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Effects of between-group competition on sexual size dimorphism in primates

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Sexual selection acting on males through intrasexual competition for mates is a well-established driver of sexual size dimorphism (SSD) in primates. However, studies typically focus on within-group competition, overlooking the potential significance of competition arising from interactions between neighbouring social groups, particularly when home ranges overlap. Here, we analysed the relationships between SSD, mating system and different proxies of range use across up to 143 species of anthropoid and strepsirrhine primates. Contrary to expectations, mating system—a commonly used proxy for male competition—did not significantly predict SSD. Instead, male-biased SSD increased with home range overlap and encounter rate between social groups, even after accounting for mating system and body size allometry. This suggests that spatial pressures, such as the latent threat of competition from rival groups, impose stronger selection on male compared with female size. Home range overlap may select for larger males to deter rivals, defend resources or monopolize females across shared territories, potentially without frequent physical contests. Our work calls for renewed attention to how spatial competition, including resource defence and mate guarding across overlapping territories, influences trait evolution in primates and other social vertebrates and to re-evaluate proxies of sexual selection.

1. Introduction

A central theme in sexual selection research revolves around understanding the evolutionary drivers of sexual dimorphism, particularly in body size [1,2]. Sexual size dimorphism (SSD) arises from differential selection pressures acting on males and females. In many species, competition for mating opportunities strongly favours increased body size in males, providing advantages in both male–male competition and female mate choice [3,4]. Extensive evidence supports a link between the intensity of sexual selection and SSD across diverse animal taxa [5–9]. However, the strength of this relationship can vary between metrics of sexual selection (e.g. Bateman gradient versus opportunity for sexual selection [variance in relativized mating success] [10]; potential for female monopolization versus realized mating success [11]) and the taxonomic group under consideration [10,12].

Primates exhibit considerable variation in SSD, primarily driven by sexual selection on male body size [5,13] (but see [10,14]). While ecological factors, such as living predominantly in terrestrial compared to arboreal habitats [8], can influence SSD, their effects are often constrained or secondary to sexual selection. For example, arboreal habitats may limit the expression of extreme male size due to limitations imposed by branch strength [13]. Yet, this constraint may not necessarily limit the *strength* of sexual selection itself, as males may still compete for mates through alternative strategies such as displays, vocalizations or sperm competition. Furthermore, as Plavcan [15] emphasizes, SSD results from complex interactions between factors affecting both male and female size, including genetically correlated changes in both sexes. Notwithstanding these considerations, sexual selection is often invoked as the primary driver of the variation observed among anthropoid primates [7,8,16].

Multiple proxies of the strength of sexual selection have been shown to covary with SSD, including mating or breeding system (a measure of male reproductive skew [7,17]), competition levels (i.e. estimates of the degree of male relative to female agonistic behaviour [8]) and the operational sex ratio (a measure of the monopolization potential of females [18]). However, these attributes do not clearly distinguish between levels of competition *within* and *between* demarcated social groups. Although the mating system is often construed as a measure of sociosexual dynamics within breeding units, it also has an important between-group component, because polygyny necessarily implies the presence of extra-group males competing for access to bisexual groups. Similarly, although Plavcan and van Schaik's [19] 'competition levels' framework is largely concerned with within-group competition, elements of between-group competition are also incorporated. For example, species classified as experiencing low-frequency competition are those in which male–male competition is typically restricted to occasional encounters with extra-group males (i.e. single-male breeding groups). To more fully reflect this broader competitive landscape, explicit measures of between-group spatial overlap and associated social and competitive dynamics are, therefore, required.

Primate groups are typically not spatially isolated entities; instead, neighbouring groups frequently interact, leading to varying degrees of between-group competition [20–23]. The causes and consequences of competition *between* groups have long been studied by socioecologists [24–29], but its role as a selective pressure on male *morphology*, with downstream consequences for SSD, has not been explicitly investigated (but see [30] for preliminary evidence in one radiation of primates). Smith *et al*. [31] demonstrate a pronounced male bias in participation in between-group conflict across social mammals, including numerous primate species. This comparative evidence provides an empirically supported rationale for expecting between-group competition to act as a sex-specific selective pressure, especially on male morphology.

