Journal of Zoology

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Correlation patterns in roe deer cranium: sexual dimorphism across different habitats

Journal:	*Journal of Zoology*
Manuscript ID	JZO-02-16-OM-029.R1
Manuscript Type:	Original Manuscript
Date Submitted by the Author:	n/a
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Keywords:	Capreolus capreolus, cranial integration, social organization, habitat selection

Abstract

Complex evolutionary interactions can cause differential responses of males and females to environmental factors which result in variations of the degree of sexual dimorphism across different habitats. Roe deer (*Capreolus capreolus*) is an excellent model species for analyzing sexual dimorphism in the context of habitat variability as the most widespread ungulate species in Europe. The impact of three different habitat types (closed, intermediate and open) on the level of cranial integration in roe deer and patterns between sexes was tested by analyzing 761 adult craniums from 11 roe deer populations in Serbia. Our results confirmed higher level of integration and more pronounced sexual dimorphism in closed habitats in comparison to open habitats. Males also showed different patterns of integration across habitats than females. The general consistency of results across different tests suggests that patterns of integration between sex and habitat groups tend to be different for males and females from different habitat types. When faced with strong selective pressures, patterns of correlations among skeletal elements can evolve even within a species as an indirect influence of social organization through habitat and sexual selection. We propose that cranial integration in roe deer evolved according to the predictions of the adaptive model of phenotypic differentiation within a taxon in closed habitats channeled by stabilizing selection. The different patterns of cranial integration between sexes after successful colonization of intermediate and open habitats can be explained by a change in overall selective pressures to disruptive/directional selection, thus breaking up observed patterns of integration, since they are treated as a constraint in changed circumstances.

Keywords: *Capreolus capreolus*, cranial integration, social organization, habitat selection

Introduction

Patterns of morphological variation in many animal species are undoubtedly linked to environmental variation, and habitat use is an important factor driving the evolution of phenotypic diversity. However, ecomorphological variation can be under strong influence of sex as many functional and morphological traits used to accomplish ecological tasks are also relevant for social functions. That is a reason why that both natural and sexual selection are frequently involved in determining how morphological traits vary across different environments (Cox, 2007). These complex evolutionary interactions can cause different response of males and females to environmental factors which results in variations of the degree of sexual dimorphism across different habitats (Stuart-Fox & Moussalli, 2007; Kaliontzopoulou, Carretero & Adams, 2015). This evolutionary influence then translates into morphological variation across habitats through biomechanical links between morphology and performance (Irschick *et al.*, 2008).

In cervids, sexual differences result from differing reproductive strategies, differential predation risks, activity budgets and social organization (Ruckstuhl & Neuhaus, 2005). The reproductive success of males depends on their physical condition with a consequence that they select higher-quality habitat patches regardless of the risk of predation. The success of females is correlated with the survival of their offspring, which are more vulnerable to predation than the adults, with females selecting habitats with more protective covering. Social organization can be predicted by habitat structure (e.g. Kurt, 1991; Strandgaard, 1972; Ellenberg, 1978; Dzieciolowski, 1979), and differences in social organization are reflected by breeding strategies. In habitats where resources are abundant, permanently available and more or less equally distributed, adult male territoriality increases personal fitness, and only territorial males rut and mate, while females and their offspring live in family clans, their ranges overlapping several of

the males'. In contrast, in habitats with seasonally changing resource availability, patterns of male territories are less stable or even absent and family bonds are hardly maintained, so mating systems are considered promiscuous (Bresinski, 1982; Stüwe & Hendrichs, 1984).

Roe deer (*Capreolus capreolus* L.) is the most widespread ungulate species in Europe which shows a high level of flexibility and success in colonizing different habitats. Adaptation to wide variety of environments and habitats influenced the social organization and spatial behavior of roe deer populations (Hewison *et al.*, 1998), where availability and configuration of woodland habitats have an important role. In habitats with high percentages of woodland where resources are predictable roe deer forms small social units (<5 individuals). Males and females pursue different lifestyles, except during the mating period. Females live in family clans, and males are solitary and maintain territories. Open plain populations (with low percent of woodland) form permanent social groups of up to 70 individuals with males and females spend much of the year together and experience similar selection pressures. In general, differences in social and spatial behavior of roe deer populations in open/field habitats in comparison to closed/woodland habitats have led to a long-standing distinction between "forest" and "field" roe deer (Pielowski, 1983; Kałuziński, 1974; Fruziński, Kałuziński & Baksalary, 1982). However, this distinction has not been unequivocally verified by current research (Hartl & Reimoser, 1988; Olano-Marin *et al.* 2014).

This distinction may open questions that involve relationships between morphology and habitat use, where habitat use reflects differences in social organization. Phenotypic integration and modularity are central to our understanding of how complex phenotypic traits evolve. Modularity of morphological structures is a widespread attribute of biological systems that explains both the integration within and the autonomy among organismal features (Goswami, 2007). Whereas integration maintains certain relationships that are necessary for proper function

and high performance of structures (Cheverud, 1996), autonomy among parts allows for components to change independently. This can facilitate adaptive responses to conflicting selective pressures, the evolution of complex phenotypes, morphological, ecological and taxonomic diversity (e.g. Williams & Nagy, 2001; Yang, 2001; Tokita, Kiyoshi & Armstrong, 2007; Esteve-Altava *et al.*, 2013). The vertebrate skull is a classic example in which the evolution of independent modules has allowed for tremendous diversity in form and function. The primary roles of the skull are feeding, housing sensory organs and encasing the brain. Regarding roe deer, the main difference between sexes is the presence of antlers in males, which contribute strongly to sexual dimorphism and influence the integration and visualization of the cranial vault as a module in males. On the other hand, feeding and running adaptations also may have additional roles in integration of roe deer skull.

The relationship of underlying phenotypic variability and the observed phenotypic variation in the cranium is determined through a complex interplay of ontogeny and natural selection acting at different levels in order to maintain structure, functional demands and evolvability in ever-changing, variable environment (Hallgrimsson *et al.*, 2007). Developmental processes constrain cranial variation subject to natural selection which in turn biases developmental processes available for subsequent generations (Willmore, Young & Richtsmeier, 2007). Pattern of interactions among cranial constituent elements reflects both common ontogeny and function in the adult cranium. Morphological integration (Olson & Miller, 1958) and modularity (Wagner, 1996) are consequences of these interactions. The modular nature of the cranium poses limitations on possible mechanisms of population differentiation and life history strategies (Zelditch & Moscarella, 2004) because individual characters cannot vary independently. Cranial correlation/covariance structure similarities and differences between studied populations can also reflect possible differential effect of natural selection gradients.

