

**SEXUAL SELECTION AND SPECIES RECOGNITION PROMOTE COMPLEX MALE COURTSHIP DISPLAYS IN  
UNGULATES**

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## **DATA AVAILABILITY STATEMENT**

Analyses reported in this article can be reproduced using the data provided by D'Ammando, G. (2024). The dataset is also available as part of the Supplementary Materials to this manuscript.

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## ABSTRACT

Identifying the evolutionary drivers of sexual signal complexity is a key challenge in the study of animal communication. Among mammals, male bovids and cervids often perform elaborate gestural displays during courtship, consisting of ritualized movements of various parts of the body but the causes underlying interspecific variation in complexity of such displays remain poorly understood. Here we apply the comparative method to investigate which factors may have either promoted or constrained gestural repertoire size.

We found that sexual selection was a strong predictor of gestural display complexity in male bovids and cervids. Repertoire size was positively correlated with breeding group size, an indicator of the intensity of sexual selection on males. Moreover, repertoires were larger in species adopting non-territorial and lek breeding mating systems than in species adopting resource-defence territoriality, a finding that can be explained by more emphasis on direct benefits than indirect benefits in resource-defence systems, where male mating success may also be less skewed due to difficulty in monopolising mates.

The results also indicate that gestural repertoire size was positively correlated with the number of closely-related species occurring in sympatry. This is consistent with display complexity being selected to facilitate species recognition during courtship and thereby avoid interspecific hybridization. At the same time, repertoire size was negatively associated with male body mass, possibly due to the energetic and mechanical constraints imposed on movements in very large species. By contrast, we found no evidence that the habitat drives selection for complex gestural courtship displays.

## INTRODUCTION

Ever since the early observations of Darwin (1871), Lorenz (e.g. 1953, 1958, 1971), and Tinbergen (e.g. 1954a, 1954b), behavioral scientists have been fascinated by the remarkable diversity in the repertoires of visual, acoustic, and olfactory displays of males during courtship. However, although a vast amount of research has advanced our knowledge of the role of sexual signals in mate choice (e.g. Møller & Pomiamkowski 1993; Ord & Stuart-Fox 2006; Muniz & Machado 2018; Lupold, Simmons & Grueter 2019), we still have only a limited understanding of why the complexity of male courtship often differs considerably among closely related species (Mitoyen, Quigley & Fusani 2019). In this study, we aim to identify the factors that explain the pronounced variation in the repertoire size of gestural courtship displays across two families of ungulates, the Bovidae and the Cervidae

Gestural courtship displays (defined as ritualized movements of the body with no mechanical function) characterize sexual interactions in a variety of taxonomic groups, from fruit flies to birds (e.g. Johnson 2000; Ord, Blumstein & Evans 2002; Fusani et al. 2007; Wong, Candolin & Lindström 2007; Dalziell et al. 2013; Ota, Gahr & Soma 2015; Kozak & Uetz 2016; Ligon et al. 2018; Miles & Fuxjager 2018a, 2018b; Ota 2020; Mukai, Takanashi & Yamawo 2022). However, such displays are rare among mammals in general, likely due to a greater reliance on olfactory communication (Coombes, Stockley & Hurst 2018). An exception is the courtship behavior of male ungulates in which such displays are ubiquitous (Leuthold 1977; Walther 1984). In bovids and cervids, the repertoires of gestural displays vary dramatically from species to species, ranging from simple head postures to virtual 'pantomimes' involving distinctive gaits with coordinated movement of neck, legs and tail (Leuthold 1977; Walther 1984; Schaller 1977, 2000; ; Estes 1991). These two families thus provide an ideal opportunity to investigate how different evolutionary forces might have promoted or constrained the evolution of courtship displays.

According to sexual selection theory, male mating competition favours the evolution of complex sexual signals to advertise good genes or Fisherian attractiveness benefits to females (*Sexual Selection hypothesis*; Darwin 1871; Kirkpatrick 1987; Andersson 1994; Mitoyen et al. 2019; Choi et al. 2022). According to the good genes hypothesis, elaborate gestural courtship displays may reveal motor skills and coordination abilities that are indicators of male genetic quality (Zahavi 1975; Byers, Hebets & Podos 2010; Barske et al. 2011; Fusani et al. 2014; Fuxjager et al. 2015, 2017). As a result, females may have evolved a mate preference for males performing more elaborate courtships as providers of good genes (Kirkpatrick 1987; Andersson 1994; Byers et al. 2010; Barske et al. 2011; Mitoyen et al. 2019; Choi et al. 2022). According to the Fisherian hypothesis, the benefits of the female mating preference accrue solely because genes for complex male displays are heritable and result in higher reproductive success of male offspring (Kirkpatrick, Price & Arnold 1990; Pomiankowski & Ywasa 1993). The strength of such sexual selection for large male repertoire size and associated female preferences is expected to be stronger in species with higher potential for polygyny and thus stronger skew in mating success among reproductive males (Emlen & Oring 1977; Wade & Arnold 1980; Kirkpatrick 1987; Shuster & Wade 2003). The potential for polygyny increases with the number of reproductive females that can be monopolized by a single male (Emlen & Oring 1977; Wade & Arnold 1980; Kirkpatrick 1987; Andersson 1994; Wade & Shuster 2004).

