurs are more terrestrial than Verreaux's sifaka and therefore experience stronger predation risk from the largest Malagasy carnivore (fosa, *Cryptoprocta ferox*; Schnoell and Fichtel 2012), but their groups were not more cohesive than those of Verreaux's sifaka. Hence, the variation in group cohesion across the three species of lemurs is unlikely to be due to variation in predation risk.

Thirdly, group size may also influence cohesion in groups. In our study, ring-tailed lemurs had a larger group size and were more cohesive than red-fronted lemurs, mirroring a similar pattern between group size and cohesion in some fish (Partridge 1980; Hemelrijk et al. 2010). However, among primates, a larger group size is usually associated with weaker cohesion (e.g. Zárate and Stevenson 2014). Stronger cohesion within groups may also arise from stronger competition between groups, for which larger group size is advantageous (LaBarge et al. 2020; Samuni et al. 2020). However, in Verreaux's sifakas at our study site, larger groups are not more likely to win in intergroup conflicts (Koch et al. 2016), suggesting that larger group sizes might be counteracted by the disadvantage of increased competition over food (Koch et al. 2016) or other costs (Rudolph et al. 2020).

Female dominance and cohesion

In our data, female dominance over males was stronger in groups from species that were more cohesive (prediction 3), and in these species, females initiated more aggression than males. In general, hypotheses regarding female dominance over males in lemurs focus on the similar body size of the sexes as well as the greater effort that females invest in conflicts because of their higher energetic demand during reproduction (cost-asymmetry hypothesis, Dunham 2008). Until recently, variation among lemur species in the degree of female dominance over males has largely been ignored but recent results show that it is more variable than previously thought (Kappeler et al. 2022). We propose here that the degree of female dominance over males may relate to differences in cohesion due to differences in the distribution of food and thus intensity of feeding competition. When food is more clumped, individuals are closer together and more likely to engage in competition for food, with females competing more strongly over food than males due to their greater energetic demands. When food is more spread out, females, however, may not need to engage that strongly in competition over food, resulting in weaker female dominance over males.

Counter-aggression and measures of dominance style

In the present study, we determined dominance style using the proportion of counter-aggression, which reflects the degree of symmetry in dyadic contests (Balasubramaniam et al. 2012; Thierry 2021). When interaction rates are low, this measure is preferable over the measure of steepness by de Vries and co-authors (2006) because steepness is biased by the proportion of unknown relationships (Klass and Cords 2011). In macaques, counter-aggression occurs relatively more often in egalitarian than despotic species supposedly because aggression in egalitarian species is milder and thus the risk of injury is lower (Thierry 2000). However, among the species of lemur in the present study, the proportion of counter-aggression differed among species even though their intensity of aggression was similar. Instead, we found that counter-aggression occurred more between individuals of a similar rank, which is an alternative explanation of why more frequent counter-aggression implies a more egalitarian dominance style. What is still unknown and requires further study is which circumstances (outside of rank differences) lead to counter-aggression and whether certain types of interactions are more likely to illicit counter-aggression as a response.

Fights that do not have a clear outcome may not induce a hormone response associated with a winner-loser effect (e.g. mirror fights in fish Teles et al. 2013; Oliveira et al. 2016)), and therefore may not affect hierarchical differentiation. Thus, a high proportion of counter-aggression may be both a cause and a consequence of an egalitarian hierarchy, because an undifferentiated hierarchy will result in frequent counter-aggression and frequent counter-aggression may prevent the hierarchy from differentiating. This is important for understanding the mechanisms underlying hierarchy formation and suggests that undecided fights should not be included in the analysis when deriving a dominance hierarchy (e.g. Elo-rating (Neumann et al. 2011)).

Future work

The relationship between spatial structure and social behaviour is often ignored in empirical studies, despite models of animal behaviour highlighting its importance (e.g. Hemelrijk et al. 2017; Tyutyunov and Titova 2017). We demonstrate here in three species of lemurs that spatial proximity among group members was associated with differences in rates of aggression, dominance style and degree of female dominance over males. Studies in captivity support our finding for the association between stronger cohesion and higher rates of aggression in other species of lemur (Digby and Stevens 2007; Cherevko 2020), as well as in other taxa such as gazelles (Cassinello and Pieters 2000), horses (Flauger and Krueger 2013), apes (Sannen et al. 2004, but see de Waal 1989), chickens (Estevez et al. 2002), cows (DeVries et al. 2004), pigs (Remience et al. 2008) and kangaroos (Höhn et al. 2000)). Yet, in our study in the wild, how and why strong cohesion in ring-tailed lemurs is maintained despite a high rate of aggression is unclear since individuals could flee or spread out to avoid costly fights. This paradox requires further study.

The generality of the relationship between cohesion, rate of aggression and dominance should be studied in more groups of lemurs and in other animals. Currently, our study offers only correlational support for this relationship based on a small dataset of three species observed at different times of year. To test this prediction more extensively, data should be collected on more groups and species of group-living animals, preferably over multiple seasons. Moreover, alternative explanations for difference in cohesion, rates of aggression and dominance style should be studied because DomWorld does not take into account many relevant biological factors such as feeding ecology, reproductive seasonality, presence of offspring and intergroup competition, all of which could influence patterns of spatial configuration and social interaction. Which factor may underlie the differences in cohesion is uncertain. We indicate three potential causes (e.g. distribution of food, predation pressure and group size) to be studied, as well as the possible interplay between cohesion, group competition and group size.

Why groups of Verreaux's sifaka did not fit the expected pattern predicted by DomWorld though they were matched in red-fronted and ring-tailed lemurs is unclear. Whether this is related to our limited data on cohesion, their strongly folivorous diet or because they evolved from a lineage separate from the other two species (Kappeler and Pozzi 2019) should be investigated further.

Conclusions

We show that among three species of lemur, spatial cohesion, rate of aggression, dominance style and female dominance over males co-vary in groups as we predicted based on the computational model DomWorld: stronger spatial cohesion among group members contributes to a more despotic dominance style (and greater female dominance over males) via higher rates of aggression and the winner-loser effect. We highlight that studies on dominance style should include the proportion of counter-aggression as a measure of dominance style and relate it to measures of spatial cohesion in groups.

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Author contribution CKH and LS conceived the study. LS conducted the data analysis. LS performed data collection for data collected in 2018, other data were provided from previous projects by CF and PMK. LS drafted the manuscript and all authors contributed to writing and revising of the manuscript.

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Data availability The datasets that were analysed for this study are deposited under the link https://doi.org/10.34894/OC4V2A.

Code availability The computer code that was used to analyse the data is available from the following link: https://doi.org/10.34894/OC4V2A.

Declarations

Ethics approval All research adhered to the legal requirements of Madagascar. Research in Kirindy Forest and Berenty Reserve was approved by a committee of the Ministry for the Environment, Water and Forests of Madagascar (MINEEF) (Permit number: 394–10/MEF/SG/DGF/SVRN/SGFF). The use of animals adheres to the guidelines set forth by the Animal Behavior Society/Association for the Study of Animal Behaviour. Further ethics approval was not required.

Consent for publication The authors consent to the publication of this manuscript in Behavioral Ecology and Sociobiology.

Conflict of interest The authors declare no competing interests.

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