In this paper, we report the results of a study specifically aimed at investigating habitat/sex differences at the single-species level and to characterize the phenotypic structure of the roe deer cranium. We attempted to provide explanations on whether these differences have a developmental or evolutionary basis in addition to environmental ones. Therefore, we raised two research questions: (1) Is there an impact of habitat type on the level of skull integration in roe deer? (2) Is there a difference in skull integration between sexes in relation to different habitat types in roe deer? Our working hypotheses were:

(1) We expected higher levels of integration in closed habitats due to stable and predictable (more homogenous) environments in comparison to open habitats which are characterized by unstable, fluctuating (more heterogeneous) environments especially in terms of food and shelter availability and higher predation stress. In predictable homogenous environments a higher level of integration is expected, integration serves as an adaptation and there is consequently selection acting to maintain or strengthen the correlations. On the contrary, in heterogeneous environments integration could be considered as a constraint with selection working against it.

(2) We expected more pronounced differences in skull integration between males and females in closed habitats, in comparison to open habitats, mainly due to stronger existing sexual segregation patterns, which we interpret as being the underlying cause of these differences. Segregation leads to different home range sizes (of sexes, among seasons etc.) which may lead to different diets of territorial males and females, different perceptions of dangers within the territory, different costs of maintaining territories among males – “the bigger the better effect”. This can be translated into sexual differences in total skull integration and differences among regions related to food acquisition (oral regions), sensory organs (orbital and nasal regions) and antler size in males (vault and basal regions of the skull).

Material and Methods

Sample

We investigated the variation in 18 cranial characters of 761 adult roe deer males and females (age >2 years) by examining the skull. Approximately half the sample, 348 of the skulls, was from the private collection of Svetlana Milošević-Zlatanović, while the remainder was obtained from private trophy collections and hunting management authorities. Age was estimated by tooth wear (height of molar, Aitken, 1975; Hewison *et al.*, 1999) and the weight of eye-lens method (Gačić *et al.*, 2007), with subsidiary criteria being the ossification stage of the *synchondrosis spheno-occipitalis* (Meijaard & Groves, 2004), strength of pedicles (males only), and architectonics of the antlers and cranium (Hrabě & Koubek, 1987).

The skulls were collected from 1990 to 1995 at 11 localities throughout the Republic of Serbia (Fig. 1, Table 1), along a transect spanning 400–450 km from northeast (NE) to southwest (SW). The localities and sampling have been described in detail by Milošević-Zlatanović, Crnobrnja-Isailović & Stamenković (2005). Samples from different localities were assigned to one of three habitat categories according to data from Milošević-Zlatanović *et al.* (2005) based on the percentage of major habitat and foraging types: open habitats included localities with predominantly agricultural landscapes, meadows and grasslands (> 80 %), closed habitats included localities situated in temperate and montane forests (> 30 % continuous forest); intermediary habitats included the remaining localities with larger proportions of forested areas in comparison to open habitats and which are frequently present as complex, patchy and heterogenous ecotonal habitats and wood/field ecotones as basic foraging areas. Sample sizes of

each population (locality) and habitat by sex, with subsamples for each habitat/sex group are presented in Table 1.

Cranial measurements were recorded with a dial calliper to the nearest 0.01mm. The cranial characters (Fig. 2) were chosen to capture most of the cranial morphology, with emphasis on functionally or developmentally related parts (Milošević-Zlatanović, Savić & Bradvarović, 1994; Milošević-Zlatanović, 2001).

Analyses

Prior to any analyses collected data were checked for normality with Kolmogorov-Smirnov test and outlier analysis (Grubbs test). Data were first log transformed, to account for scaling of variances with the mean, and then standardized to zero mean within each of the habitat/sex group before pooling (Bookstein *et al.*, 1985; Merila & Bjorlund, 1999). A preliminary 2-way (habitat/sex) MANOVA was performed to analyze the effect of habitat and sex on cranial characters. As the results showed significance of both the main effects and their interaction, further analyses were conducted on habitat/sex groups as objects of the analyses.

Matrix comparisons, Repeatability, and Adjusted Matrix Correlations

To avoid confounding the correlations by mixing samples with different means, we standardized all cranial characters to zero mean. All measurements were ln-transformed and to enhance the normality of distributions, Merila & Bjorlund, 1999).

Correlation matrices of six analyzed groups (males and females from three habitat types) were compared using matrix correlation. We applied the Mantel test (1000 replicates) to explore

whether the matrices were more similar to each other or to randomly generated matrices. Two matrices were considered significantly similar when the observed matrix correlation exceeded 95% of the randomly generated correlations.

As noted by Cheverud (1996), maximum observed correlations between two matrices may not be equal to 1, due to differences in sample sizes. To estimate the impact of sampling error, the original dataset was resampled with replacement and the correlation matrices were re-estimated 1000 times. These matrices were compared with the original observed matrix using the mean matrix correlation as an estimate of matrix repeatability *t*. Repeatability was then used to estimate the theoretical maximum matrix correlation ($R_{max} = (t_a \times t_b)^{1/2}$, where t_a and t_b are the repeatabilities of the matrices being compared. The maximum matrix correlation was then used to obtain an adjusted matrix correlation ($R_{adj} = R_{obs}/R_{max}$) between the two matrices (Cheverud, 1996).

Morphological integrations

Cranial modularity was assessed according to hypotheses based on functional or developmental relationships among cranial characters. Specifically our hypotheses were based on models which were derived from tissue origin (Zelditch, 1988) and modified functional matrix models of modularity in the mammalian cranium (Cheverud, 1982; Goswami, 2006; Willmore, Leamy & Hallgrímsson, 2006). The entire suite of cranial characters was divided into subsets reflecting the predominant developmental origin of cranial bones, either from neural crest cells (NC) or paraxial mesoderm (PM). Five groups of characters were further constructed according to shared functions of the respective bones in the adult cranium and were used as cranial modules in our analyses: Base, Oral, Nasal, Temporal, and Vault. Further, all analyses

were performed considering a two-module organization of the cranium: the Face module consisting of the oral and nasal modules and a Cranial module consisting of all the other modules (base, temporal and vault). As a final hypothesis we used an overall connectivity matrix (total correlation), summing all five subregions to test for integration in the cranium as a whole (Fig. 3).

Magnitude of integration

The overall magnitude of integration was estimated by the index of integration, which was calculated as the variance of eigenvalues (VE) for the entire skull, following the method by Wagner (1984, 1990). Higher correlation between traits and related higher values of VE, corresponds to smaller subspace in the overall multivariate phenotypic space. Lower correlation between traits corresponds to lower VE indicates a more even distribution of variance. Phenotypic covariation among traits, used to estimate integration, reflects the underlying genetic covariance matrix, which has been shown in several studies (Cheverud, 1988; Roff, 1995; Ackermann & Cheverud, 2000; Porto et al., 2009).