Here, we aimed to explicitly examine the effects of between-group male–male competition on SSD across a broad sample of primates. We hypothesized that SSD is shaped by between-group competition. To test this hypothesis, we used comparative data from 146 primate species. We employed three measures of the potential for between-group competition: the daily encounter rate, the proportion of between-group encounters that are agonistic and home range overlap. The rate of between-group encounters can be used to quantify the direct pressure exerted by neighbouring groups [32,33], particularly in the case of agonistic encounters. Home range overlap could also be construed as a quantitative measure of the extent to which groups are encroached by neighbouring groups, providing an indirect measure of the potential for resource competition and territorial encounters between groups. Building on [30], we analysed SSD across a broader taxonomic sample using multiple between-group competition proxies.

2. Methods

(a) Data collection

We collated information from the literature on home range overlap, between-group encounter rate, the rate of agonistic between-group encounters, sexual dimorphism in body mass and mating system for up to 146 primate species (both strepsirrhine and anthropoid). Home range overlap was defined as the percentage of a group's total range that is shared with neighbouring groups. Encounter rate refers to the number of encounters between the focal group and neighbouring groups per day. Agonistic encounters were defined as encounters including any of the following behavioural elements: physical altercations, displays, avoidance, displacement, vigilance and vocal exchanges. Data on home range overlap, between-group encounter rates and proportion of between-group encounters that are agonistic were compiled predominantly from the primary literature (to ensure accuracy) and not secondary sources. If the requisite data were available for multiple study sites of the same species, we calculated an average across sites. Data on home range overlap were available for 135 primate species, on encounter rate for 99 species, and on the rate of agonistic interactions for 72 species. Solitary primates were excluded because our hypotheses and predictor variables focus explicitly on within- and between-group competitive processes, which are not readily defined for species lacking stable social groups. When collating the data, we disregarded heavily food-provisioned populations (e.g. some Japanese macaque groups) and populations in non-native habitats (i.e. Cayo Santiago rhesus macaques). For a study to be included, it had to exceed a duration of five months. Species with multilevel societies (multiple core units embedded within larger groups [34]) are characterized by complete range overlap among core units and were given a default between-unit encounter rate of 1 per day. The full dataset containing all variables is provided in the electronic supplementary material. Data on sexual dimorphism in body mass and mating system were sourced for 144 and all 146 primate species, respectively.

Plavcan & van Schaik [8,19] devised categorical estimates of the degree of male–male intrasexual agonistic competition. These 'competition levels' factor in both the intensity and potential frequency of contests, with the former being approximated by the observed tolerance among adult males towards each other and the latter being a function of the proximity of males to each other. We did not use this scheme to measure within-group competition for two reasons: (i) The competition levels are largely collinear with mating systems (see e.g. [11]), so we relied exclusively on the latter; (ii) it is unclear to what degree competition levels measure within versus between-group competition (see Introduction).

(b) Data analyses

We conducted all analyses in R v. 4.5.1 [35], with log SSD (log male mass – log female mass) as the response variable. We did not include body size as a covariate, because there is no consensus that sexual size dimorphism arises as a simple allometric consequence of body size, and sexual selection may influence overall size and dimorphism concurrently rather than independently (e.g. [7,13,36]). However, results were qualitatively unchanged when body size was included as a covariate. The focal predictors included the mating system (polygyny, monogamy, polygynandry and polyandry), proportional home range overlap between social groups, daily encounter rate, rate of agonistic encounters and proportion of encounters that were agonistic (electronic supplementary material, figure S1). Due to non-independence between the variables related to between-group encounters and varying missing data between variables, we examined their effects on SSD in separate models.

To account for uncertainty in phylogenetic relationships, taxonomic representation due to missing values and species-specific estimates of the variables themselves (e.g. due to often only 1–2 reported trait means per species), we conducted all analyses in a resampling framework across 1000 iterations. As the core analyses, we ran phylogenetic generalized least-squares models across 1000 trees that we randomly sampled from the set of 10 000 molecular species-level mammalian trees by Upham *et al.* [37] and pruned to the primate species represented in our dataset. Four species that were missing from these trees were manually inserted based on recent phylogenetic studies. Specifically, we placed *Piliocolobus temminckii*, *Piliocolobus tephrosceles* and *Trachypithecus leucocephalus* using time-calibrated colobine phylogenies to decide on insertion and branch lengths [38]. The fourth species, *Piliocolobus epieni*, was not represented in any of these phylogenies, so we inserted it as a sister species to *P. tephrosceles* rather than to *P. temminckii*, following Ting [39], who identified morphological and molecular similarities between these taxa. These 1000 tree-based models represent the primary estimates of the relationships between the predictor variables and sexual size dimorphism while explicitly incorporating phylogenetic uncertainty.

