**MANUSCRIPT TITLE:**

**LIVING IN MIXED-SEX GROUPS LIMITS SEXUAL SELECTION AS A DRIVER OF PELAGE DIMORPHISM IN BOVIDS.**

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**ABSTRACT**

Among mammals, bovids provide some of the most striking examples of sexual dimorphism in colouration and pelage appendages, such as beards and manes. This dimorphism is usually assumed to have evolved through sexual selection on males in the context of intra- or intersexual communication. However, the sexes colouration and pelage appendages look similar between the two sexes in several bovid species thought to be characterized by large opportunities for sexual selection, hinting at fitness costs of dimorphic traits due to other selection pressures. This study applies the comparative method with phylogenetic control to identify the factors promoting and constraining the evolution of dimorphism in colouration and pelage appendages across bovids.

We found that trait dimorphism correlated positively with large breeding group size, an indicator of the intensity of sexual selection, and negatively with male territoriality, which is also likely to affect the operation of sexual selection. The relative rarity of colour and pelage dimorphism in species with territorial mating systems may be explained by weaker sexual selection due to difficulty in monopolizing females and/or sexual selection targeting other traits, such as territorial quality as an extended phenotype. We also found that dimorphism in colour and pelage was reduced in species spending more time in mixed-sex groups outside the breeding season, possibly due to increased predation costs from non-uniformity. This suggests that benefits from integration into mixed-sex groups selects against the extravagant male morphologies otherwise promoted by sexual selection.

**KEY WORDS**: sexual selection; Bovidae; ungulates; sexual dimorphism; colouration; ornaments; mixed-sex groups; confusion effects

**INTRODUCTION**

Marked differences in morphology between males and females can be found in a wide range of taxa, and often encompass a variety of traits, from body size and weaponry (Pérez-Barberìa et al. 2002; Cassini 2020) to colouration and various appendages (e.g. in birds: Møller & Pomiankowski 1993; Cooney et al. 2019; in primates: Grueter et al. 2015; Lüpold et al. 2019). Darwin’s formulation of sexual selection presented a breakthrough in our understanding of the evolutionary origin of sexual dimorphism (Darwin 1871). However, aspects of the taxonomic distribution of sexually dimorphic traits continue to puzzle evolutionary biologists (Lande 1980; Andersson & Iwasa 1996; Shultz & Burns 2017). In particular, why is sexual dimorphism seemingly weak in a large number of species thought to be characterized by intense sexual competition?

Among mammals, the Bovidae offers striking variation in sexual dimorphism, from the practically monomorphic wildebeest (*Connochaetes taurinus*) and duikers (*Cephalopus* sp.), to species where the bold appearances of males contrast conspicuously with those of females, such as the blackbuck (*Antilope cervicapra*), many wild goats and sheep, and members of the bushbuck tribe (Schaller 1977; Estes 1991a). What may explain these differences between species? Whilst previous research has demonstrated that dimorphism in body size and horns is linked primarily to the opportunity for sexual selection (Loison et al 1999; Bro-Jørgensen 2007), dimorphism in colouration and the presence of manes, beards, hair tufts and other pelage appendages is less well understood.

According to sexual selection theory, sexual dimorphism in colouration and pelage appendages may result from stronger reproductive competition in males: such competition could lead to sex-specific benefits from signalling individual quality to mates and/or competitive ability to rivals (Lande & Arnold 1985; Andersson & Simmons 2006). Theoretically, inter- and intrasexual signals exclusive to males are expected to be more widespread in species with a high opportunity for sexual selection (Clutton-Brock et al. 1980; Grueter et al. 2015; Cassini 2020). The opportunity for sexual selection depends on the variance in mating success among reproductive males, which is in turn affected by the female group size and the male mating strategy: these factors influence the number of mates one male can potentially monopolize (Shuster 2009; Bro-Jørgensen 2011).