Owing to the uneven sample sizes between males and females from each habitat types, the estimates of variation and covariation may be unreliable (Cheverud, Wagner & Dow, 1989), so we applied corrections for uneven sample sizes: E(V(l)) = (M-1)/N, where *M* is the number of traits, N is the sample size, and E(V(l)) is the expected VE (Wagner, 1984; Cheverud *et al.*, 1989). We use this correction to obtain a corrected observed variance of the eigenvalues for each sample as well as correcting the bootstrapped values for tests of significance.

The significance of the differences between species VE was calculated by resampling the data with replacement and recomputing the VE (Manly, 2006). We used the ratio of the VE of

the two compared groups as a test statistic. The P-value corresponds to the number of times VE in the group with smaller VE exceeds the bootstrapped values in the group with larger VE, divided by the number of iterations (1000) (Rolian, 2009).

Patterns of integration

Several methods were used to investigate patterns of correlation (i.e. integration).

The correlation matrices for each group were statistically compared with connectivity matrices constructed for each developmental/functional integration hypothesis. Connectivity matrices were constructed by placing a one where two traits are hypothesized to be integrated and a zero where integration was not hypothesized (Marroig & Cheverud, 2001). Correlation of the group matrix to the connectivity matrices was measured using a matrix correlation, which is a measure of the structural similarity of two matrices. Significance was assessed by a Mantel's test (Mantel, 1967; Marroig & Cheverud, 2001) where the observed matrix correlation is compared to an empirically derived distribution of matrix correlations. This matrix distribution is produced by randomly permuting the rows and columns of the reference matrices and then computing their matrix correlation. This process is repeated 1.000 times and if the observed correlation exceeds 95% of the random correlations, then the matrices are considered to be significantly similar at P=0.05 (Manly, 2006).

Additionally, we calculated the average within-module correlation and the average correlation among all other traits not in the module using the data from the phenotypic correlation matrices. This ratio give us an idea of how much a given module is visible against the background variation in the rest of correlations and can be thought as a modularity ratio (see Porto *et al.*, 2009).

To explore the patterns of skull integration in roe deer without a priori assumptions of expected developmental modules, we employ method of the conditional independence among the traits described by Magwene (2001). We calculated the partial correlation matrix and corresponding edge exclusion deviance for each group (Whittaker, 2009; Magwene, 2001). Edge exclusion deviance (EED) measures the strength of association between traits after conditioning on all other variables: $EED = -N \ln(1-\rho^2_{ij\cdot[K]})$, where N is sample size and $\rho^2_{ij\cdot[K]}$ is the squared partial correlation of the i_{th} and j_{th} linear distances with all other traits held constant (Magwene, 2001). The EED-value is tested using $\chi 2$-distribution with one degree of freedom (Whittaker, 2009). Two traits are considered conditionally independent if they have an EED value of less than 3.84 which corresponds to $P = 0.05$, with $df = 1$, from the $\chi 2$ distribution. Traits that have an $EED > 3.84$ are conditionally dependent and therefore, are considered to be significantly integrated. To measure the edge strength (ES) of this conditional dependence between variables we used the formula: $ES = 0.5 \ln(1-\rho^2_{ij\cdot[K]})$; where again, $\rho^2_{ij\cdot[K]}$ is the squared partial correlation of variables *i* and *j*, with all other traits held constant (Magwene, 2001). These analyses were performed for two scenarios of skull integration: the basic five-module organization and a derived two-module organization.

All statistical analyses were performed by the software packages PopTools 2.62, CSIRO, Canberra (Hood, 2004) and Statistica 10 (StatSoft Inc., 2010).

Results

Multivariate morphological differences

The overall difference in the craniometric characters between sexes and among habitat categories is significant (two-way MANOVA: factor habitat category Wilks' λ (2.36) = 0.64578, $P < 0.0001$; factor sex Wilks' λ (1.18) = 0.40886, $P < 0.0001$; factor habitat*sex Wilks' λ (2.36) = 0.88126, $P < 0.0001$).

Matrix comparisons, Repeatability, and Adjusted Matrix Correlations

Observed and adjusted matrix correlations between roe deer correlation matrices between habitat types and sexes, along with the respective matrix repeatabilities, are present in Table 2. All raw matrix correlations were significant at the 0.001 level. Raw correlations ranged from 0.37 to 0.85 and adjusted correlations ranged from 0.40 to 0.88. The biggest difference between sexes are in closed habitats (correlation of 0.42), while sexes are most similar in open habitats (correlation of 0.85). Intermediate habitats had medium matrix correlation between males and females in relation to other groups (correlation of 0.66). Also, correlations between males from different types of habitat are higher than correlations between females. In general, all comparisons involving closed habitats have lower correlations, especially those with females from closed habitats.

All resulting correlation matrices displayed high levels of repeatability consistent with their sample sizes (open habitats with 0.97 and 0.96 for males and females respectively, intermediate habitats with 0.96 and 0.91 and closed habitats with 0.93 for both sexes). Adjustment for matrix repeatability did not change the general pattern of similarity (Table 2).

All this results indicates the specificity of correlation structure between habitats and the complexity of correlation structure of habitats and sexes in roe deer. Therefore, we expect to

observe differences of the correlation structure and therefore of the integration pattern, between different habitat types and sexes.

Magnitude of integration

The variance of eigenvalues (VE) calculated for each sex and habitat type indicates that the level of integration varies between habitat groups (Fig. 4). Higher VE values indicate that most variance can be explained by fewer eigenvalues, which corresponds to higher integration between the characters in question.

Statistically significant difference between sexes was observed only in closed habitats with higher levels of integration in females (females VE=1.88, $CI_{99\%}$: 1.85-1.91, and males VE=1.36, $CI_{99\%}$: 1.34-1.38; p= 0.000). In open (females VE=1.29, $CI_{99\%}$: 1.27-1.31, and males VE=1.15, $CI_{99\%}$: 1.13-1.17; p= 1.000) and intermediate habitats (females VE=1.47, $CI_{99\%}$: 1.44-1.50 and males VE=1.42, $CI_{99\%}$: 1.41-1.43; p= 0.622) males and females did not differ concerning levels of integration.

When we look at each sex separately, significant differences exist, in the case of males, between open habitats, and the other two habitats (males: open/intermediate p= 0.001, open/closed p= 0.002), which are separated by lower levels of integration in open habitats. For females, closed habitats showed higher levels of integration relative to other two (females: open/intermediate p= 1.000, open/closed p= 0.000).

Patterns of integration

Connectivity matrices were constructed for each hypothesis and statistically compared with the correlation matrices using Mantel's tests. The correlation coefficients for all habitat groups and sexes are highest with the theoretical matrix for the temporal module as well as in some cases (male from intermediate and closed habitats) with the matrix representing all modules or complete integration. These correlations are statistically significant with significance of $p<0.05$ or nearly statistically significant $0.05<p<0.10$ (Table 3). Exceptions to this pattern are related to closed habitats with females which do not show clear patterns in relation to the theoretical matrix and in males with the visibility of base cranial module. This implies differences in cranial correlation structure especially among sexes of closed habitats.

