

AGGREGATION PATTERN OF KASHMIR MARKHOR (*CAPRA FALCONERI CASHMERICENSIS*) POPULATION AT CHITRAL GOL NATIONAL PARK, PAKISTAN

Original Article

Shah Fahad Ali Khan^{1*}, Muhammad Khisroon¹, Mehroon Nisa², Shagufta Naz²

¹Department of Zoology, University of Peshawar, Peshawar, Pakistan.

²University of Chitral, Pakistan.

Corresponding Author: Shah Fahad Ali Khan, Department of Zoology, University of Peshawar, Peshawar, Pakistan, fahad@uoch.edu.pk.

Acknowledgement: We extend our sincere gratitude to the researchers, park authorities, and all contributors who made this study possible.

Conflict of Interest: None

Grant Support & Financial Support: None

ABSTRACT

Background: Grouping behavior in large mammals is influenced by various environmental and biological factors, including habitat type and seasonal variations. Understanding these dynamics is critical for the conservation of species like the Kashmir Markhor (*Capra falconeri cashmeriensis*), an endangered ungulate inhabiting rugged terrains. Despite its ecological significance, limited information exists on the seasonal and habitat-specific aggregation patterns of this species, particularly in regions like Chitral Gol National Park, Pakistan.

Objective: This study aimed to evaluate the effects of seasonal and habitat variations on the group size of Kashmir Markhor, providing insights into their behavioral ecology and informing conservation strategies.

Methods: Long-term observational data were collected from April 2019 to March 2021 in Chitral Gol National Park. Surveys were conducted biweekly using binoculars at randomly selected transects and vantage points. Seasonal variations in group size were analyzed using ANOVA, with a significance level of 0.05. Habitat types were categorized based on dominant vegetation, and differences in group size across habitats were assessed. Statistical analyses were performed using SPSS (version 22). Grouping criteria followed established methodologies, defining groups as individuals within a 75-meter radius.

Results: Markhor group size varied significantly across seasons ($p < 0.0001$). The largest groups were observed during winter (mean = 13.73) and the rut season (mean = 15.17), while the smallest groups were recorded in autumn (mean = 8.71) and the non-rut season (mean = 7.92). Female Markhor consistently formed larger groups than males, with significant seasonal variations ($p < 0.00001$). Habitat type had no significant impact on group size ($p = 0.979$), with the largest groups found in Chilghoza Forest (mean = 11) and the smallest in Mixed Woodland (mean = 9.57).

Conclusion: Seasonal variations significantly influenced the grouping patterns of Kashmir Markhor, with larger groups forming during resource-scarce and reproductive periods. Habitat types had minimal impact, emphasizing the importance of incorporating seasonal dynamics into conservation efforts.

Keywords: Aggregation, behavior, *Capra falconeri*, Chitral Gol National Park, ecology, group size, season.

INTRODUCTION

The aggregation patterns and grouping behaviors of prey species are a critical focus in ecological research, as grouping often serves as an adaptive defense mechanism against predation. The primary advantages of such behavior include a reduced predation risk and diminished individual vigilance requirements, allowing group members to allocate resources toward other essential activities (1, 2). Additionally, grouping behavior can be influenced by the distribution of resources (3), foraging benefits (4), social interactions (5), and thermoregulation (6). These factors often operate in tandem, interconnected in complex ways, and the dynamics of grouping behavior may vary depending on the ecological context or temporal framework of assessment (7). In mammals, several studies have indicated that group size is influenced by density-dependent factors and predator-prey interactions, as higher densities can increase predator contact rates and subsequent kill rates (8). For instance, research on elk (*Cervus elaphus*) in Yellowstone National Park demonstrated that population density significantly influenced group size, which in turn affected predator encounter rates and established a mechanism for density-dependent predation (9). Seasonal variations further modulate grouping behaviors, as documented in numerous studies across different species. For example, long-term research on red deer in Poland's Białowieża Primeval Forest revealed that group sizes varied seasonally, with the largest aggregations observed during fall and winter, correlating with increased vulnerability to wolf predation and the severity of winter conditions (Jędrzejewski et al., 1992). Similar patterns have been observed in other species, such as Japanese serow (11), white-tailed deer (12), sika deer (13), chital (14), and elk (15), underscoring the universal relevance of seasonality in shaping social structures and survival strategies.

