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Original scientific paper

DOES SEX AFFECT THE GENETIC STRUCTURE OF JACKALS IN NORTHERN LOWLANDS OF BOSNIA AND HERZEGOVINA?

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Abstract

Sex-biased dispersal may affect the genetic structure of wild populations, often leading to distinct patterns of relatedness between males and females. We examined this phenomenon in the golden jackal (*Canis aureus*) population from the northern lowlands of Bosnia and Herzegovina (BiH) by analyzing 36 individuals (18 males and 18 females) using 16 polymorphic microsatellite loci. The population exhibited moderate genetic diversity, consistent with the diversity in the region. Analyses of population structure, including STRUCTURE, PCoA, and pairwise Fst (Fst = 0.004; p = 0.190), revealed no significant genetic differentiation between males and females, suggesting a lack of sex-biased structuring. This pattern may be further explained by recent demographic expansion. Analyses of local relatedness showed that the observed patterns reflect local kinship rather than relatedness determined by sex. Although the corrected Assignment Index (AIc) indicated a trend consistent with male-biased dispersal, this difference was not statistically significant. However, male dispersal warrants further investigation with an increased sample size and broader sample distribution.

Keywords: Bosnia and Herzegovina, *Canis aureus*, genetic structure, relatedness, sex-biased dispersal.

INTRODUCTION

Sex-biased dispersal may affect the genetic structure of animal populations, with one sex dispersing more frequently or over longer distances, thus influencing patterns of gene flow among populations and relatedness of individuals (Handley and Perrin, 2007). Males and females of various species often differ in their tendency to leave the natal population and establish populations at new territories. For example, females may be more philopatric (remaining close to their birthplace), while males disperse further-or vice versa. In mammals, dispersal is typically male-biased, with females remaining philopatric, which can lead to

detectable differences in population genetic structure (Greenwood, 1980; Handley and Perrin, 2007).

The effect of sex-biased dispersal on population structure has been well documented in *Canis* species. Male-biased dispersal has been demonstrated in golden jackals (*Canis aureus*) (Rutkowski *et al*., 2015), as well as in wolves (*Canis lupus*) (Pilot *et al*., 2006; Fabbri *et al*., 2014). These studies consistently reported higher female relatedness within populations, followed by more extensive male-mediated gene flow. Similar trends were observed in other highly mobile species. For example, in African wild dogs (*Lycaon pictus*), female-biased dispersal can significantly shape genetic structure by enhancing gene flow among populations (Girman *et al*., 1997), while in brown bears (*Ursus arctos*), sex-specific dispersal rates and behaviors influence population genetic structure, with males typically driving gene flow (Bellemain *et al*., 2005).

In Bosnia and Herzegovina (BiH) population-genetic studies have suggested the existence of population structure (K=2) in jackals, however, without a clear spatial pattern. This is likely due to a limited sampling territory (Nikitović *et al*., 2023). Previous studies have shown that the northern lowlands represent a distribution hotspot, with jackals originating from Serbia and northeastern Croatia (Selimović *et al*. 2021), while their presence in the south has been connected with the Dalmatian population (Milenković, 1987; Kryštufek *et al*., 1997; Mitchell-Jones *et al*., 1999).

Understanding whether dispersal is sex-biased is important for interpreting the genetic structure of wild populations. Despite various analyses, many studies neglect sex-specific effects, particularly when sampling is geographically restricted. A robust assessment of the relationship between sex-biased dispersal and genetic structure requires multi-locus markers and a stratified sampling design that allows direct comparisons between males and females across populations. In our study, sampling was limited to the northern lowlands of BiH; however, the application of 16 polymorphic microsatellite loci enabled us to investigate patterns of relatedness, genetic differentiation, and individual assignment within this region. Specifically, we tested whether males and females differ in their genetic structure, as would be expected under sex-biased dispersal.

MATERIALS AND METHODS

Sample collection and sampling area. Tissue samples from jackals were collected in the lowland northern area of Bosnia and Herzegovina between 2018 and 2021. Samples were obtained from individuals that died due to various circumstances (e.g., legal hunting, traffic accidents, etc.). Immediately after collection, tissues were preserved in 96% ethanol and stored at -20◦C until DNA extraction.