These results are supported by comparisons of the average correlations for presumed integrated and non-integrated characters (Table 4).

The greatest difference in the correlation strength of presumed integrated and non-integrated characters (i.e. lowest percentage) occurs with the temporal and cranial base modules and the module which implies total integration. This pattern is present in almost all groups. Exceptions are females from intermediate and closed habitats, with higher correlations within hypothetically integrated oral, vault and nasal modules (Table 4). This implies different functional demands in these groups.

Edge exclusion deviance was also used to explore patterns of cranial correlation. The conditional independence matrix for these groups is shown in Fig. 5. All illustrated edges are significant. Out of the 153 potential edges between these 18 characters, many were not significant and therefore absent. We found 43 significant edges for males and 38 for females in open habitats, 39 significant edges for males and 33 for females from intermediate habitats, and 33 and 42 significant edges for males and females from closed habitats. Thus, about 75% of all potential edges were absent, i.e. these edges may either never have been present or could have

been broken up. Conditional independence analyses revealed several conserved patterns across sexes and habitat types. The patterns that are present in all groups includes two significant and particularly strong edges, which include the links between greatest occipital width (GWO) and greatest width of the cranium (GWC), and between distance of interorbitale (LI) and *lacrymale* (LL).

Males and females from open habitats display comparable edges and therefore are assumed to share comparable patterns of cranial correlation. On the other hand, significant edges and their strength are different between sexes within intermediate and closed habitats indicating different patterns of cranial correlations. However, these differences originate mostly due to the specific correlation pattern present in females from both habitat types (Fig. 6). If we assume that the roe deer cranium has a two-module organization, then the situation could be understood as follows: females from intermediate, to a lesser extent, and females from closed habitats are ones that differ from the basic pattern.

Discussion

According to the goals of this study, roe deer craniums were used as a model system to investigate the degree to which patterns of morphological integration are stable in different habitat types and whether sexes differ in that context. We adopted a comparative approach that allows us to determine the relative impact of differing functional demands within the context of relationships between social organization and habitat type. Our results confirmed both our hypotheses which imply higher level of integration and more pronounced sexual dimorphism in skull integration in closed habitats in comparison to open habitats.

The differences between open and closed habitats and relationship between males and females from these habitats are in effect differences in their social organization and sexual segregation caused by the availability and configuration of woodland habitats, or different choices made by males and females with respect to security and food availability in their living areas. The roe deer has two main resource requirements: nutrient-rich forage and cover, which offers escape from predators and disturbance (Putman 1986; Cibien *et al.*, 1995; Mysterud & Østbye, 1995, 1999; Tufto, Andersen & Linnell, 1996; San José *et al.*, 1997; Mysterud, 1999). In open habitats, where cervids are generally more gregarious, females tend to look more like young males. By being less dimorphic, females also blend into the herd and are less likely to be selected as prey due to a smaller body size. Further, by being gregarious, males and females spend much of the year together and undergo similar selection pressures, so sexual segregation is lower. The observed patterns of correlation in the roe deer skull are in line with these facts with similar patterns and level of integration in males and females from open habitats. In closed habitats, males and females pursue different lifestyles, only to come together for mating, sexual segregation being higher. Males invest energy in large body size and large antlers with pronounced territoriality, while females invest in the security of their young. These differing selection pressures are likely to lead to high sexual dimorphism of skull integration. The only statistically significant difference between sexes was found in closed habitats which confirm our starting hypothesis that relates sexual segregation to the level of integration in the skull. The link between sexual segregation and skull morphology can be derived from sex-related differential space, habitat and diet use as well as foraging behavior differences (Conradt 1998; Barboza and Bowyer, 2000; Mysterud, 2000; Yearsley and Pérez-Barbería, 2005).

Generally, our results show a relatively high level of total skull integration followed by pronounced visibility of the module representing total integration, with only the temporal module

standing out as independent. Strong phenotypic integration means that only a subset of possible trait combinations will exist within a species – even in cases where one or more of the traits display considerable variation (Schlichting, 1989a). Phenotypic integration may therefore limit how a species can respond to environmental variation, as traits must respond in correlated ways to change (Schlichting, 1989b). Regarding roe deer as the most widespread ungulate species in Europe where it has colonized many different habitats (Linnell, Duncan & Andersen, 1998) we can say that the integration is limited to the braincase allowing a high level of flexibility and success. Haber (2015) reported high variation of integration among closely related species of Artiodactyla suggesting that integration can respond relatively quickly to selection. Differences in level of integration between closed to open habitats in roe deer are in line with our prediction that closed habitats are more stable/less variable thus providing for stronger canalizing selection pressures. For a forest species this is a reasonable proposition. In intermediate and open habitats, the higher level of variation and heterogeneity in almost all environmental variables can lead to greater variability which by itself causes lower integration. Furthermore, a more environmentally canalized population response will lower the effect of such selective responses as is the pattern of sexual dimorphism, a result corroborated by our data.

Regarding correlation patterns, the overall patterns among skull elements are not consistent across habitat types and sexes. Across habitat types, males and females from open and intermediate habitats are more similar, while correlations between sexes from these two habitat types and closed habitats are much lower. The highest difference in correlation patterns was exhibited between closed and intermediate habitats in both sexes. The high repeatability of the correlation matrices suggest that it is not likely that these results are biased due to measurement error or sampling. These results are different from those published previously, which showed similarities in correlation patterns across species and sexes (Ackermann & Cheverud, 2000;

Marroig & Cheverud, 2001; Goswami, 2006). Although these studies did not analyze variability within any single species, and especially not with respect to habitat differentiation, the similarity of correlation matrices among species and sexes suggested a general (evolutionary) trend. With respect to models of phenotypic differentiation among members of a taxon, our results are more in accordance with the predictions of the "adaptive" model rather than with the results of the "constraint" model. The adaptive model emphasizes the interplay between genotype and the currently acting selection pressure, and maintains that the correlation among traits can be broken up if (with respect to the ancestral population) selection changes from stabilizing to directional/disruptive as we presume happens in the transition between closed and open habitats. The "constraint" model, on the other hand, predicts that the change in selective pressure will act as a constraint on the achieved level of correlations, preventing them to be broken up.

Within the skull, the temporal module has the highest integration and was the only functional module to show significant similarity with the theoretical modules (full correlations as expected by theory). It also showed the least significant (absence of significance) level of sexual and habitat differentiation. As this region supports the antlers (*frontale*), the eyes (*jugale, orbitosphenoideum*) and the mastication muscles (*squamosum, jugale*, *processus zygomaticus* i.e. the zygomatic arch), it provides the roe deer with three basic functions of such importance that variability in this region would likely be detrimental in terms of survival and overall fitness. Also high average correlations were found for the base module, as well as some significant edges between elements of base, vault and temporal modules, regardless of sex or habitat type, implying that the posterior parts of the skull were the most conserved (variation in the back part of the skull is constrained) and that other parts could respond more quickly to different selective pressures.