In bovids, male mating strategies can be divided into territorial and non-territorial. In territorial species, males defend defined areas attractive to females, due to either the resources they contain, or their location (notably in lek systems). Conversely, males of non-territorial species follow and defend females directly, particularly when they are in oestrus (Gosling 1986; Isvaran 2005).Although molecular paternity studies remain few (Coltman et al. 2002; Festa-Bianchet et al. 2019), evidence from behavioural studies suggests that territoriality may reduce the potential for polygyny, as females often range over multiple territories, forcing males to share reproductive opportunities with rivals (Gosling 1986; Bro-Jørgensen 2007, 2011). By contrast, access to oestrous females in non-territorial systems is generally controlled by males that attain top rank in dominance hierarchies and monopolize breeding groups by excluding subordinates from mating (Gosling 1986; Bro-Jørgensen 2007, 2011). For a given female group size, non-territorial strategies may therefore be expected to show a greater potential for male polygyny, which translates into heightened competition and stronger selection for male dimorphic traits than in territorial systems.

Male mating strategies can also affect the evolution of signalling systems by determining which male traits are primarily targeted by sexual selection (Andersson 1994). In territorial ungulates, attributes of male territories may substitute for morphological signals as sources of information in intra- and inter-sexual interactions (Owen-Smith 1977; Jarman 1983;Apollonio et al. 1989; Vanpé et al. 2008, 2009). Females in these systems often choose mating partners based on territorial location or availability of resources, rather than on male physical characteristics (e.g. Balmford et al. 1992; Bro-Jørgensen 2002; Bro-Jørgensen & Durant 2003). By using territorial quality in mate selection, females may obtain both direct benefits associated with increased resource availability and indirect genetic benefits because only competitively superior males can acquire high-quality territories (Owen-Smith 1977; Jarman 1983). If territorial properties are widely used as a spatial reference for male quality, it is possible that information encoded in costly morphological signal traits becomes redundant, resulting in reduced dimorphism. Specifically, in the handful of bovids that facultatively adopt lek territoriality, selection may not necessarily favour conspicuous signalling traits in males even if male mating skew is often thought to be pronounced. We therefore hypothesised that the evolution of male ornaments as signals of individual quality may be more pronounced (i) in species forming larger groups and (ii) in non-territorial species, the latter both because of a greater potential for polygyny and because territorial quality may serve as an alternative indicator of individual quality in territorial species(*Sexual Selection hypothesis*).

Differences in the intensity of sexual selection and in mating strategies, however, cannot account for why dimorphic colourations and appendages failed to evolve in many highly polygynous non-territorial bovids. A possibility is that variation in predation costs also influence differences between species in their degree of sexual dimorphism. The antipredator strategy of many social animals, from fish to mammals, rely on uniformity in morphology which makes it easier to confuse predators and prevent them from singling out a target in a group (Landeau & Terborgh 1986; Ruxton & Krause 2002). Because bovid species differ markedly in the degree to which they form mixed-sex groups, variation in sexual dimorphism may depend on the propensity for the sexes to aggregate outside the breeding season. Sexual segregation may be caused by sex-differences in predation risk, driving females to seek safer areas, differences in forage requirements, leading females to prioritise food quality more over quantity, and - especially - differences in activity budgets, with females spending more time feeding due to smaller body size (Ruckstuhl & Neuhaus 2002). We hypothesised that the selective pressure for monomorphism to facilitate predation confusion is strongest in species that spend more time in mixed-sex groups outside the breeding season (*Visual Integration hypothesis*).

Habitat-related differences in antipredator strategy may also affect the intensity of selection for conspicuous morphologies in males. Whereas open habitat species typically rely on safety-in-numbers for protection against predators, species in closed habitats rely more on concealment, which is expected to select for similar morphology in the two sexes (Zuk & Kolluru 1998; Stuart-Fox & Ord 2004; Caro 2005a). Moreover, closed habitats may also interfere with transmission of visual signals (Bradbury & Vehrencamp 2011; Bossu & Near 2015; Price 2017). Previous studies have found that grassland bovids are characterized by more elaborate and sharper pelage markings than the generally uniform or disruptive colourations of forest species, leading to the suggestion that the latter might be less reliant on vision than on other sensory channels (Stoner et al. 2003; Caro & Stankowich 2010). We thus hypothesised that colour and pelage dimorphism is more pronounced in open habitats, where the predation cost of conspicuousness is lower and visual communication is not obstructed by physical barriers(*Habitat hypothesis*).