DNA extraction, microsatellite amplification, and genotyping. Genomic DNA was isolated following Sambrook and Russell (2001). Sex determination was performed by amplifying the Amelogenin gene using the Canine Genotypes™ Panel 1.1 kit (Finnzymes, Thermo Fisher Scientific, Finland). To assess genetic diversity and population structure, eighteen microsatellite loci were amplified. Genotyping was conducted on an ABI3730xl Genetic Analyzer (Applied Biosystems, California), and allele sizes were determined using GeneMarker V.4 (Softgenetics). Potential genotyping errors, such as allelic dropout and null alleles, were examined using MicroChecker 2.2.3 (Van Oosterhout *et al*. 2004).

Genetic diversity and population structure. The dataset of 36 individuals was divided into two groups based on sex: 18 females and 18 males. Individuals were randomly selected from the larger dataset using the *dplyr* package in R (v4.4.1) with the aim of standardizing the sample size. All subsequent analyses were performed on this sex-standardized dataset.

Genetic parameters, including the mean number of alleles per locus (Na), effective number of alleles (Ne), observed (Ho) and expected (He) heterozygosities, and the number of private alleles, as well as deviations from the Hardy–Weinberg equilibrium (HWE) and pairwise fixation index (Fst) were calculated using GenAlex v6.5 (Peakall and Smouse, 2006). Allelic richness was calculated using the *allelic.richness()* function from the *hierfstat* package in R (v4.4.1); the statistical significance of the results was assessed using a Welch's two-sample t-test (Yuen, 1974).

Population structure was analyzed using the Bayesian clustering method implemented in STRUCTURE v2.3.4 (Pritchard *et al*. 2000; Hubisz *et al*. 2009). The analyses included the following parameters: an admixture model, a correlated allele frequency, 10^6 MCMC iterations, and a burn-in of 10^5. The number of genetic clusters (K) ranged from 2 to 5, and the analysis for each K was repeated three times. The optimal number of clusters (K) was determined by applying the ΔK method using Structure Harvester (Earl and vonHoldt, 2012) and subsequently visualized using the PopHelper package in R (Francis, 2016). The spatial distribution of the detected clusters was visualized in QGIS v.3.4.11 (QGIS, 2018).

Relatedness. Genetic relatedness among individuals was assessed by calculating pairwise Euclidean genetic distances (Shirk *et al*. 2015). The analysis was conducted in R v4.4.1 using the packages *adegenet* (Jombart, 2008), and *ade4* (Dray and Dufour, 2007). Genetic relationships and population structure were visualized using two complementary approaches: i) Principal Coordinates Analysis (PCoA) was performed on the distance matrix, and the results were displayed in two dimensions using the function *s.label()*, and ii) a genetic relatedness dendrogram was constructed by applying hierarchical clustering *hclust()* on the distance matrix, using Ward’s method (Murtagh and Legendre, 2014). The dendrogram describes hierarchical relationships among individuals, where branch height reflects the level of genetic distance, and thus relatedness. The Mantel test *mantel.randtest()* with 999 permutations was used to assess the statistical significance of the results.

Sex-biased dispersal. To test for sex-biased dispersal, the corrected Assignment Index (AIc) method, as implemented in GenAlEx v6.5 (Peakall and Smouse, 2006), was employed. The AIc estimates the likelihood of an individual's genotype originating from the sampled population. Individuals with negative AIc values are generally considered likely dispersers/immigrants, while positive values indicate residents (Mossman and Waser, 1999; Goudet *et al*. 2002). Mean AIc values were calculated separately for males and females. A Mann–Whitney U-test was applied to compare the distribution of AIc values between the sexes, testing whether one sex exhibited a significantly lower mean AIc (Herrero *et al*. 2021).

RESULTS AND DISCUSSION

Genetic diversity. Null alleles were identified at two loci (FH2054 and INU005), which were consequently excluded from further analyses. All subsequent genetic analyses were performed using the remaining 16 microsatellite loci. A total of 154 alleles were detected, including 76 in females and 78 in males. Although females showed a higher average number of alleles (Na=4.75) compared to males (Na=4.44), males exhibited a slightly higher effective number of alleles (Na=2.86 vs. Ne=2.56 in females), suggesting a more even distribution of allele frequencies in the male group (Tab. 1). The mean allelic richness was highly similar between the sexes (4.44 for females and 4.52 for males), and a Welch's t-test confirmed that this minimal difference was not statistically significant (p=0.8235).