In bovids and cervids, the degree of polygyny is affected by the species-specific mating systems adopted by males to secure copulations (Clutton-Brock 1989, 2017; Bro-Jørgensen 2007). A key distinction is between territorial mating systems, where males defend an area that is attractive to females, and non-territorial mating systems, where males defend access to oestrous females directly, usually depending on the male's status in a dominance hierarchy (Isvaran 2005; Bro-Jørgensen 2007). Territorial systems can be divided into resource territoriality, where females are attracted to territorial resources (usually food) and lek territoriality where females are attracted to tiny resource-less territories clustered on mating arenas ('leks') (Apollonio et al. 1992; McComb & Clutton-Brock 1994; Höglund & Alatalo 1995; Isvaran & Jhala

2000; Bro-Jørgensen 2002; Bro-Jørgensen 2011). The common female preference for central lek males, who tend to be the strongest competitors, can generate a strong skew in male mating success. By contrast, in resource territorial systems, female herds often range over multiple male territories, increasing the likelihood that multiple males end up sharing breeding opportunities within a female herd (Isvaran 2005; Bro-Jørgensen 2007), thereby attenuating the expected strength of sexual selection for elaborate courtship displays (Bro-Jørgensen 2007, 2011). Furthermore, whereas resource availability is key to attracting females in resource defence systems, female choice in lek systems may focus more on male display as an indicator of mate quality (Andersson 1989).

Another possibility is that complex courtship displays have evolved under selection pressures for conspecific mate recognition (*Species Recognition hypothesis*; Ord & Stamps 2009; Bradbury & Vehrencamp 2011; Hill 2015; Mitoyen et al. 2019; Ota 2020; Gray 2022). Given the high costs of hybridization (e.g. low offspring viability, miscarriages), male sexual signals are expected to be under strong selection to diverge into distinctive species-specific forms among species that have the potential to interbreed, as this allows females to reject costly matings with heterospecific partners (Kirkpatrick 1982; Grant & Grant 1997; Hoskin & Higgie 2010; Rosenthal 2013; Scholes & Laman 2018). Such selection for species recognition is expected to lead to more elaborate courtship displays where several closely-related species co-exist in sympatry (Ord, King & Young 2011; Freeberg, Dunbar & Ord 2012; Taylor & Ryan 2013; Hill 2015; Miles, Cheng & Fuxjager 2017; Miles, Goller & Fuxjager 2018; Gray 2022). The fact that hybridization has been widely documented in both bovids and cervids under natural conditions (e.g. Robinson et al. 2015; Vaz Pinto et al. 2016) supports the relevance of species recognition as a potential driver behind larger courtship display repertoires in these lineages.

Finally, the habitat in which a species occur affects the efficacy of transmitting signals in different modalities and habitat may thus also have influenced the size of the repertoire of visual signals used in male courtship displays (*Habitat Drive hypothesis*; Ord, Blumstein & Evans 2002; Candolin 2003; Doucett,

Mennill & Hill 2007; Ord & Stamps 2008; Munoz & Blumstein 2012; Partan 2013, 2017; Fuxjager & Schlinger 2015; Miles & Fuxjager 2018b; McGinley et al. 2023). Open habitats are usually conducive to visual communication, as shown by the revealing colorations and contrasting pelage markings in grassland-dwelling ungulates (Estes 2000; Stoner, Caro & Graham 2003; Caro & Stankowich 2010). On the other hand, dense habitat types with low light and obstruction from vegetation generally impede vision and forest-dwelling species are primarily cryptic in colouration, relying on other sensory channels for socio-sexual signalling (e.g. olfaction; Estes 2000; Stoner et al. 2003; Caro & Stankowich 2010). It is thus possible that open habitats might have exerted a positive selection pressure for the evolution of large repertoires in gestural courtship displays.

Here we apply the comparative method with phylogenetic controls to test the three main evolutionary hypotheses proposed above, i.e. the Sexual Selection, Species Recognition, and Habitat Drive hypotheses. Following previous authors, we used the repertoire size of gestural displays (i.e. the overall number of gestures) as a measure of courtship display complexity (cf. Ord, Blumstein & Evans 2001; Ligon et al. 2018; Miles & Fuxjager 2018b). According to the Sexual Selection hypothesis, we predict that repertoire size is positively correlated with breeding group size, an indicator of the degree of polygyny (Bro-Jørgensen 2007a; Cassini 2020). We also predict larger repertoires in species with non-territorial and lek mating systems than in resource territorial species, where male mating skew is likely to be less pronounced and female mate choice more dependent on direct benefits from resource access than indirect benefits from evaluation of male courtship displays. According to the Species Recognition hypothesis, gestural display complexity is predicted to increase with the number of closely-related species in sympatry (henceforth “degree of sympatry”), which is used as an indicator of hybridization risk (Santana et al. 2012, 2013). According to the Habitat Drive hypothesis, open habitats promote display complexity as they are favourable to the evolution of visual communication systems and a positive correlation between gestural repertoire size and habitat openness is therefore predicted. We furthermore tested for an association

between repertoire size and male body mass, since large body size might impose energetic costs on movements that restrict the ability to perform elaborate gestural displays (Taylor et al. 1982). Hypotheses and their predictions are summarized in Table 1.