Despite the extensive research on the ecology and behavior of Markhor (*Capra falconeri cashmeriensis*), including their population dynamics and conservation status (16, 17, 18), there remains a paucity of knowledge regarding the specific factors influencing their grouping behavior. Understanding these dynamics is critical, as group size and structure are essential behavioral responses to seasonal and habitat variations. A comprehensive investigation into these aspects will not only contribute to the broader ecological understanding of the species but also inform effective conservation strategies. This study aims to elucidate the aggregation patterns and behavioral responses of Markhor populations to environmental and seasonal variations, providing critical insights into their ecology and facilitating evidence-based management practices.

METHODS

The study was conducted at Chitral Gol National Park (CGNP), covering an area of 7,750 hectares within the Chitral district. Located at elevations ranging from 1,500 to 4,950 meters, the park comprises rugged Rocky Mountains and diverse land cover, including snow-covered zones, subalpine areas, herbaceous vegetation, mixed woodland, broad-leaved forest, desolate land, and barren ground (18, 19). It serves as a critical habitat for over 173 bird species, 42 mammalian species, and three amphibian species (19). The accessibility of the park was facilitated by a jeep route from Chitral town, allowing for transportation on foot or by vehicle. A map of the study area is provided to illustrate the terrain and ecological zones. Primary data collection was undertaken through direct field surveys of Markhor populations conducted between December 2019 and January 2022. Observations were systematically made on weekends, employing binoculars to monitor the species from randomly selected transects and vantage points. Surveys categorized the data into summer and winter seasons, following Beauchamp's (2007) grouping criteria, where any cohesive unit of individuals located within a 75-meter radius was considered a group. The study adhered to a detailed habitat classification system based on dominant vegetation types, following the guidelines proposed by Arshad et al. (2012). The identified habitats included subalpine coniferous forests, subtropical pine forests, mixed woodlands, scrub forests, and grasslands.

The statistical analysis utilized Analysis of Variance (ANOVA) to assess seasonal and habitat-based variations in group size, with significance levels set at 0.05. SPSS (version 22) was employed for all analyses, ensuring robust and reliable interpretations of the data. Ethical approval for this research was obtained from the institutional review board. The study complied with ethical research standards, and informed consent was not applicable as the study involved no direct interaction with human participants.