Mean observed (Ho) and expected (He) heterozygosities were moderately low and highly similar across both sexes. Observed heterozygosity was Ho=0.53 for females and Ho =0.52 for males, while expected heterozygosity was He=0.56 for females and He=0.59 for males. This moderately low genetic diversity observed in jackals from Bosnia and Herzegovina aligns with findings from other studies (e.g., Fabbri *et al.* 2014; Kemenszky *et al*. 2022). Hardy-Weinberg equilibrium tests highlighted significant departures in several loci, often differing between sexes. Highly significant deviations ($p<0.001$) were observed in both sexes for loci AHTk211 and AHT137, while other loci showed highly significant deviations in only one sex (e.g., FH2848 in males; REN247M23 in females) (Table 1). Significant deviations from Hardy-Weinberg equilibrium may be influenced by inbreeding rather than the Wahlund effect. Furthermore, it is possible that males and females originate from different source populations or that dispersal is sex-biased, as both scenarios can affect Hardy-Weinberg equilibrium. However, we cannot exclude the possibility that the observed pattern results from random variation alone, given the small sample size, which can lead to apparent deviations.

Table 1. Basic genetic parameters of the jackal (*Canis aureus)* population from Bosnia and Herzegovina by gender, based on 16 microsatellite loci (M – males, F – females, Na - number of alleles per locus, Ne - effective number of alleles, Ho - observed heterozygosity, He - expected heterozygosity, HWE - Hardy-Weinberg equilibrium; ns=not significant, * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

Locus	Na		Ne		Ho		He		HWE	
	F	M	F	M	F	M	F	M	F	M
AHTk211	4	4	2.05	2.78	0.00	0.06	0.51	0.64	***	***
CXX279	3	3	2.37	1.98	0.72	0.22	0.58	0.49	ns	*
REN169O18	4	5	2.88	2.86	0.78	0.72	0.65	0.65	*	ns
INU055	4	3	2.34	1.98	0.56	0.56	0.57	0.49	ns	ns
REN54P11	6	4	3.01	3.43	0.72	0.72	0.67	0.71	ns	ns
INRA21	4	5	3.43	3.95	0.67	0.61	0.71	0.75	ns	ns
AHT137	11	9	4.98	6.11	0.39	0.56	0.79	0.84	***	***
REN169D01	2	3	1.38	1.67	0.22	0.33	0.28	0.40	ns	*
AHTh260	6	6	2.28	3.39	0.56	0.72	0.56	0.70	ns	*
AHTk253	3	2	1.55	1.25	0.44	0.22	0.36	0.19	ns	ns

INU030	4	5	3.26	3.66	0.78	0.72	0.69	0.73	ns	ns
FH2848	4	4	1.91	2.88	0.56	0.72	0.47	0.65	ns	***
AHT121	7	5	1.74	2.06	0.50	0.44	0.43	0.51	ns	ns
REN162C04	4	4	1.69	1.82	0.39	0.50	0.41	0.45	ns	ns
AHTh171	6	4	3.11	2.60	0.67	0.61	0.68	0.62	ns	ns
REN247M23	4	5	2.93	3.41	0.50	0.56	0.66	0.71	***	ns
Mean	**4.75**	**4.44**	**2.56**	**2.86**	**0.53**	**0.52**	**0.56**	**0.59**		
SD	**0.53**	**0.39**	**0.23**	**0.29**	**0.05**	**0.05**	**0.04**	**0.04**		

The majority of private alleles occurred at low frequencies, appearing in only a few individuals. However, certain loci showed relatively higher frequencies, such as INU055, REN54P11 and AHTh121 in females, suggesting some alleles are more common within sex-specific groups (Figure 1). The presence of private alleles does not necessarily indicate strong genetic differentiation between the sexes. Instead, the slightly higher number of private alleles in females may be a consequence of random sampling, demographic processes specific to that sex group (e.g., differing reproductive strategies or migration patterns), or a larger effective female population size in the past (Lucotte *et al*. 2016).