## **METHODS**

### *Scoring gestural display complexity as the response variable*

Data on gestural courtship displays of bovids and cervids were collected from peer-reviewed publications and scientific books in English, French, German, Italian, and Spanish (data sources listed in Appendix II). We only considered descriptions that detailed full courtship behavior sequences leading to copulation and excluded sources which only mentioned specific displays without describing an entire courtship sequence. This resulted in a dataset of 73 out of 136 bovid species and 21 out of 47 cervid species. Although we failed to find descriptions of courtship behavior for some species, the dataset is representative of the overall diversity in that it includes at least one species from each genus, except for the poorly studied monospecific genus *Pseudoryx* (Bininda-Emonds et al. 2007). Domesticated species were excluded from the study because human intervention is likely to have modified their behavioral traits.

We used the repertoire size of gestural courtship displays as a quantitative measure of species-specific display complexity (Ord & Blumstein 2002; Dunn & Smaers 2018; Miles & Fuxjager 2018b). Repertoire size was scored as the total number of distinctive body movements performed by males during courtship, henceforth referred to as “display components” (Table 2; Appendix I). Definitions and classification of display components were based on the seminal work of Fritz R. Walther (1974, 1984). Some display components (e.g. ear and horn orientation) are subtle modifiers of other movements (such as head-up and low-stretch postures; Walther 1984; Appendix I) and are not consistently described across species;



these were excluded from the calculations. Also, following Walther (1984), executive behaviors with particular functions were not scored as display components; these include licking, smelling, grooming and naso-genital contact with *Flehmen* response (olfactory investigation of sexual receptivity). A small number of gestural courtship display components involved movements aimed at enhancing the expression of another behaviour, e.g. squatting during urine spraying (Walther 1984; Schaller 2000). We conducted the statistical analyses also without adding them to the final gestural repertoire score, and obtained qualitatively similar results (not shown).

#### *Independent variables*

The explanatory variables included in the study included mating system, which was scored as a categorical variable, and the following continuous variables: breeding group size, degree of sympatry with closely related species, habitat openness, average male body mass (in kg) and research effort (data sources listed in Appendix II). Mating system was classified as either resource defence territoriality, lek territoriality or non-territorial female defence.

Males in a few ungulate species are reported to adopt alternative mating systems in different populations, and sometimes also within the same population (Bro-Jorgensen 2011; Corlatti & Lovari 2023). We assigned these species to the predominant mating system in the population for which the repertoire size had been calculated. For example, male red deer (*Cervus elaphus*) defend resource-based territories in some areas (Carranza, Alvarez & Redondo 1990), but descriptions of courtship displays were only available for populations where non-territorial female defence was the main mating system, and this species was therefore classified as non-territorial. In species that lek, lek and resource-based territoriality usually co-exist in lekking populations; however, mating success is usually skewed in favour of lekking males (Isvaran & Pongshe 2013; Isvaran 2021) and this affects also the mating success of resource defenders (Bro-

Jørgensen & Durant 2003). Even in populations that are not forming classical leks, more successful territories are often clustered and can be considered as lek precursors or “exploded leks” (Bro-Jørgensen 2008). Therefore, species that form leks in at least some populations were classified as lek territorial.

The degree of sympatry with closely-related species was quantified as the number of other species from the same tribe with whom distribution ranges overlapped. Bovid and cervid tribes were defined following Vrba & Schaller (2000) and all corresponded to monophyletic groups in the phylogeny used for the comparative analysis (Bininda-Emonds et al. 2007). We chose to focus on sympatry on the tribal rather than the generic level because interspecific hybridization has been observed also between bovid species not in the same genus (e.g. Jorge, Butler & Benirschke 1976; Douglas et al 2011). Overlap in geographic distribution was assessed visually by plotting distribution polygons for all species within the tribe using QGIS 3.4.3 (QGIS Development Team 2019). Any observable overlap in geographic range was considered as evidence for sympatry (Santana et al. 2013). Polygons of distribution range were obtained from the IUCN Red List database ([www.iucnredlist.org](http://www.iucnredlist.org)). We scored the degree of sympatry based on current distribution ranges because spatial data on historical occurrence is inadequate for the majority of the species included in this study.