In this study, we applied the comparative method with phylogenetic control to test the key hypotheses proposed above to explain variation among bovid species in the dimorphism of colouration and pelage appendages, such as manes and beards (Table 1). According to the Sexual Selection hypothesis, we predicted that trait dimorphism increases with the potential for male polygyny, i.e. breeding group size (an indicator of the number of females per mating male; Wade & Shuster 2004), and with male non-territoriality (an indicator of female monopolisability as well as the importance of morphological rather than spatial attributes as targets for sexual selection). According to the Visual Integration hypothesis, we predicted that trait dimorphism would decrease with the propensity to form mixed-sex groups outside the breeding season. Finally, according to the Habitat hypothesis, we predicted that trait dimorphism would increase with the openness of habitats occupied.

**METHODS**

*Indices for sexual dimorphism in colouration and pelage appendages*

Data on sexual dimorphism in colouration and pelage appendages were collected for 110 of the 136 bovid species. The data used in the final analyses relate to the subspecies for which the most detailed information could be obtained. Domesticated subspecies were excluded from the study (e.g. in *Bos frontalis*, *B. grunniens*, and *Capra aegagrus*), because domestication is likely to alter adaptive colourations and morphologies. Sexual dimorphism was scored from photographs in lateral view compiled from Costello (2016) and online resources ([www.arkive.com](http://www.arkive.com); [www.encyclopediaoflife.com](http://www.encyclopediaoflife.com); [www.ultimateungulate.com](http://www.ultimateungulate.com)). Depending on availability, between two (one male, one female) and eight (four males, four females) images were selected for each species. All images used depicted the same subspecies and - for boreal species with different summer and winter coat – represented the same season.

Sexual dimorphism in colouration (CSD) was assessed on eight distinct body regions, following Caro & Stankowich (2010): (i) head; (ii) neck; (iii) flank, shoulder, humerus; (iv) rump, femur; (v) upper front leg (i.e. elbow, ulna); (vi) lower front leg (i.e. podials, metapodials); (vii) upper hind leg (i.e. knee, tibia); and (viii) lower hind leg (i.e. podials, metapodials). Colouration in bovids cannot be considered independently from the presence of contrasting white or black markings, in the form of distinctive stripes, blotches, or spots, against lighter or darker background hair (Stoner et al. 2003; Caro & Stankowich 2010). In order to account for variation in both hair pigmentation and presence/absence of contrast markings, dimorphism for each body region was scored according to a three-point scale: 0 - no difference; 1 - difference in background colour or contrast markings (i.e. presence in one sex only); 2 - difference in both background colour and contrast markings. Background hair colour was compared to a reference of five colour categories (modified from Caro et al. 2017): (i) white (de-pigmented); (ii) phaeomelanin - yellow/red; (iii) eumelanin - brown; (iv) eumelanin – grey; and (v) eumelanin - black (**Figure 1**). Background colour was scored as dimorphic if the same body region was assigned to different categories in males and females. Differences in nuances within the established colour categories (e.g. dark versus light brown) was not evaluated, because variable lighting conditions, hair length, and gland secretions could have affected the perceived intensity (Caro 2005b; Caro et al. 2017). Following Caro et al. (2017), the CSD index was calculated as the sum of the scores for all eight body regions.

Sexual dimorphism in pelage appendages (PASD) was scored as an index based on inter-sexual differences in: (i) frontal hair tuft; (ii) beard or ventral mane; (iii) dorsal mane; (iv) cape (covering both dorsal and ventral parts of the neck); (v) front leg pantaloons; and (vi) hind leg pantaloons (based on Estes 2000). A four-point visual scale was used: 0 - no difference in the pelage appendage between the sexes; 1 – the appendage differs in either size or colour between the sexes; 2 – the appendage differs in both size and colour between the sexes; 3 – the appendage is present in one sex only (always male; Grueter et al. 2015). The PASD index was calculated as the sum of scores for all the pelage appendages present in a given species.