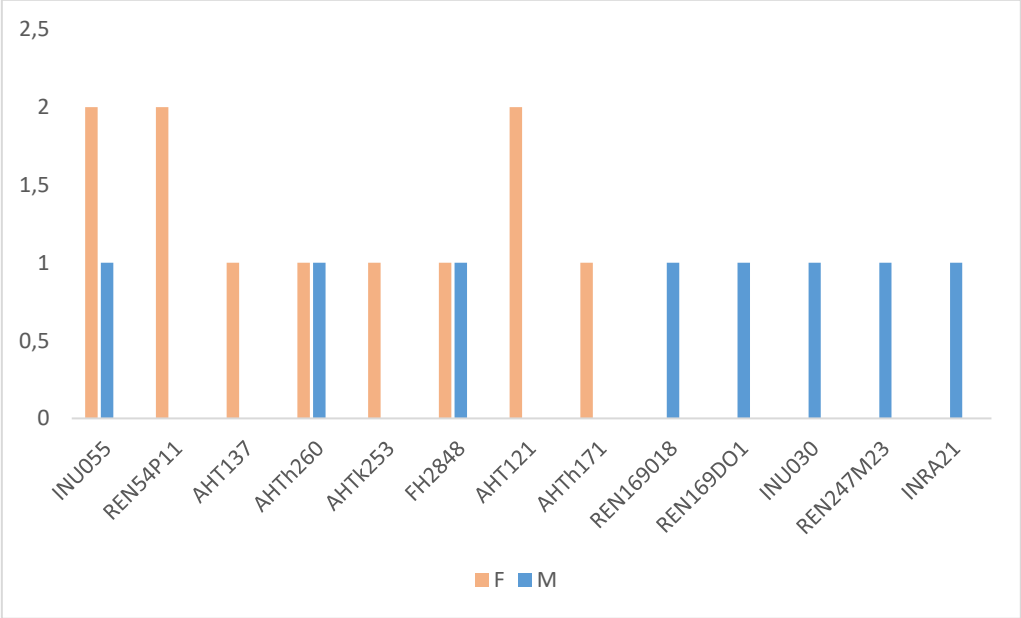

Figure 1. Distribution of detected private alleles per locus between females (F) and males (M)

Population structure, relatedness and sex-biased dispersal. STRUCTURE analysis revealed four genetic clusters (K=4) within the jackal population of Bosnia and Herzegovina; however, spatial visualization showed no distinct geographic patterns (Figure 2A). Pairwise Fst between males and females was non-significant (Fst=0.004; p=0.190), indicating an absence of significant intersexual genetic differentiation.

The PCoA (Figure 2B) further confirmed the absence of sex-based structuring, demonstrating that females and males overlap substantially and do not form distinct genetic clusters. Similarly, the dendrogram (Figure 2C) supported the lack of sex-based clustering, as

clustering patterns primarily reflected local relatedness rather than sex effect. Overall, these analyses demonstrate that the observed genetic variation is predominantly structured within the sexes (a pattern consistent with local kinship/philopatry) rather than between them.

While previous studies in Europe (e.g., Rutkowski *et al*., 2015; Nikitović *et al*., 2023) primarily assessed population-level rather than sex-specific genetic structure, they similarly reported weak or unclear spatial structuring across broad regions, with pronounced structure observed only in certain localized populations such as Dalmatia (Stronen *et al*., 2021).

Our finding of no intersexual differentiation is further supported by studies explicitly analyzing sex-biased dispersal in golden jackals (Bogdanowicz *et al*., 2024), which found no evidence for male- or female-biased dispersal at range-wide or expansion-front scales. This suggests that the absence of intersexual genetic structure in our population is consistent with broader patterns in the species and may be influenced by recent demographic expansion or colonization of new areas, which could mask finer structures. However, methodological limitations, including the number of microsatellite loci and sample size, may reduce the power to detect subtle sex-biased dispersal, supporting the need for larger and more spatially comprehensive sampling.