Following Stankowich & Campbell (2016), habitat openness was scored as the probability of detection for terrestrial mammals in each of the seven main habitat categories in the IUCN Red List classification scheme ([www.iucnredlist.org](http://www.iucnredlist.org)),: (i) 0.10 tropical rainforest; (ii) 0.20 temperate forest; (iii) 0.30 wetland; (iv) 0.50 shrubland; (v) 0.70 grassland (tropical and temperate); (vi) 0.80 rocky areas; and (vii) 0.95 deserts. Scores were assigned only to habitats reported as “suitable”, and the overall species-specific habitat openness score was calculated as the average detection probability across all habitat categories.

Because gestural repertoire sizes calculated from literature may conceivably be biased towards more well-studied species, we controlled for research effort using the number of publications mentioning the

Linnean binomial name of each species in the ISI Web of Knowledge ([www.webofknowledge.com](http://www.webofknowledge.com)) between 1960 and 2018 (as no accounts of courtship behavior have been published since then). The search was restricted to the categories likely to include behavioral accounts, i.e. (i) Zoology; (ii) Behavioral Sciences; (iii) Ecology; and (iv) Evolutionary Biology.

### *Statistical analyses*

All analyses were conducted in R v. 3.5.2 (R Development Core Team 2019) with the packages *ape* and *caper* loaded in the workspace (Orme et al. 2018; Paradis et al. 2019). We used phylogenetic least squares (PGLS) regressions to identify statistically significant predictors of gestural repertoire size. The PGLS methods accounts for autocorrelations in the dataset generated by shared ancestry by including phylogeny as a variance-covariance matrix in the error structure of a least squares regression models (Harvey & Pagel 1991; Housworth, Martins & Lynch 2004). The phylogeny for this study was derived from the ultrametric molecular tree of mammals in Bininda-Emonds et al (2007) and pruned to include only the species included in the dataset. This phylogeny was selected as it offers the best species coverage for both cervids and bovids, incorporating both molecular and morphological data. Branch lengths were scaled with Pagel's lambda set to maximum likelihood (Freckleton, Harvey & Pagel 2002) as this transformation best fitted the dataset after graphical comparisons with delta and kappa estimators (using the `profile.pgls` function in *caper*; Orme et al. 2018).

Gestural repertoire size was entered as the response variable in PGLS models together with the following explanatory variables: breeding group size, degree of sympatry, habitat openness, male body mass, research effort (all continuous) and mating system (categorical). Male body mass and breeding group size were log-transformed (using the natural logarithm) prior to analyses in order to meet the assumptions of residual normality and homoscedasticity (graphically checked using the `plot.pgls` function in the package

capere; Orme et al. 2018). Model simplification was conducted by progressive removal of non-significant predictors in order of least significance ( $p \leq 0.05$ ; Murthaugh 2014). The results presented here pertain to the final model including only significant predictors; statistics for non-significant predictors were obtained by separately adding each of them separately to the final model. Variance inflation factors (VIFs) were calculated to estimate multicollinearity between independent variables. All VIFs were  $\leq 2.04$ , and thus well below the commonly accepted threshold of concern (5-10; McClave & Sincich 2003). We moreover tested for correlations between gestural repertoire size and each of the predictors separately in bivariate models.

Finally, to further explore the Sexual Selection hypotheses, we also tested for sexual size dimorphism (SSD) (measured as male body mass:female body mass) as a predictor of courtship display repertoire size. SSD is commonly used as an indicator of sexual selection on males (e.g. Cassini 2020), however correlation between SSD and both breeding group size and male mating strategy prevented us from including all three variables in the same analysis due to multicollinearity issues. Since SSD, unlike the two other variables, is primarily a consequence rather than a cause of sexual selection, we report the results of the effect of SSD in Appendix III only.

## RESULTS

The repertoire size of gestural courtship displays in male bovids and cervids was significantly predicted by breeding group size, male mating strategy, degree of sympatry and male body mass in multiple regression analysis ( $F_{5,88} = 9.336$ ;  $\lambda = 0.41$ ;  $p < 0.001$ ;  $R^2 = 0.35$ ; Table 3). As predicted by the Sexual Selection hypothesis, repertoire size correlated positively with breeding group size (in both bivariate and multiple regression models; Table 3; Figure 1) and it was significantly larger both in species with non-territorial and lek mating systems than in species with resource-based territoriality (again in both bivariate and multiple

regression models; Table 3 and 4; Figure 2). As predicted by the Species Recognition hypothesis, gestural repertoire size was moreover positively associated with the degree of sympatry with other species from the same tribe (Table 3; Figure 3). Male body mass was negatively related to gestural repertoire size: larger species presented less elaborate displays than smaller species (Table 3; Figure 4), consistent with the hypothesis of size-based constraints on the complexity of gestural displays. Both the degree of sympatry and male body mass only emerged as significant predictors of repertoire size in multiple regression models, which accounted for the effects of group size and mating system (Table 4). No effects of either habitat openness or research effort could be detected (Table 3; Table 4).