To assess repeatability of the scoring system, CSD and PASD was scored by a second observer blind to the study hypotheses based on two randomly selected pictures (one male and one female) for each study species (n=110). The two sets of scores were highly correlated (CSD: Kendall’s T = 0.978; p < 0.0001; PASD: Kendall’s T = 0.923; p < 0.0001).

*Independent variables*

Data on average breeding group size and male mating strategy was derived from literature sources listed in the Appendix. Male mating strategy was classified as a binary trait: territorial (T), or non-territorial (NT). Lek breeding territoriality is reported from only four bovid species, and always co-exists with resource-defence territoriality (Clutton-Brock et al. 1993); due to this small sample size, lekking species were not considered separately from other territorial species.

Following Estes (1991a) and Roberts (1996), a three-point scale was used to score the tendency for sexual aggregation outside the breeding season: 1 – never forming mixed-sex groups with multiple males (including species in which males are solitary or live in segregated, unisexual groups, only joining female groups in search of mating opportunities); 2 - sometimes forming multi-male mixed-sex groups (including species in which only some males are found in multimale mixed-sex groups, either because not all males join these groups or because associations are temporary, e.g. during migrations); and 3 - generally forming multi-male mixed-sex groups (including species in which the sexes typically aggregate, although some males may temporarily join bachelor groups; Jarman 1983). The scoring was based on available published material (Supplementary Material).

Following Cabrera & Stankowich (2018), habitat openness was scored based on the probability of detecting large mammals in each of the nine different IUCN habitat categories (www.iucnredlist.org): tropical forest (0.1), temperate forest (0.2), wetland (0.3), tropical shrubland (0.5), temperate shrubland (0.6), savannah (0.7), grassland (0.8); rocky areas (0.8), and desert (0.95). The species-specific score for habitat openness was calculated as the mean detection probability across all habitat categories occupied by the species (Cabrera & Stankowich 2018).

*Statistical analyses*

All analyses were conducted in R 3.5.2 (R Development Core Team 2019), with the packages ape (Paradis et al. 2019) and caper (Orme et al. 2018) loaded in the main workspace. Phylogenetic Generalized Least Squares (PGLS) analyses were conducted to identify statistically significant predictors of colour and pelage dimorphism (Freckleton et al. 2002; Mundry 2014). The PGLS algorithm controls for correlations arising due to shared ancestry, which do not reflect independent evolutionary events, by including phylogeny as a variance-covariance matrix of branch lengths in the error structure of an ordinary least squares regression model (Freckleton et al. 2002). Branch lengths were scaled using Pagel’s lambda to estimate maximum likelihood (Freckleton et al. 2002), selecting the best fitting branch transformation using the profile.pgls function in the package caper (Orme et al. 2018). Delta and kappa branch transformations produced qualitatively similar results (not reported here). The phylogenetic tree was obtained from Bininda-Emonds et al. (2007), which incorporates both molecular and morphological data and offers a comprehensive species coverage for bovids. When using the phylogenetic tree in Upham et al. (2019), similar results (not shown) were obtained.

Dimorphism in colouration and pelage appendages (CSD and PASD) were modelled as response variables in separate PGLS models. Explanatory variables initially included in both models were breeding group size, male mating strategy, sexual association pattern, and habitat openness. Normal distribution of residuals was achieved by log(x+1) transformation of CSD, log-transformation of all continuous variables in the CSD models, and square-root-transformation of PASD and all continuous variables in the PASD models. Assumptions of residual normality and heteroscedasticity were tested using the plot.pgls function in the package caper (Orme et al. 2018). The final models were constructed by removing predictors in order of least significance until only significant predictors remained (P<0.05, two-sided; Murtaugh 2014). Coefficient estimates for non-significant predictors refer to the results obtained when adding each of them separately to the final models. Variance Inflation Factors (VIFs) were calculated to assess the effect of multicollinearity between explanatory variables; in all cases, VIFs were ≤ 3 and thus below the accepted threshold of concern at 5-10 (Kutner et al. 2005).