Our result corroborate the recent findings of Haber (2015) who showed that an analogous module has not been important in the divergence of bovids and cervids, and that it is not subject to strong sexual selection. On the other hand, modules corresponding to feeding and running adaptations – which were identified to have a major role in the differentiation of Artiodactyls – did not show overall significant visibility according to theoretical considerations. However, we found higher average correlations in these modules (oral and nasal module) for females from intermediate and closed habitats, which indicate more specialized feeding and running adaptations in these groups. Specificity of females from closed and partly of intermediate habitats is probably caused by selective and protective life strategies or specific features of foraging and predator escape patterns in these habitats. Further, females from closed habitats show specific patterns of partial correlations with higher values within the face module, in contrast to all other groups, where correlation strengths were higher for the braincase module. That indicates specific selective pressures related to feeding and running.

The general consistency of results across tests suggest that patterns of morphological integration between sex and habitat groups tend to be different for males and females from different habitat types implying that when faced with strong selective pressures, patterns of correlations among skeletal elements can evolve even within a species as an indirect influence of social organization through habitat and sexual selection.

This study reveals the roe deer`s high adaptability as maintained by the influence of ecological factors on key covariance-generating developmental processes which can enhance selection response both through ecotypical and behavioural adaptation.

Acknowledgements

We are grateful to Mark Hewison and Sabrina Curran for their helpful comments and criticisms on previous versions of the manuscript. We thank all the workers employed in game management organizations of Serbia and we acknowledge the help of Jovan Bradvarović, Mihajlo Hadži-Pavlović, Slobodan Kastratović, Laslo Knehtl, Goran Jevremović and Ivan Tadein for collecting samples. This study was partially funded by the Ministry of Agriculture, and Environmental Protection of Serbia (Grant No. 401–00–3288/2014–10) to SMZ, and by the Ministry of Education, Science and Technological Development of Serbia (Grant No. III 43001) to SŽS.

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Figure 1. Map of Serbia with sampled localities. Circles designate populations samples from open habitats, squares from closed habitats, triangles from intermediate habitats (see Table 1 for full description).

Figure 2. Cranial characters used in the analysis: (a) ventral projection, (b) dorsal projection, (c) lateral projection. The characters, according to their affiliation to the analysed modules were: **BASE**: (1) LB: Length of base, Basion (Ba) – Posterior edge of M^3; (2) CW: Condylar width, Distance of the tips of *condylus occipitalis*; (3) GWO: Greatest width of occipital region;

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Figure 3. Cranium of a roe deer, *Capreolus capreolus*, showing the five cranial modules tested in this study: (a) ventral projection, (b) dorsal projection, (c) lateral projection.

Figure 4. The overall magnitude of integration (variance of eigenvalues - VE) for analysed habitat groups and sexes (black – females, white – males). The group VE's with 99% bootstrapped confidence intervals are presented.

Figure 5. Conditional independence graph for a five-module organization of roe deer cranium for males and females within three types of habitats (value represents strength of association between traits).

Figure 6. Conditional independence graph for a two-module organization of roe deer cranium matrices for males and females within three types of habitats (value represents strength of association between traits). (Black circles-males; white circles-females).

Table 1. Population samples and habitat characteristics of the 11 localities from Serbia used in the analyses. The first two columns denote sample sizes (N- males/females) while the remaining columns present areas (ha) of major vegetation features used in categorizing the habitats as open (O), intermediate (I) and closed (C).

Population/habitat	N males	N females	Forested areas (ha)	Meadow & grassland (ha)	Ploughland (arable land, ha)	Remaining area (ha)
1. Novi Kenževac (O)	38	15	780	3 900	22 600	3 300
2. Ada-Bečej (O)	51	104	1 100	819	61 600	7 800
3. Novi Bečej (O)	23	20	1 200	12 930	38 900	7 700
4. Zrenjanin (O)	56	19	5 000	24 100	156 600	27 600
Open habitats	**168**	**158**				
5. Smederevska Palanka (I)	70	12	2 300	4 200	30 000	2 700
6. Deliblatska peščara (I)	74	11	19 200	12 100	65	2 300
7. Petrovac na Mlavi (I)	21	23	18 100	9 600	58 900	11 400
8. Negotin (I)	82	21	22 200	22 800	48 000	3 400
Intermediate habitats	**247**	**67**				
9. Severni Kučaj (C)	15	12	41 000	6 300	3 200	13 100
10. Južni Kučaj (C)	36	14	81 000	38 300	39 800	15 900
11. Stara planina (C)	25	19	56 600	46 300	55 200	8 500
Closed habitats	**76**	**45**				

Table 2. Matrix correlations between different sex (males/females) and habitat type groups (Open/Intermediate/Closed). Matrix repeatabilities are on the diagonal in boldface, lower triangle of matrix presents raw correlations, and upper triangle adjusted correlations.

Habitat/sex		Open		Intermediate		Closed	
		males	females	males	females	males	females
Open	males	**0.97**	0.88	0.82	0.73	0.72	0.62
	females	0.85	**0.96**	0.80	0.72	0.74	0.56
Intermediate	males	0.79	0.77	**0.96**	0.71	0.56	0.54
	females	0.69	0.67	0.66	**0.91**	0.48	0.40
Closed	males	0.68	0.70	0.53	0.44	**0.93**	0.45
	females	0.59	0.53	0.51	0.37	0.42	**0.93**