## DISCUSSION

We found that the most significant predictors of the gestural courtship complexity in male bovids and cervids were the drivers of sexual selection. Specifically, the repertoire size of gestural courtship displays was positively correlated with breeding group size and with both non-territorial and lek mating systems, all expected to intensify sexual selection on males. Further support for the Sexual Selection hypothesis was provided by a positive correlation between repertoire size and sexual size dimorphism (Appendix III). The comparative analyses simultaneously pointed to species recognition as a driver of complexity in gestural courtships in that bovids and cervids living in sympatry with multiple closely-related heterospecifics also had larger gestural repertoires. Finally, larger species had smaller gestural repertoires, possibly due to constraints imposed by body size on displays involving motion.

The majority of bovids and cervids adopting resource-based territoriality had very small gestural repertoires (< 5), likely due to the reduced potential for polygyny associated within this mating system (Bro-Jørgensen 2007; Plard, Bonenfant & Gaillard 2011; Bowyer et al. 2020). On the other hand, the large gestural repertoires exhibited by several species with dominance-mediated access to reproduction (e.g.

reindeer *Rangifer tarandus*, Himalayan tahr *Hemitragus jemlahicus*, wild goats *Capra* spp.) suggest that courtship display complexity represents a key target of sexual selection in non-territorial systems (Owen-Smith 1977; Jarman 1983). Although direct female defence by males in non-territorial mating systems may impose restrictions on the expression of female preferences (Bro-Jørgensen 2007, 2011; Clutton-Brock & McAuliffe 2009), evidence exists that also females in dominance-based societies actively avoid mating with subordinate males (e.g. bighorn sheep *Ovis canadensis*; Geist 1971; Hogg 1987; American bison *Bison bison* Berger & Cunningham 1994; Bowyer et al. 2007; moose *Alces alces* Bowyer et al. 2011). The evolutionary interests of females and dominant males may thus to some extent coincide in non-territorial systems and the elaborate courtship displays of the males, together with their greater ornamentation (D'Ammando, Franks & Bro-Jørgensen 2022), might thus influence female mate choice by providing cues to male rank (Jarman 1983; Clutton-Brock, Albon & Guinness 1986; Pelletier & Festa-Bianchet 2006). By contrast, female mate choice in resource defending species may rather be based on the quality of the resources on territories (Bro-Jørgensen 2011; Bowyer et al. 2020).

Lek-breeding bovids and cervids also present larger gestural repertoires than species defending resource-based territories. This may again be because female mating patterns are shaped primarily by resource availability on male territories in resource territorial species (Balmford, Rosser & Albon 1992) whereas assessment of male quality as sires is more important in lek systems (Balmford, Albon & Blakeman 1992). The finding is also consistent with stronger selection for courtship complexity in lekking species due to the larger skew in male mating success (Höglund & Alatalo 1995). However, previous studies have found mating preferences of female ungulates on leks to be largely determined by territory location (e.g. central versus peripheral; Bro-Jørgensen & Durant 2003; Bro-Jørgensen 2011), and there is thus scope for future studies to look at the interactions between territorial, phenotypic, and behavioral traits in determining male mating success on leks.

We note that some noise in the data may be explained by the presence of alternative mating tactics within populations (Isvaran 2005; Bowyer et al. 2020; Corlatti & Lovari 2023). Examples include sneaky matings close to territory boundaries and coursing tactics in non-territorial systems; these tactics are generally adopted by immature individuals and not preceded by courtship (Hogg & Forbes 1997; Willis et al. 2012). As more quantitative information on the prevalence of such alternative mating tactics become available, the analyses presented in this study may be refined.

The effects of the degree of sympatry on gestural repertoire size was significant only after controlling for breeding group size and male mating strategy. Courtship displays in bovids and cervids tend to be more complex in species overlapping in distribution with several closely-related heterospecific species. For example, the wild goat (*Capra aegagrus*) and markhor (*Capra falconeri*) of the species-rich Himalayan region (Schaller 1977), exhibited larger gestural repertoires than the Alpine ibex (*Capra ibex*), which does not occur in sympatry with other members of the same tribe (despite equal or smaller breeding group size in the former). Similar patterns were observed within the duikers of the genus *Cephalophus*, generally characterized by breeding pairs. Co-existence with closely related species thus appears to promote further elaboration of sexually-selected gestural courtship displays by addition of more display components, supporting the hypothesis that complexity in courtship displays has evolved as a pre-copulatory barrier against hybridization. Behavioral mechanisms of reproductive isolation are of crucial importance to bovids and cervids, whose inability to identify conspecifics as mating partners innately is demonstrated by the development of mating preferences for other species in cross-fostering experiments (Walther 1991; Kendrick et al. 2001). Larger gestural repertoires might offer a greater opportunity for display divergence among closely-related species and facilitate recognition of conspecifics as mating partners during courtship (Johnson 2000; Wagner, Pavlicev & Cheverud 2007; Freeberg et al. 2012; Gray 2022). In passerine birds, gestural display complexity has indeed been connected to geographical patterns of speciation (Miles et al. 2017). Also worth noting is that pairing trials between species with small gestural

repertoires have resulted in hybridization: female red brocket deer (*Mazama* spp.; repertoire size  $\leq 3$ ) readily accept copulations with heterospecific males (Carranza, Roldan & Duarte 2018). Now it is necessary to test whether the opposite is also true, that higher levels of courtship display complexity can prevent interspecific mating.