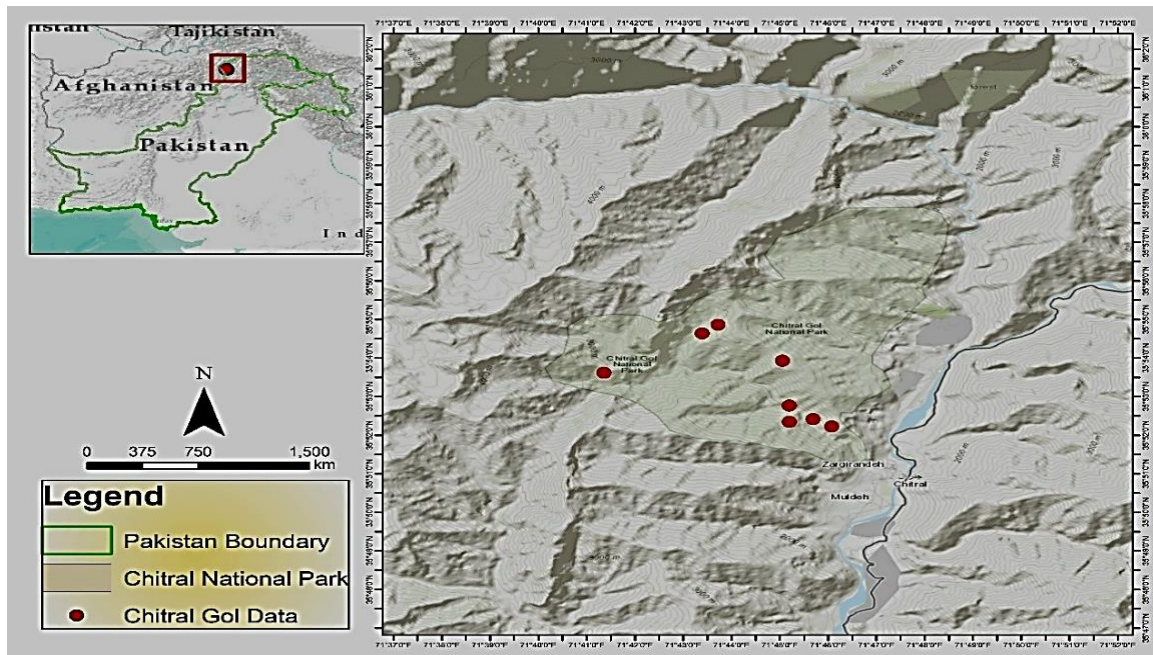
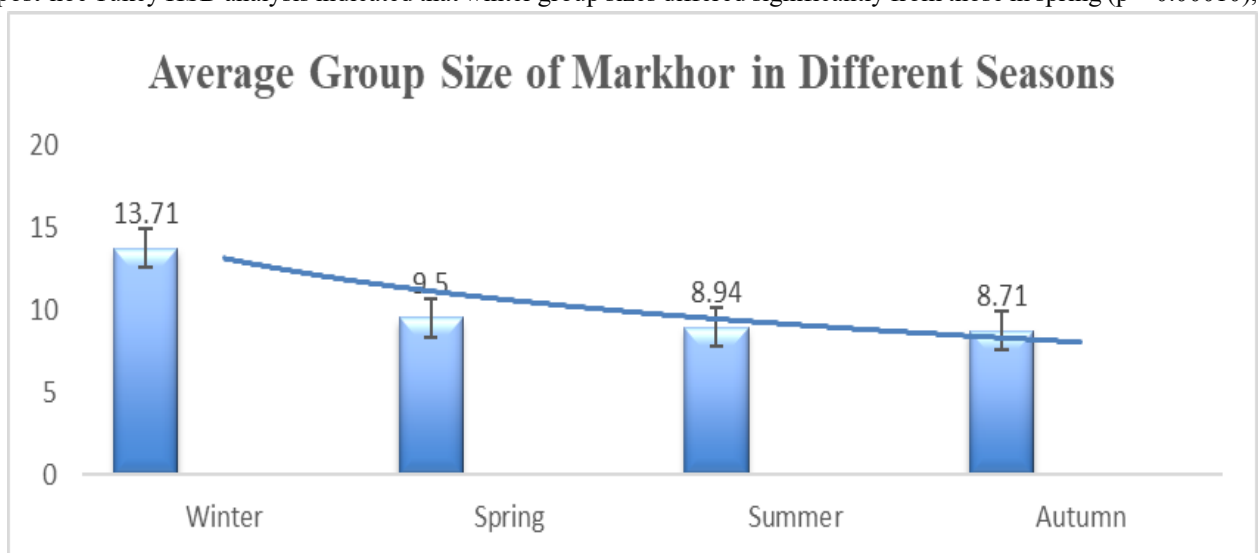