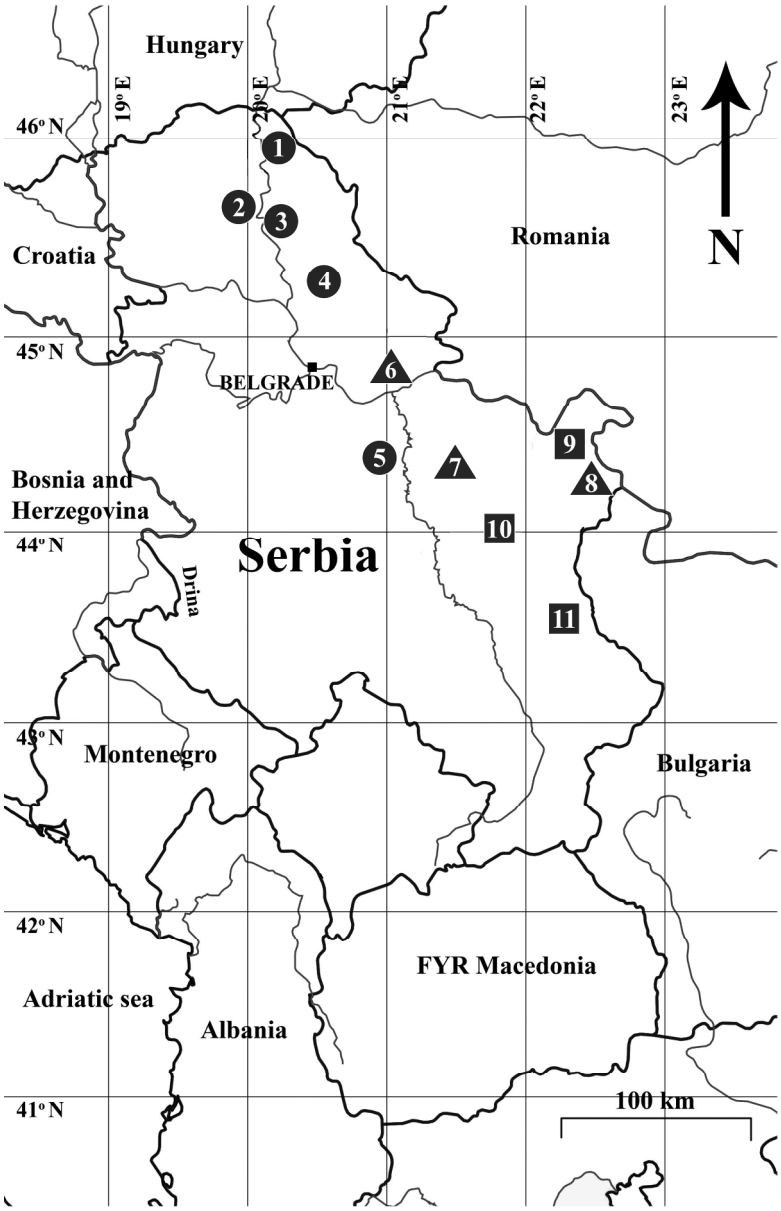
Table 3. Correlations and significance values (bolded entries – $P<0.05$, italic entries – $0.05<P<0.1$) of habitat/sex groups correlation matrices with integration hypotheses. The five hypothesized cranial regions (Base, Oral, Nasal, Temporal, Vault), two developmental regions (NC - neural crest, PM - paraxial mesoderm) and total skull integration (All) are presented.

		Cranial and developmental regions							
Habitat/sex		Base	Oral	Nasal	Temporal	Vault	NC	PM	All
Open	males	0.08	-0.06	-0.06	*0.18*	-0.13	0.08	0.00	0.05
	females	0.05	-0.07	-0.02	**0.26**	-0.12	0.00	0.09	*0.10*
Intermediate	males	0.09	-0.11	0.01	**0.21**	-0.04	0.01	0.04	**0.10**
	females	0.05	-0.09	*0.12*	*0.15*	-0.08	0.16	-0.08	*0.09*
Closed	males	**0.20**	-0.13	-0.07	**0.25**	-0.08	-0.15	0.13	*0.12*
	females	0.05	0.03	-0.04	-0.10	0.02	0.04	0.04	-0.04

Table 4. Average within-module correlation (INT – integrated characters) and correlation among all other traits not in the module (NonINT – non-integrated characters), with the modularity ratio (%). The five hypothesized cranial regions (Base, Oral, Nasal, Temporal, Vault), two

developmental regions (NC - neural crest, PM - paraxial mesoderm) and total skull integration (All) are presented.

Habitat/sex			Cranial and developmental regions							
			Base	Oral	Nasal	Temporal	Vault	NC	PM	All
Open	males	INT	0.53	0.39	0.43	0.47	0.37	0.33	0.30	0.44
		NonINT	0.25	0.26	0.26	0.24	0.26	0.24	0.25	0.21
		%	47.7	65.7	60.2	52.1	69.4	73.84	81.28	48.7
	females	INT	0.52	0.37	0.45	0.48	0.39	0.30	0.32	0.44
		NonINT	0.25	0.25	0.25	0.23	0.25	0.24	0.23	0.20
		%	47.3	66.6	55.2	48.7	64.2	79.62	72.89	45.7
Intermediate	males	INT	0.57	0.37	0.50	0.50	0.47	0.31	0.29	0.47
		NonINT	0.28	0.28	0.28	0.27	0.28	0.29	0.29	0.24
		%	49.3	77.6	55.9	53.9	60.6	93.24	100.29	50.3
	females	INT	0.51	0.33	0.62	0.52	0.43	0.37	0.31	0.48
		NonINT	0.28	0.29	0.28	0.27	0.28	0.26	0.28	0.24
		%	55.1	86.6	44.8	51.3	65.7	69.60	90.02	49.9
Closed	males	INT	0.66	0.31	0.38	0.54	0.39	0.24	0.34	0.46
		NonINT	0.24	0.25	0.24	0.22	0.24	0.25	0.22	0.19
		%	35.9	78.6	64.9	41.4	62.2	104.49	64.06	41.6
	females	INT	0.36	0.47	0.36	0.46	0.59	0.34	0.32	0.46
		NonINT	0.28	0.27	0.28	0.27	0.27	0.26	0.27	0.24
		%	76.7	57.5	76.6	57.4	46.5	78.82	83.82	51.6