A limitation in our test of the Species Recognition hypothesis is that we were restricted to using current rather than historical distributions of the study species. The exact evolutionary context under which larger display repertoires have evolved – including the sequence of events - thus remains largely unknown. As new paleontological and biogeographical data accumulate, we can further test how suited current distributions are to estimate historical distributions during the evolution of species-specific courtship behaviour (which may occur partly after speciation). We also note that olfactory communication, which was not the focus of our study, could be important in avoiding heterospecifics as mating partners (Coombes et al. 2018). However, lack of data for the vast majority of the study species prevents quantitative tests of this possibility at present. Despite the potential sources of noise in our analysis, we still found significantly larger repertoire sizes in species living in areas with a larger number of more closely related species. We are unaware of any hypothesis more plausible than the Species Recognition hypothesis to explain this finding at present.

The negative correlation between repertoire size and male body mass needs further exploration. Movements require higher energetic expenditures in large-bodied mammals (Blanckenhorn 2000) and could thus impose costs selecting against elaboration of gestural displays. Moreover, large ungulates also frequently possess exaggerated cranial weapons and neck appendages (Bro-Jørgensen 2016), which may reduce agility during courtship (cf. the very small repertoires of bovines and moose *Alces alces*, all characterized by large horns/antlers and dewlaps; Estes 1991). We therefore suggest that physiological and morphological disadvantages might both limit the repertoire of gestural courtship displays in large species.



In summary, our study provides evidence from interspecific comparisons that the complexity of gestural courtship displays in male bovids and cervids, as expressed in repertoire size, is likely promoted by both sexual selection and the need for species recognition (as reflected in the degree of range overlap with closely related species). Specifically, lekking species and species with non-territorial mating systems have larger repertoires than resource-territorial mating systems, and males also have larger repertoires where females form larger breeding groups. We hope that future studies will uncover the generality of these patterns in other taxa, especially the Species Recognition hypothesis warrants further attention. Also, the present study focused on explaining complexity in courtship behaviour in a single modality, and a fruitful area for future studies may also be how complexity in sexual signals in different modalities interact with each other (Bro-Jorgensen 2010).

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## TABLES

**Table 1:** Hypotheses on the evolution of complex gestural courtship displays in male bovids and cervids.

Symbols in cells refer to the predicted correlation between repertoire size of gestural courtship displays and independent variables (+ = positive correlation; - = negative correlation; 0 = no correlation).

Hypothesis	Group size	Mating system	Degree of sympatry	Habitat openness	Male body mass
<i>Sexual selection</i>	+	+ Lekking + Non-territorial	0	0	0
<i>Species recognition</i>	0	0	+	0	0
<i>Habitat drive</i>	0	0	0	+	0
<i>Body size constraints</i>	0	0	0	0	-

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**Table 2:** Components of gestural courtship displays in bovids and cervids. in relation to the body parts involved (see Appendix I for further details).

<b>Gestural display component</b>	<b>Body parts</b>
<i>Low-stretch</i>	Head and neck
<i>Head-down</i>	Head and neck
<i>Head-turn</i>	Head and neck
<i>Nose-up</i>	Head and neck
<i>Head twisting</i>	Head and neck
<i>Swan neck</i>	Head and neck
<i>Tongue flicking</i>	Head and neck
<i>Empty biting</i>	Head and neck
<i>Foreleg kick</i>	Front legs
<i>Kneeling/squatting</i>	Front legs
<i>Flank stroke</i>	Front legs
<i>Pawing</i>	Front legs
<i>Hunching</i>	Hind legs
<i>Cavorting</i>	Hind legs
<i>Bipedalism</i>	Front and hind legs
<i>High-lift gait</i>	Front and hind legs
<i>Crouching</i>	Front and hind legs
<i>Tail erection</i>	Tail
<i>Neck fighting</i>	Other display elements
<i>Chin-resting</i>	Other display elements
<i>Erectile display</i>	Other display elements
<i>Urine spraying</i>	Other display elements

**Table 3:** PGLS correlations between repertoire size of gestural courtship displays and socio-ecological traits in male bovids and cervids. Statistics refer to the inclusion of variables in the final multiple regression model with significant predictors only; resource defence territoriality is the reference mating system (B=0).

	B	S.E.	t	P
Lek mating system (categorical)	3.018	0.759	3.977	<0.001
Non-territorial mating system (categorical)	2.174	0.531	4.097	<0.001
Breeding group size (ln)	0.696	0.217	3.214	0.002
Male body mass (ln)	-0.578	0.221	-2.615	0.011
Degree of sympatry	0.186	0.068	2.740	0.007
Habitat openness	-0.049	1.167	-0.042	0.967
Research effort	0.001	0.001	1.036	0.303

**Table 4:** PGLS correlations between repertoire size of gestural courtship displays and socio-ecological traits in male bovids and cervids. Statistics refer to bivariate regression models with one explanatory only; resource defence territoriality is the reference mating system (B=0).