Figure 1 Map of the study area, Chitral Gol National Park

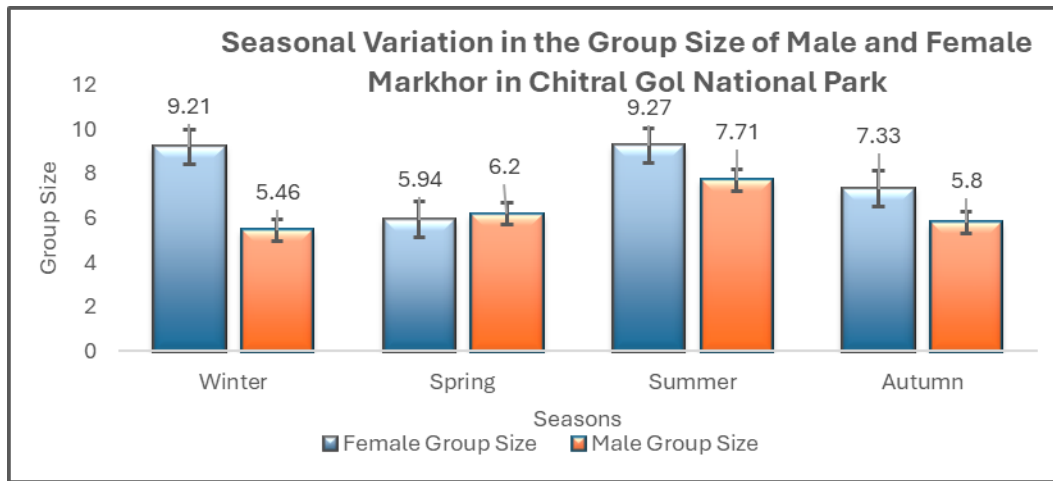
RESULTS

The study revealed significant seasonal variations in the group size of Markhor in Chitral Gol National Park. The largest average group size was observed in winter, with a mean of 13.73, while the smallest group sizes were recorded in autumn and summer, with means of 8.71 and 8.94, respectively. Statistical analysis using ANOVA confirmed a significant difference in group size across seasons ($p < 0.0001$). Further post-hoc Tukey HSD analysis indicated that winter group sizes differed significantly from those in spring ($p = 0.00010$), summer ($p = 0.00001$), and autumn ($p = 0.00000$).

During the rut season, group sizes were notably higher, with a mean of 15.17 compared to 7.92 during the non-rut season ($p < 0.00001$).

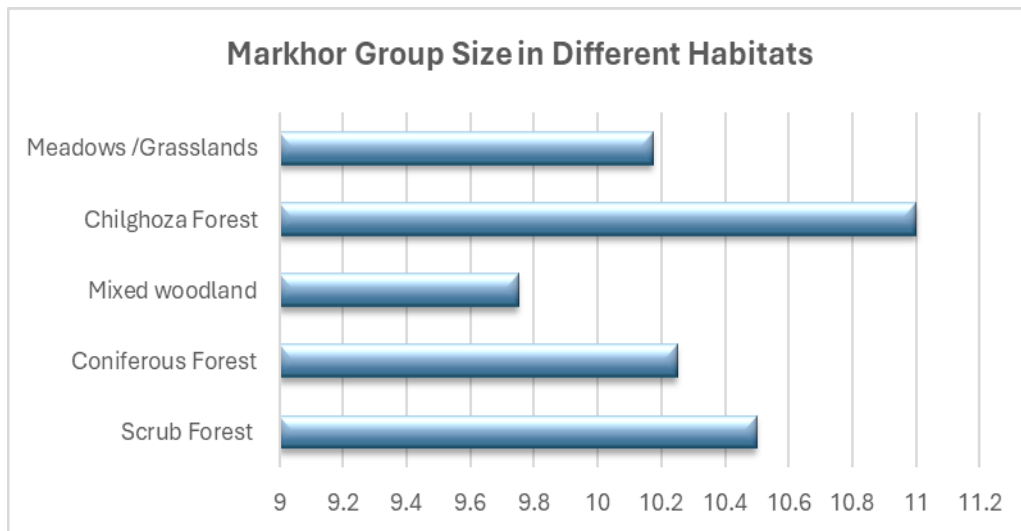


Female Markhor displayed significant seasonal variations in group size, with the largest groups recorded in summer (mean = 9.27) and winter (mean = 9.21), while the smallest groups were observed in spring (mean = 5.94) and autumn (mean = 7.33). ANOVA results indicated a significant difference in female group sizes across seasons ($p < 0.00001$). Post-hoc Tukey HSD analysis showed significant differences in winter compared to spring ($p = 0.00000$) and autumn ($p = 0.00778$). Similarly, summer group sizes significantly differed from spring ($p = 0.00000$) and autumn ($p = 0.00563$). However, no significant differences were observed in other pairwise seasonal comparisons.