**RESULTS**

The degree of sexual dimorphism in colouration (CSD) and in pelage appendages (PASD) in bovids were both predicted by breeding group size, male mating strategy, and sexual aggregation (CSD: F3,83 = 20.320; λ= 0.066; p = <0.001; R2 = 0.403; PASD: F3,83 = 4.785; λ = 0.952; p = 0.003; R2 = 0.117; **Table 2**; **Table 3**). Both measures of dimorphism were positively correlated with breeding group size and non-territorial mating strategies, as predicted by the Sexual Selection hypothesis (**Figure 2**). Only 4 of 64 territorial species exhibited some form of colour dimorphism, in contrast to 26 of the 46 non-territorial species. Similarly, pelage dimorphism characterized 19 of 46 non-territorial bovids, but only one out of 64 territorial species (the sable antelope *Hippotragus niger*). Supporting the Visual Integration hypothesis, both CSD and PASD were negatively correlated with the level of sexual aggregation (**Table 2**; **Table 3**), with none of the species that consistently aggregate in mixed-sex groups outside the breeding season scored as dimorphic (**Figure 3**). Finally, no support was found for the Habitat hypothesis, as no correlation was found between habitat openness and neither CSD or PASD (**Table 2**; **Table 3**).

**DISCUSSION**

This study provides evidence that sexual dimorphism in colouration and pelage appendages of bovids is promoted by sexual selection on males. Dimorphism in both traits correlated positively with breeding group size and non-territorial rather than territorial mating strategies, two factors affecting the level of male polygyny and hence the intensity of sexual selection. The results also revealed negative correlations between sexual dimorphism in the two traits studied and the tendency to aggregate in mixed-sex groups outside the breeding season, suggesting that a selective pressure for monomorphism in such groups limits the evolution of divergent male morphology.

Male territoriality characterizes nearly two-thirds of the bovid species, and the reduced dimorphism in colouration and pelage appendages found in these species may derive from a smaller potential for polygyny due to difficulty in monopolizing female groups (Gosling 1986; Cassini 2020). A parallel can be drawn to male weaponry, as horns and antlers are generally shorter and less elaborate in territorial ungulates (Bro-Jørgensen 2007; Plard et al. 2011). Furthermore, as mentioned above, sexual selection in territorial systems could target male traits other than morphological signals, including behaviours associated with territorial advertisement, such as scent marking and vocalizations (Owen-Smith 1977). Hence several highly polygynous bovids in which males defend territories, showed negligible differences between the sexes in colouration and pelage appendages (e.g. Alpine chamois (*Rupicapra rupicapra*; Corlatti et al. 2015; and impala; *Aepyceros melampus*; Jarman 1979). The preponderance of colour and pelage dimorphism in non-territorial species, on the other hand, suggests that in these taxa conspicuous and elaborate colour and hair designs have a widespread function as signals in inter- or intrasexual interactions. Since female mate choice may have a more modest role in determining mating success than competition between males (with forced copulations by dominant individuals reported in some non-territorial taxa, e.g. Pelletier et al. 2006; Mainguy et al. 2008; Ihl & Bowyer 2011), dimorphic traits may have been selected through their role in male intrasexual confrontations (Loehr et al. 2008; Bowyer et al. 2020). Several field studies have indeed found support for male colouration and pelage appendages as signals of competitive ability, with trait expression mirroring changes in dominance rank of males in eland (*Tragelaphus oryx*; Bro-Jørgensen & Beeston 2015), Himalayan tahr (*Hemitragus jemlahicus*; Lovari et al. 2015) as well as in other mammalian families, most notably primates (Setchell & Wickings 2005; Bergman et al. 2009).

Our study found morphological dimorphism in bovids to be weaker in species where multiple males and females aggregate outside the breeding season. This was exemplified by the complete absence of CSD and PASD in all species which usually form mixed-sex groups (African buffalo *Syncerus caffer*, muskox *Ovibos moschatus*, addax *Addax nasomaculatus*, and oryx antelopes *Oryx* spp.), despite the fact that their large breeding group sizes and male non-territoriality suggest high potential for polygyny. Conversely, some of highest scores for the CSD and PASD indices were assigned to species that usually segregate into unisexual groups, even though their smaller group sizes point to lower potential for polygyny (e.g. sitatunga *Tragelaphus spekii* and greater kudu *Tragelaphus strepsiceros*). Limited evidence suggests that similar variation may be observed within species: in the mountain bongo (*Tragelaphus eurycerus isaaci*), which is reportedly more sexually segregated than the lowland subspecies (*T. e. eurycerus*), males have a more distinctive colour, sometimes nearly black rather than reddish brown (Hillman 1986; Estes 1991b). The evidence thus suggests that extravagant male morphology might impose significant costs in mixed-sex groups, offsetting the fitness benefits deriving from sexual signalling.