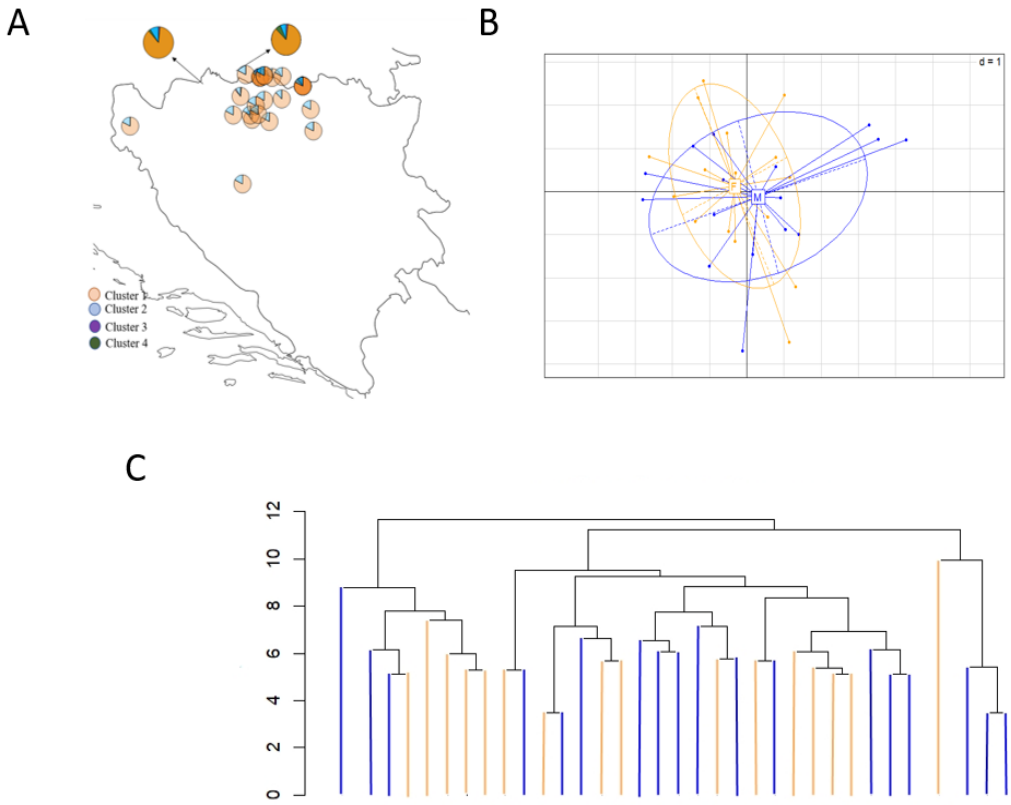

Figure 2. A) Visualization of the detected genetic clusters in STRUCTURE using QGIS; the map also illustrates the geographical distribution of the analysed samples. B) The PCoA result shows the absence of population structure. C) Dendrogram illustrates the hierarchical clustering of individuals and supports the absence of strong sex-based partitioning. Each terminal branch represents one individual, and the height of lines reflects the genetic distance between clusters; the longer the joining line, the less related the individuals are; blue lines correspond to the males, whereas orange corresponds to the females.

Sex-Biased Dispersal Analysis. The mean corrected assignment index (AIc) differed between sexes, with males showing negative mean values (Mean AIc = -0.345) and females showing positive mean values (Mean AIc = +0.345). This indicates a trend in which males are more likely to act as dispersers, while females tend to remain resident. However, the difference between sexes was not statistically significant (Mann-Whitney U-test: Z = 0.918, p = 0.359). Thus, although males exhibited a stronger tendency towards dispersal than females, the evidence was not significant given the available sample size.

CONCLUSION

Our results demonstrate an absence of significant genetic structuring between the sexes, indicating that sex is not a major factor currently shaping the population's genetic make-up. This finding is consistent with broader patterns of low genetic structure across rapidly expanding golden jackal populations in Europe. Although some evidence, such as negative AIc values in males, suggests a potential trend of male-biased dispersal, the hierarchical genetic clustering of individuals observed in the jackal population appears to be primarily driven by local relatedness among individuals within the analyzed dataset, rather than by sex. However, removing related individuals would substantially reduce our sample size; therefore, a more robust conclusion regarding sex-biased dispersal will require a larger sample and a broader sampling area.

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DA LI POL UTIČE NA GENETIČKU STRUKTURU ŠAKALA NA SJEVERU BOSNE I HERCEGOVINE?

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Sažetak

Disperzija zasnovana na polu može uticati na genetičku strukturu populacija divljih životinja, često dovodeći do različitih obrazaca srodstva između mužjaka i ženki. U našoj studiji, ovaj fenomen istražili smo u populaciji zlatnog šakala (*Canis aureus*) iz sjevernih nizijskih područja Bosne i Hercegovine, analizirajući 16 polimorfnih mikrosatelitskih lokusa kod 36 jedinki (18 ženki i 18 mužjaka). Dobijeni rezultati ukazali su na umjeren genetički diverzitet, u skladu sa rezultatima iz regiona. Analize populacione strukture, uključujući STRUCTURE, PCoA i Fst (Fst = 0,004; p = 0,190), nisu otkrile značajnu genetičku diferencijaciju između mužjaka i ženki, što sugeriše na nedostatak strukturiranja zasnovanog na polu. Nedavna demografska ekspanzija može dodatno doprinijeti odsustvu divergencije. Analize lokalnog srodstva pokazale su da posmatrani obrasci odražavaju lokalno srodstvo, a ne srodstvo određeno polom. Iako je korigovani indeks pripadnosti (AIc) ukazao na veću disperziju mužjaka, ova razlika nije bila statistički značajna. Ipak, uočeni rezultat zahtijeva dalje istraživanje sa većim uzorkom i širom prostornom distribucijom.

Ključne riječi: Bosna i Hercegovina, *Canis aureus*, pol, genetička struktura, genetička varijabilnost

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