ANOVA results indicated a significant difference in female group sizes across seasons ($p < 0.00001$). Post-hoc Tukey HSD analysis showed significant differences in winter compared to spring ($p = 0.00000$) and autumn ($p = 0.00778$). Similarly, summer group sizes significantly differed from spring ($p = 0.00000$) and autumn ($p = 0.00563$). However, no significant differences were observed in other pairwise seasonal comparisons.

In contrast, no significant seasonal variation was detected in the group sizes of male Markhor ($p = 0.1301$). The largest male group size was observed in summer (mean = 7.71), while the smallest was recorded in winter (mean = 6.20). The f-ratio value for males was calculated to be 1.9617. Tukey HSD analysis revealed that group size in summer was significantly larger than in spring ($p = 0.04417$), but no significant differences were found in other seasonal comparisons.



Group sizes across different habitat types exhibited no significant variation. The largest groups were observed in Chilghoza Forest, with a mean size of 11, while the smallest were recorded in Mixed Woodland Trees, with a mean size of 9.57 ($p = 0.979$). Female Markhor demonstrated the largest group sizes in grasslands (mean = 9) and the smallest in Mixed Woodland Trees (mean = 7.69), with no significant differences among habitat types ($p = 0.6154$). Male Markhor exhibited the largest group sizes in grasslands (mean = 7) and the smallest in scrub forests (mean = 4.71). While the differences in male group sizes across habitats approached significance ($p = 0.057$), they did not reach the threshold for statistical significance. The findings indicate that Markhor exhibit distinct seasonal grouping behaviors, particularly among females, while habitat type appears to have a less pronounced impact on group size.

While the differences in male group sizes across habitats approached significance ($p = 0.057$), they did not reach the threshold for statistical significance. The findings indicate that Markhor exhibit distinct seasonal grouping behaviors, particularly among females, while habitat type appears to have a less pronounced impact on group size.

Table 1 Seasonal variation in group size of Kashmir Markhor *Capra falconeri* in Chitral Gol National Park

	Winter	Spring	Summer	Autumn	Total
N	19	38	17	21	95
$\sum X$	261	361	152	183	957
Mean	13.73	9.5	8.94	8.71	10.07
$\sum X^2$	3815	3745	1432	1833	10825
Std.Dev.	3.57	2.92	2.13	3.45	3.54

Result Details

Source	SS	Df	MS	F Ratio	P value
Between-treatments	328.0731	3	109.35	11.62	0.0001
Within-treatments	856.4111	91	9.4111		
Total	1184.4842	94			

SS= Sum of Squares, Df= Degree of freedom, MS=Mean sum of squares, F value= F statistics, *Significantly different at 0.05 level

Table 2 Seasonal variation in group size of female Kashmir Markhor *Capra falconeri cashmerieinsis* in Chitral Gol National Park

	Winter	Spring	Summer	Autumn	Total
N	19	17	11	12	59
$\sum X$	175	101	102	88	466
Mean	9.21	5.94	9.27	7.33	7.89
$\sum X^2$	1641	619	968	696	3924
Std.Dev.	1.2727	1.088	1.4894	2.1462	2.0485

Result Details

Source	SS	Df	MS	F ratio	P value
Between-treatments	122.4423	3	40.8141	18.5599	< .00001
Within-treatments	120.9476	55	2.199		
Total	243.3898	58			

SS= Sum of Squares, Df= Degree of freedom, MS=Mean sum of squares, F value= F statistics, *Significantly different at 0.05 level

Table 3 Seasonal variation in group size Male Kashmir Markhor *Capra falconeri cashmerieinsis* in Chitral Gol National Park

	Winter	Spring	Summer	Autumn	Total
N	25	13	7	15	60
$\sum X$	155	71	54	87	367
Mean	6.2	5.46	7.71	5.8	6.11
$\sum X^2$	1057	441	446	565	2509
Std.Dev.	2	2.1062	2.2147	2.0771	2.1161