To examine the robustness of these baseline results, we repeated the same analyses under two additional resampling schemes. First, we generated 1000 datasets in which we excluded either 10%, 20% or 30% of species from each iteration to test the sensitivity to taxonomic representation. This ‘species sampling’ procedure evaluated whether results depended on the inclusion of specific taxa or were stable across varying species subsets.

Second, to account for uncertainty in species-level trait estimates (e.g. due to measurement error, sampling bias or natural variation among populations), we introduced stochastic noise into all trait values (separately for each variable) and repeated the full analysis across 1000 perturbed datasets. For continuous traits, we applied multiplicative Gaussian noise, multiplying each value by $(1 + x)$, where x was a random value drawn from a normal distribution with a mean of 0 and a standard deviation of either 0.1 or 0.2 (i.e. corresponding to average noise of ± 10 or ± 20% around trait values, respectively). This approach preserved the original scale and relative variation across value ranges. For proportional traits, we used a logit-normal approach to ensure perturbed values remained within biologically plausible bounds (0–1). To this end, we first transformed trait values using the logit function, then added Gaussian noise in logit space before back-transforming values to their original scale. To reflect the empirical pattern of greater uncertainty near intermediate proportions, we scaled the standard deviation according to the distance of each proportion (p) from 0.5, using a linear scaling function: scaling factor $(SF) = 1 - 2 \times |p - 0.5|$. This factor peaks at $p = 0.5$ and approaches 0 near the extremes. We then calculated the scaled standard deviation as: $SD_{scaled} = SD \times (1 + SF)$, where s.d. was either 10 or 20%, matching the levels of deviation used for continuous traits. To handle boundary cases (i.e. trait values of exactly 0 or 1), we used truncated normal distributions to add small, bounded positive or negative noise while ensuring values remained in plausible ranges (i.e. 0–5% of the boundary). This perturbation procedure preserved the overall data structure while introducing biologically informed within-species variation for a conservative test of the robustness of model estimates.

All p-values and 95% confidence intervals (percentile-based) around the reported effect sizes (r) were derived from the percentiles of bootstrapped distributions based on sampled phylogenies or data.

3. Results

Across 133 species, SSD increased with the proportion of overlapping home ranges (r [resampled 95% confidence limits] = 0.17 [0.14, 0.19], $p < 0.001$, $\lambda = 0.92$ [0.91, 0.94]; figure 1a). This relationship was robust to all levels of species subsampling (30%: $n = 94$, $r = 0.20$ [0.06, 0.31], $p = 0.008$) or intraspecific noise added (20%: $r = 0.15$ [0.04, 0.24], $p = 0.014$; electronic supplementary material, figure S2). The daily encounter rate was also positively associated with SSD ($n = 97$, $r = 0.15$ [0.11, 0.19], $p < 0.001$; $\lambda = 0.95$ [0.93, 0.97]; figure 1b), consistent across all levels of sampling (30% species subsampling: $n = 68$, $r = 0.15$ [0.01, 0.28], $p = 0.036$; 20% intraspecific error: $n = 97$, $r = 0.12$ [0.01, 0.23], $p = 0.026$; electronic supplementary material, figure S3).

In contrast, there was mixed evidence for evolutionary covariation between SSD and the proportion of encounters reported to be agonistic. The baseline model across the 1000 trees suggested a weak but significant negative effect of agonistic encounters ($n = 71$, $r = -0.09$ [−0.10, −0.07], $p < 0.001$; $\lambda = 0.87$ [0.86, 0.89]; figure 1c), as did the model with 10% of species removed in each sampling iteration ($n = 64$, $r = -0.09$ [−0.17, −0.01], $p = 0.036$). However, higher exclusion rates weakened the support of this pattern (20%: $n = 57$, $r = -0.10$ [−0.22, 0.02], $p = 0.084$; 30%: $n = 50$, $r = -0.11$ [−0.27, 0.04], $p = 0.172$; electronic supplementary material, figure S4). Similarly, adding 10% intraspecific noise to each trait value yielded at best a weak negative trend ($n = 71$, $r = -0.08$ [−0.16, 0.00], $p = 0.058$), with no statistical support at 20% noise (−0.08 [−0.22, 0.07], $p = 0.32$). Overall, these results indicate that any evolutionary association between SSD and the proportion of agonistic encounters is, at best, weak and not robust across the species with available data.