	B	S.E.	t	P
Lek mating system (categorical)	2.851	0.792	3.599	0.001
Non-territorial mating system (categorical)	1.919	0.494	3.888	<0.001
Breeding group size (ln)	0.634	0.205	3.100	0.003
Male body mass (ln)	0.141	0.224	0.632	0.529
Degree of sympatry	0.099	0.078	1.273	0.206
Habitat openness	1.441	1.154	1.249	0.215
Research effort	0.001	0.001	1.415	0.160

## FIGURE LEGENDS

**Figure 1:** Repertoire size of gestural courtship displays in male bovids and cervids in relation to breeding group size (log-transformed). The regression line was obtained from multiple regression using the PGLS algorithm and points indicate residuals in repertoire size from the final model.

**Figure 2:** Repertoire size of gestural courtship displays in male bovids and cervids according to mating system. Points correspond to individual species, and the violin plot describes the probability distribution of the data.

**Figure 3:** Repertoire size of gestural courtship displays in male bovids and cervids in relation to number of sympatric species from the same tribe. The regression line was obtained from multiple regression using the PGLS algorithm and points indicate residuals in repertoire size from the final model.

**Figure 4:** Repertoire size of gestural courtship displays in male bovids and cervids in relation to average male body mass (log-transformed). The regression line was obtained from multiple regression using the PGLS algorithm and points indicate residuals in repertoire size from the final model.

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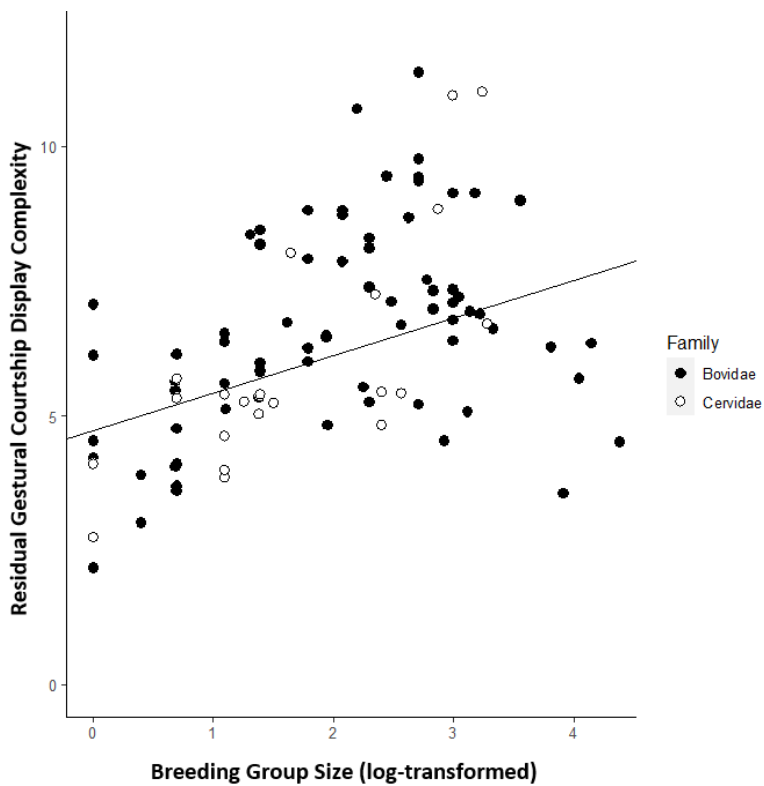
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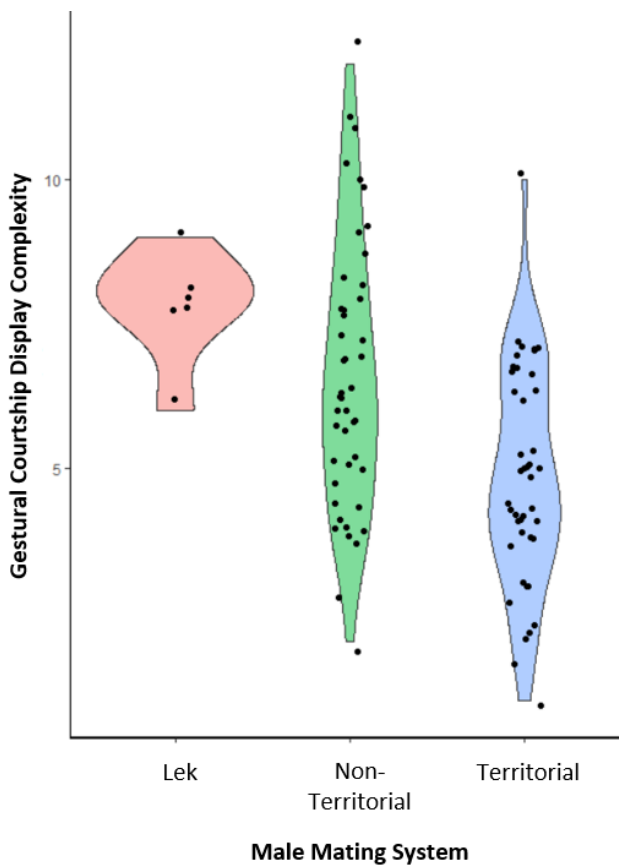
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Figure 1