The lack of dimorphic pelage ornaments in taxa where mixed-sex groups predominate agrees with our Visual Integration hypothesis. Although the exact function of female horns is still debated, previous studies suggest that also horns are less dimorphic in species forming mixed-sex groups (Estes 1991b; Roberts 1996), pointing to a general pattern of reduced sexual dimorphism in species where the sexes aggregate. In schooling fish, “confusion effects” generated by multiple, indistinguishable targets decrease the attack success of predators (Penry-Williams et al. 2018; Rystrom et al. 2018), and a selective advantage from reduced predation risk may thus cause male and female phenotypes to converge. Confusion effects are also employed in the antipredator tactics of gregarious ungulates (Geist & Bayer 1988; Caro et al. 2004; Caro 2005a), and this may promote monomorphism of species forming mixed-sex groups. Morphological dimorphism tends to be rare also in species where males join females only for shorter periods of time, but when this happens at times of the year when exposure to predation risk is particularly high, such as during resource shortages or mass movements (Owen-Smith 2008).

An alternative proposition attributes monomorphism in species forming mixed-sex groups to costs that subordinate males incur from sex-specific morphologies because revelation of sexual identity triggers aggression from dominants (Estes 1991a, 2000). Studies of oryx antelope (*Oryx beisa*) have thus linked the observation that subordinate males are not evicted from social groups as long as they do not attempt mating to their visual resemblance of females, which is thought to reduce intrasexual aggression (Walther 1978), presumably through some form of sensory exploitation. However, sexual identity is often detected through olfactory rather than visual cues in ungulates (Gosling & Roberts 2001).

We found no evidence that closed habitats attenuated selection on male visual signals due to reduced transmission efficacy or an antipredator strategy relying on hiding in that no correlation was found between habitat openness and CSD or PASD. Hence some closed habitat species (habitat openness <0.5) were highly dimorphic. e.g. in the bushbuck tribe (Estes 1991b). A general association between sexual monomorphism and dense habitats reported previously (e.g. Estes 2000) may thus be primarily due to smaller breeding group size in closed environments, which restrict opportunities for sexual selection in forest species (Jarman 1974).

A limitation of our study is that it relies on assumptions about the relationship between socioecological factors and male mating skew, which still awaits confirmation by molecular paternity assignment for the vast majority of bovid species in the wild (the few species from which information is available include the bighorn sheep *Ovis canadensis* and the mountain goat *Oreamnos americanus*; Coltman et al. 2002; Festa-Bianchet et al. 2019). From interspecific comparative studies, positive associations between both non-territoriality and female group size on one side and traits used in male combat, such as horn length and body size, on the other indirectly supports reduced potential for polygyny in territorial species and species with smaller female groups (Jarman 1983; Bro-Jørgensen 2007). However, additional genetic studies on individual variance in lifetime reproductive success will be necessary to fully understand the association between different mating strategies and the intensity of sexual selection on males for dimorphic ornaments.

We conclude that interspecific variation in sexual dimorphism in colouration and pelage appendages in bovids reflects underlying differences in the intensity of sexual selection, and in the propensity to form mixed-sex groups outside the breeding season. It is possible that the selective advantage of monomorphism in taxa where the sexes aggregate is a more pervasive evolutionary force than previously acknowledged. For example, the absence of dimorphism in colouration and ornaments in other highly polygynous lineages of mammals, such as equids, kangaroos, and some primates (e.g. savannah baboons *Papio* spp. Jarman 1983; Dixson et al. 2005), may be explained by their tendency to aggregate in mixed-sex groups, and warrants further comparative studies to test the applicability of our visual integration hypothesis at a broader taxonomic scale.