Finally, we found no support for an overall effect of social mating system on SSD once phylogenetic covariance was accounted for. Across the 1000 tree samples, the omnibus test was never statistically significant (mean $F_{3,140}$ [95%CI] = 1.46 [1.61,

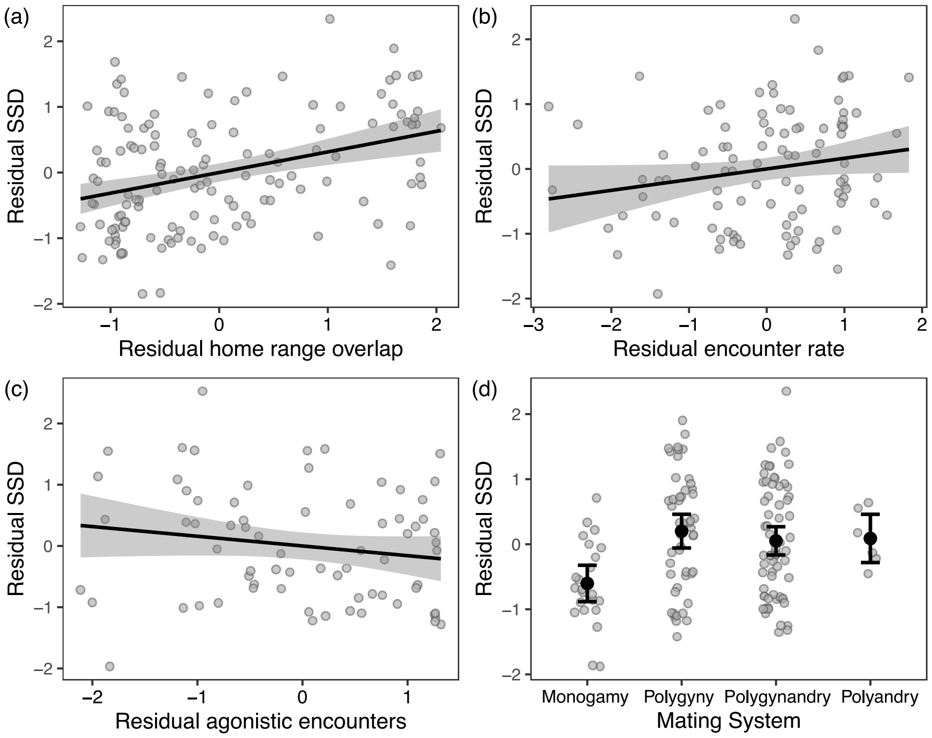

Figure 1. Associations of SSD with the (a) proportional home range overlap, (b) daily encounter rate, (c) proportion of agonistic encounters and (d) social mating system across primate species. These plots are based on the original dataset (species means) and the consensus tree, with standardized continuous variables. The distributions across the resampled phylogenies and datasets are shown in electronic supplementary material, figures S2–S6.

1.85], all $p > 0.10$), and this result was largely robust to resampling of species or trait values, with fewer than 4% of omnibus tests yielding $p < 0.05$. Nevertheless, individual contrasts consistently indicated higher SSD values for polygynous and polygynandrous mating systems relative to monogamous or polyandrous systems (figure 1d; electronic supplementary material, figure S5). This apparent discrepancy is likely driven by the very strong phylogenetic signal in SSD (λ = 0.92 [0.90, 0.93]), which suggests that apparent differences in SSD among mating system categories largely reflect deep phylogenetic structure in SSD rather than repeated, independent evolutionary responses to mating system transitions, despite multiple inferred transitions in mating system within clades (electronic supplementary material, figure S1). Consistent with this interpretation, artificially constraining λ to lower values revealed strong overall effects, with statistical significance emerging when $\lambda \leq 0.76$. The same general patterns were also observed in analyses restricted to the 128 haplorhine primates in our dataset, a clade in which an association between social mating system and SSD has previously been documented [7], in contrast to strepsirrhines, which exhibit minimal sexual dimorphism [40] (electronic supplementary material, figure S6).

4. Discussion

We provide the first comparative evidence that between-group competitive pressure plays a central role in shaping SSD in primates. Across species, SSD increased with greater home range overlap and higher predicted encounter rates between social groups. These patterns suggest that male size evolves not only in response to competition between groupmates but also to the persistent spatial pressure of rival groups in overlapping home ranges. Our study complements Grueter & van Schaik's [30] work on colobines by demonstrating that between-group competition may shape SSD across primates more broadly. Home range overlap likely selects for larger male body size to deter incursions, monopolize resources, reduce the risk of reproductive losses through extra-group mating or defend access to females across shared space, even without frequent physical contests. Thus, spatial overlap itself—not just realized aggression—creates a landscape of latent competition favouring larger males.