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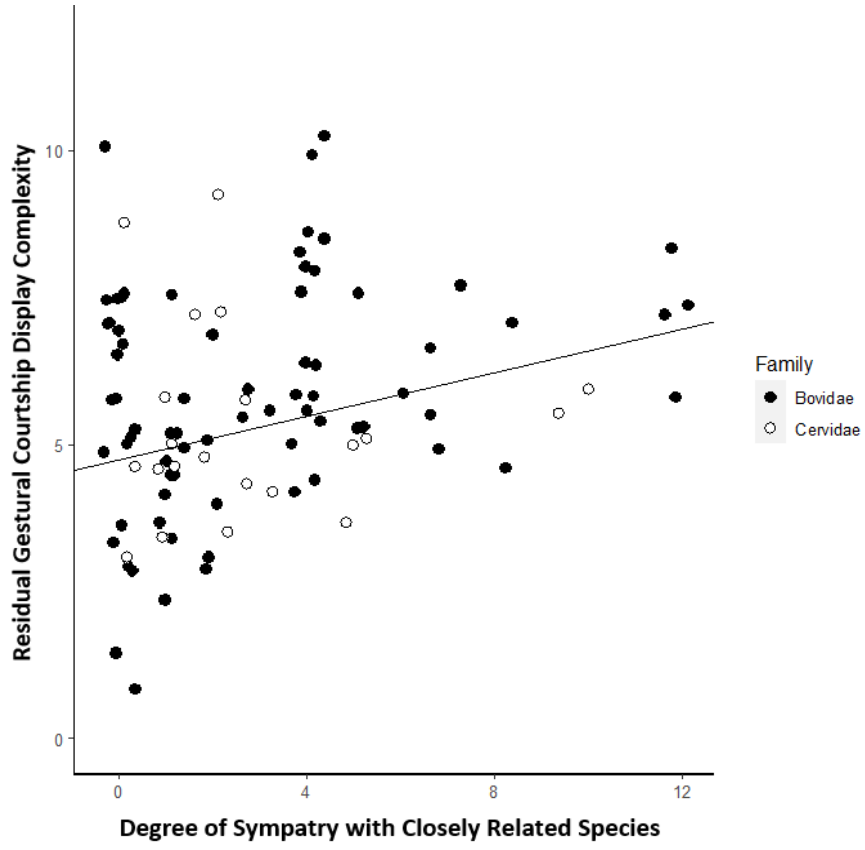
Figure 2



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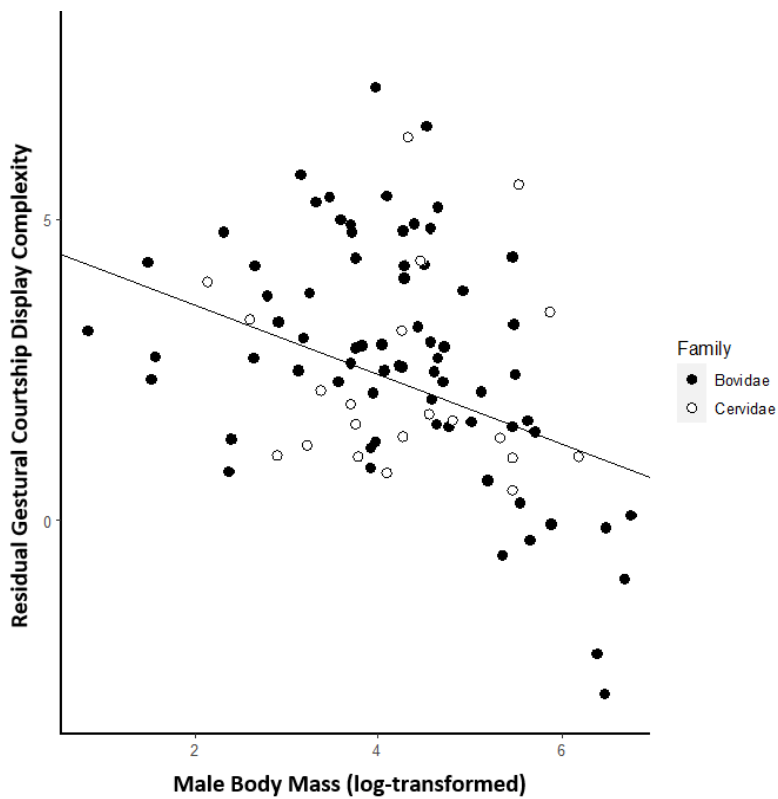
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Figure 3



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Figure 4



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