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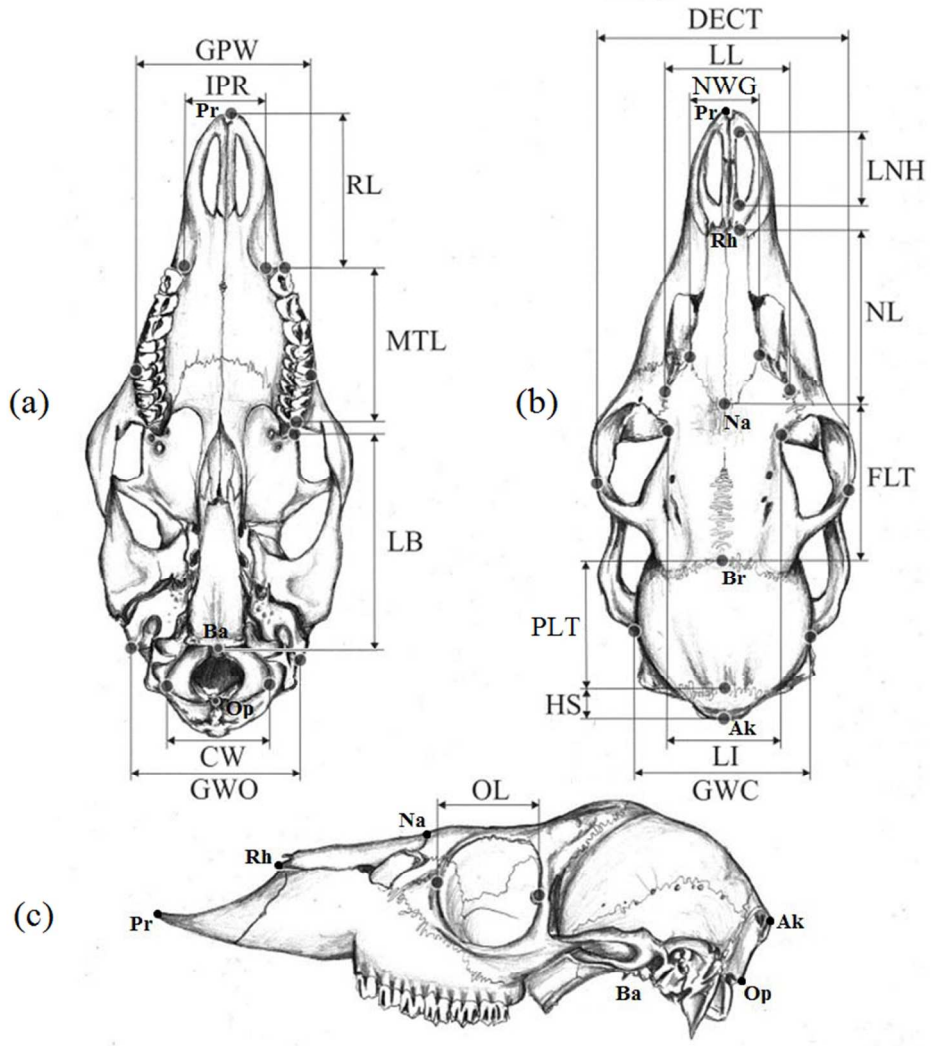

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232x251mm (96 x 96 DPI)

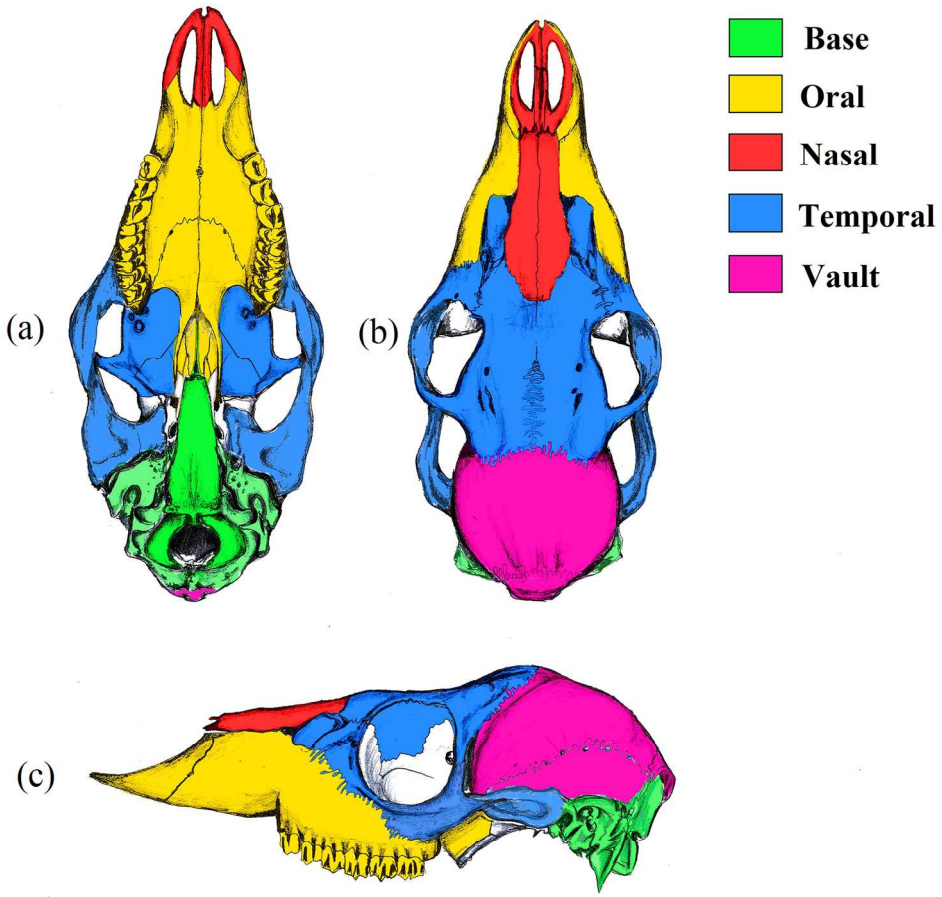

Figure 3. Cranium of a roe deer, Capreolus capreolus, showing the five cranial modules tested in this study: (a) ventral projection, (b) dorsal projection, (c) lateral projection.
160x155mm (300 x 300 DPI)