This interpretation is supported by a previous comparative analysis demonstrating that another type of premating secondary sexual trait, ornamentation, is associated with greater home range overlap [41]. Notably, Grueter & Lüpold [41] also found that species with more extensive range overlap tend to experience fewer agonistic encounters. The apparent discrepancy between that finding and the present result—namely, a positive association between home range overlap and sexual size dimorphism—can be reconciled as follows. Intruder pressure may favour greater investment in body size or strength, but this does not necessarily translate into more frequent intergroup agonism. This may be because pronounced physical traits that signal male competitiveness function as effective deterrents, reducing the likelihood of escalation during intergroup encounters even as selective pressure from overlap remains high. This further suggests that the potential for conflict (proxied by overlap/encounter rate) drives selection more than the observed intensity of fights.

Although the ecological variables used here to index between-group competition reflect resource distributions that are relevant to both sexes—and thus align with socioecological assumptions that female fitness is often constrained by access to resources—males and females may differ in how these pressures translate into selection. Comparative evidence indicates that direct participation in aggressive between-group conflict is strongly male biased across social mammals, including primates [31]. Consequently, between-group competition may impose more direct selection on male traits associated with physical contest competition, whereas its effects on females are more likely to be mediated indirectly through resource access and social dynamics. This sex difference in involvement provides a plausible explanation for why similar competitive environments yield sex-specific morphological consequences. Future work integrating direct measures of sex-biased participation in between-group conflict with comparative morphological data—such as those compiled by Smith *et al*. [31]—would provide an important next step for testing and refining the hypotheses advanced here.

In contrast to the strong effect of between-group competition, we found no significant relationship between mating system and SSD *after* accounting for phylogenetic non-independence. Earlier studies reported elevated SSD in polygynous systems [6,7,11,42], but our findings align with more recent work showing that SSD is not always a reliable predictor of pre-copulatory sexual selection across taxa [10,43]. Discrepancies among studies may reflect differences in their approaches to accounting for phylogenetic non-independence, taxonomic distribution or mating system classification. The strong phylogenetic signal in the model ($\lambda \approx 0.92$) indicates that SSD is highly conserved, whereas mating system appears comparatively labile, such that apparent differences in SSD among mating system categories primarily reflect deep clade-level structure in SSD rather than repeated, independent evolutionary responses to mating system transitions—consistent with simulations showing emergent effects only when λ is artificially reduced. Further, mating system classification itself ranges from three- to five-category schemes, while we used a four-category framework (monogamous, polyandrous, polygynous and polygynandrous). Although monogamous species consistently show lower SSD, it remains unclear whether polygynous versus polygynandrous systems reliably differ [13,42]. Another source of potential error is that species are often classified by social organization (i.e. group composition) rather than actual mating behaviour. Classifying species as monogamous, polygynous, polyandrous and polygynandrous ignores substantial intraspecific variation, as well as variation in reproductive skew within polygynandrous species and the occurrence of extra-pair reproduction in monogamous and polygynous species. For example, *Rhinopithecus* groups are often labelled as 'polygynous' yet genetic and behavioural evidence indicates that they are in fact polygynandrous [44,45]. Moreover, variance in male reproductive success does not consistently map onto mating system, as shown in both primates and pinnipeds [11,46]. Together, these issues highlight the limitations of using mating system alone to infer the strength of sexual selection.

By establishing between-group spatial competition as a previously underappreciated driver of SSD, our findings expand our understanding of the evolution of primate SSD. While within-group mating competition remains important, it does not operate in isolation. This conceptual expansion, integrating spatial pressures into models of sexual selection, challenges the traditional focus on within-group interactions and emphasizes that male traits can evolve in response to broader socioecological pressures. This has implications for predicting SSD patterns in species with fluid or overlapping home ranges, including some of humans' closest relatives. Furthermore, these findings call for a re-evaluation of sexual selection proxies to incorporate spatial pressures, such as resource defence or mate-guarding across shared ranges, which may drive trait evolution irrespective of direct contest frequency. Our findings extend existing socioecological frameworks by demonstrating how between-group spatial pressures are associated with morphological evolution, offering new insights for studies on sexual dimorphism in other social vertebrates with territorial overlap (e.g. cooperative birds, social carnivores).

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data supporting the findings of this study are available from Figshare (https://figshare.com/s/edcfad181d745e82d8c1). The same data are also provided in the Supplementary Files accompanying this article [47].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. C.C.G.: conceptualization, data curation, investigation, methodology, writing—original draft; X.Q.: conceptualization, writing—review and editing; S.L.: formal analysis, methodology, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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