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**TABLES**

**Table 1:** Hypotheses and predictions for the evolution of morphological dimorphism in bovids. Symbols in cells refers to the expected correlation between the degree of colour and pelage dimorphism, and selected independent variables (0 = no correlation; + = positive correlation; - = negative correlation).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| ***Hypotheses*** | ***Predictors of morphological dimorphism*** | | | | |
| Group size | Mating  strategy | Sexual  Aggregation | Habitat  Openness |
| *Sexual selection* | + | + (non-territorial) | 0 | 0 |
| *Visual integration* | 0 | 0 | - | 0 |
| *Habitat* | 0 | 0 | 0 | + |

**Table 2:** PGLS correlations between the degree of colour dimorphism in bovids and various socio-ecological traits. Coefficients estimates and statistical significance are provided for a multivariate model containing all significant predictors (F3,83 = 20.320; λ= 0.066; p = <0.001; R2 = 0.403).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  |  |  | | | |
|  | Coefficient | S.E. | t | | P |
| Group Size (log) | 0.261 | 0.081 | 3.213 | **0.002** | |
| Non-territorial  Mating Strategy | 0.795 | 0.172 | 4.621 | **<0.001** | |
| Sexual Aggregation | -0.772 | 0.161 | -4.791 | **<0.001** | |
| Habitat Openness | -0.386 | 0.382 | -1.012 | 0.314 | |

**Table 3:** PGLS correlations between degree of dimorphism in pelage appendages in bovids and various socio-ecological traits. Coefficients estimates and statistical significance are provided for a multivariate model containing all significant predictors (F3,83 = 4.785; λ = 0.952; p = 0.003; R2 = 0.117).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  |  |  | | |
|  | Coefficient | S.E. | t | P |
| Group Size (log) | 0.076 | 0.037 | 2.064 | **0.042** |
| Non-Territorial  Mating Strategy | 0.517 | 0.232 | 2.232 | **0.028** |
| Sexual Aggregation | -0.326 | 0.117 | -2.793 | **0.006** |
| Habitat Openness | -0.263 | 0.318 | -0.828 | 0.501 |

**FIGURE LEGENDS**

**Figure 1**: Bovid hair colour based on the dominant type of pigment (i.e. no pigment, phaeomelanin, or eumelanin). For each colour category, different gradations are presented as examples of variability in pigment saturation. Bovids were conservatively scored as dimorphic for differences between these categories. This classification was based on examination of high-quality pictures where single hair could be easily detected by the naked eye. (Numbers indicate the species used for reference: 1. Dall’s sheep male (*Ovis dalli*); 2. Banteng female (*Bos javanicus*); 3. Oribi male (*Ourebia ourebi*); 4. Four-horned antelope male (*Tetracerus quadricornis*); 5. Bongo female (*Tragelaphus eurycerus*); 6. Barbary sheep male (*Ammotragus lervia*); 7. European bison female (*Bison bonasus*); 8. Alpine ibex male (*Capra ibex*); 9. Muskox male (*Ovibos moschatus*); 10. Blue sheep female (*Pseudois nayaur*); 11. Lesser kudu male (*Tragelaphus imberbis*); 12. Nilgai male (*Boselaphus tragocamelus*); 13. Asiatic wild water buffalo male (*Bubalus bubalis*); 14. Sable antelope male (*Hippotragus niger*)).

**Figure 2**: Colouration dimorphism in bovid species with territorial (T) and non-territorial (NT) male mating strategies. The points correspond to the single species included in the study, while the violin plot describes the probability distribution of the data.

**Figure 3**: Proportion of species dimorphic in colour (A) and pelage appendages (B) according to sexual aggregation (n = 110).

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**DATA AVAILABILITY STATEMENT**

Analyses reported in this article can be reproduced using the data provided by D'Ammando, G, Franks, DW, Bro-Jorgensen, J. (2022). Living in mixed-sex groups limits sexual dimorphism in colouration and pelage appendages in bovids, Dryad, Dataset. DOI <https://doi.org/10.5061/dryad.w0vt4b8tb>. The dataset compiled by the authors is also available as part of the Supplementary Materials to this manuscript.



Fig 1



Fig 2



Fig 3