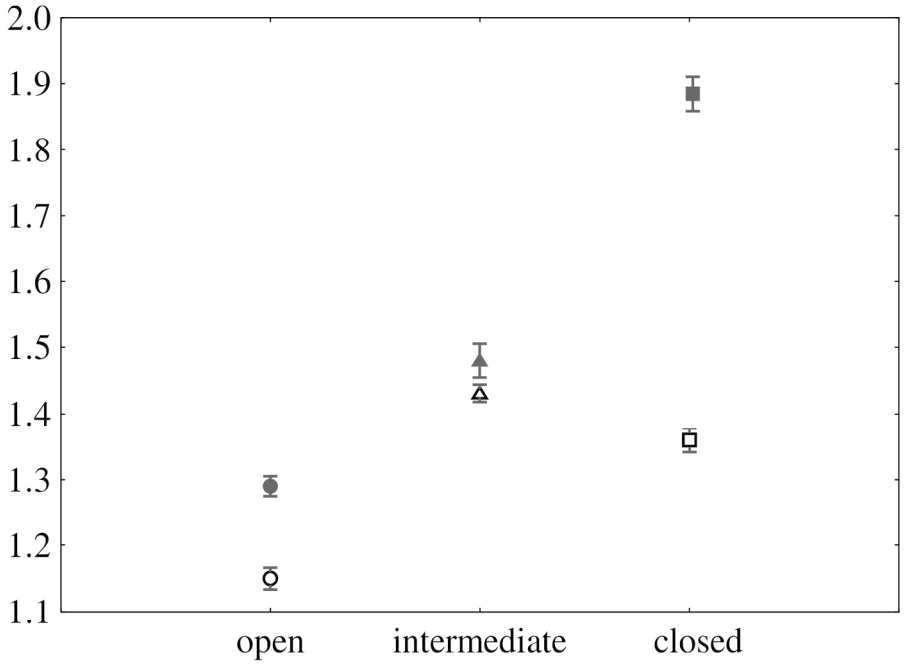

Figure 4. The overall magnitude of integration (variance of eigenvalues - VE) for analysed habitat groups and sexes (black – females, white – males). The group VE's with 99% bootstrapped confidence intervals are presented.
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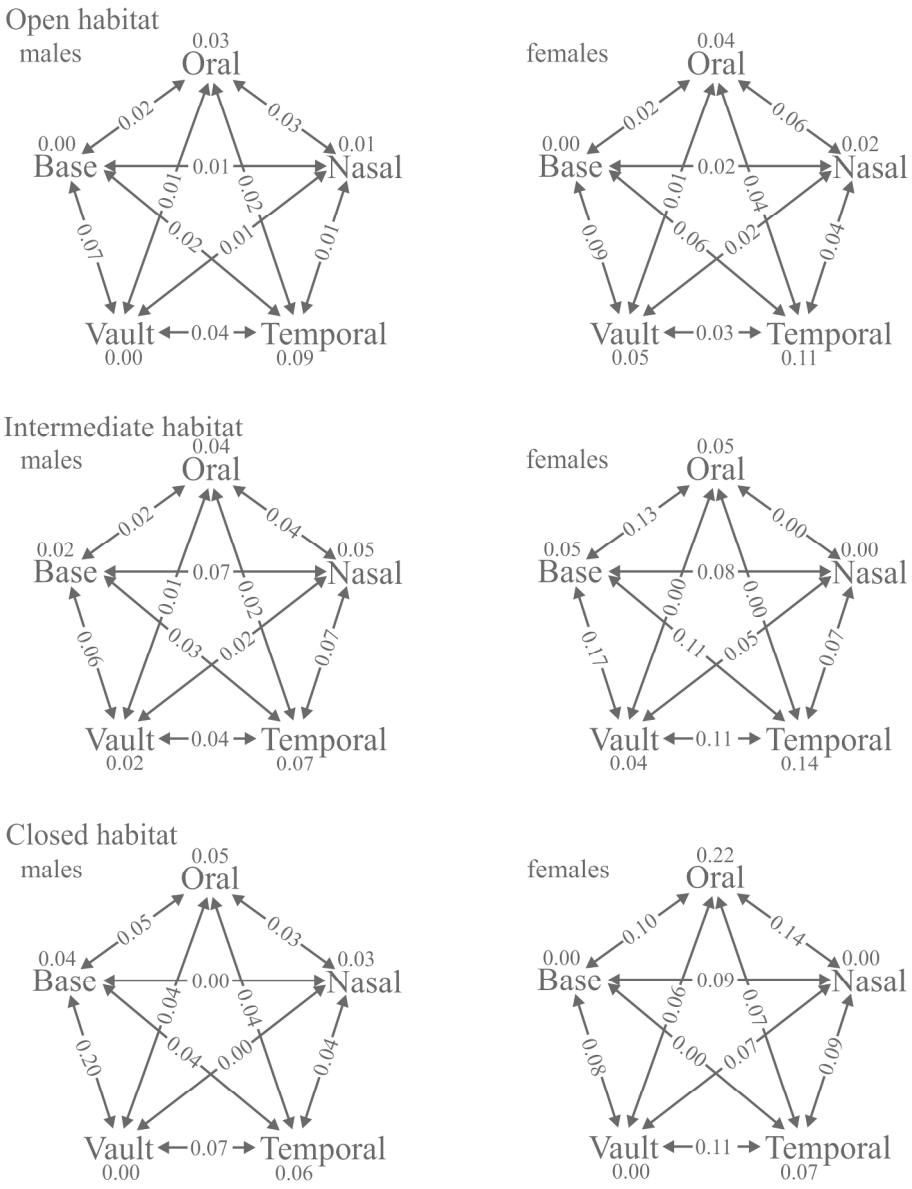

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192x256mm (299 x 299 DPI)

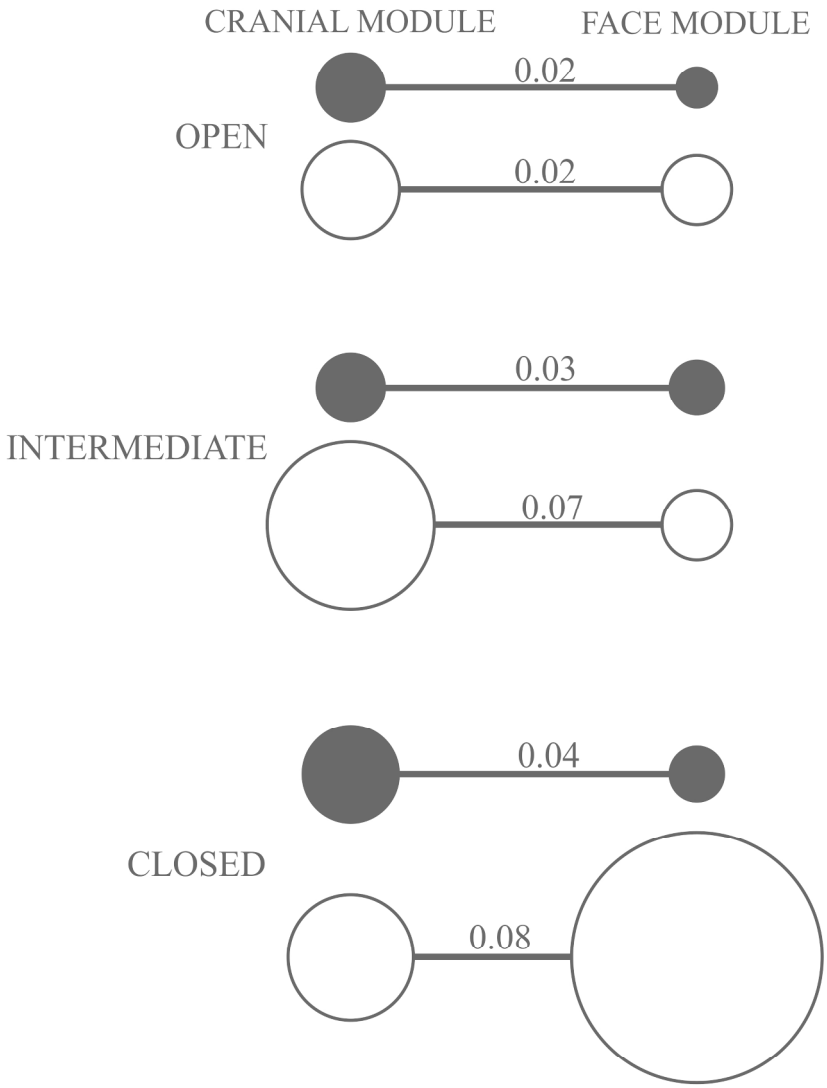

Figure 6. Conditional independence graph for a two-module organization of roe deer cranium matrices for males and females within three types of habitats (value represents strength of association between traits). (Black circles-males; white circles-females).
204x268mm (299 x 299 DPI)