Result Details					
Source	SS	Df	MS	F ratio	P value
Between-treatments	25.124	3	8.3747	1.961	0.1301
Within-treatments	239.0593	56	4.2689		
Total	264.1833	59			

SS= Sum of Squares, Df= Degree of freedom, MS=Mean sum of squares, F value= F statistics, *Significantly different at 0.05 level

Table 4 Variation in group size Kashmir Markhor *Capra falconeri cashmeriensis* in different habitats in Chitral Gol National Park

	Scrub Forest	Coniferous Forest	Mixed woodland	Chilghoza Forest	Grasslands	Total
N	10	40	16	6	23	95
$\sum X$	105	410	156	66	234	971
Mean	10.5	10.25	9.75	11	10.174	10.221
$\sum X^2$	1283	4908	1790	820	2794	11595
Std.Dev	4.4783	4.2532	4.2348	4.3359	4.3343	4.2154

Result Details					
Source	SS	Df	MS	F ratio	P value
Between-treatments	8.05	4	2.0134	0.109	0.9790
Within-treatments	1662.3	90	18.47		
Total	1670.4	94			

SS= Sum of Squares, Df= Degree of freedom, MS=Mean sum of squares, F value= F statistics, *Significantly different at 0.05 level

Table 5 Variation in group size of female Kashmir Markhor *Capra falconeri cashmeriensis* in different habitats in Chitral Gol National Park

	Scrub Forest	Subalpine Coniferous Forest	Mixed Woodland	Subtropical Pine Forest	Grasslands	Total
N	9	32	13	6	11	71
$\sum X$	71	262	100	49	99	581
Mean	7.88	8.18	7.69	8.16	9	8.18
$\sum X^2$	581	2248	850	417	947	5043
Std.Dev	1.615	1.8217	2.5944	1.8348	2.3664	2.0306

Result Details					
Source	SS	Df	MS	F ratio	P value
Between-treatments	11.253	4	2.8133	0.66944	0.6154
Within-treatments	277.366	66	4.2025		
Total	288.619	70			

SS= Sum of Squares, Df= Degree of freedom, MS=Mean sum of squares, F value= F statistics, *Significantly different at 0.05 level

Table 6 Variation in group size of Male Kashmir Markhor *Capra falconeri cashmeriensis* in different habitats in Chitral Gol National Park

	Scrub Forest	Subalpine Coniferous Forest	Mixed Woodland	Subalpine Forest	Pine	Meadows/ Grasslands	Total
N	7	26	11	6		19	69
$\sum X$	33	143	54	32		133	395
Mean	4.71	5.5	4.90	5.33		07	5.72
$\sum X^2$	185	957	306	176		999	2623
Std.Dev.	2.2147	2.6115	2.0226	1.0328		1.9437	2.3065
Result Details							
Source		SS	Df	MS		F value	P value
Between-treatments		47.5971	4	11.899		2.424	0.0570
Within-treatments		314.171	64	4.9089			
Total		361.7681	68				

SS= Sum of Squares, Df= Degree of freedom, MS=Mean sum of squares, F value= F statistics, *Significantly different at 0.05 level

DISCUSSION

The findings of this study indicate that seasonal variations had a more pronounced influence on the mean group sizes of Markhor compared to habitat types. This observation aligns with prior research on ungulates, which highlights the significant role of environmental changes in shaping group dynamics. Larger group sizes recorded during the winter may reflect a survival strategy driven by resource scarcity and heightened vulnerability to predation, as previously documented in similar species (22). The increase in group sizes observed during the rut season underscores the influence of reproductive behaviors on social structures, a phenomenon widely recognized in ungulate ecology (23). These findings suggest that seasonal shifts in resource availability and mating patterns are pivotal drivers of social aggregation among Markhor populations, with implications for conservation strategies that should account for these temporal dynamics. Consistent with earlier studies, the tendency of larger groups to form in forested areas near grasslands highlights the importance of habitat heterogeneity in supporting social interactions among ungulates. Such environments may provide optimal conditions for foraging and predator avoidance, enabling group members to allocate more time to essential activities like feeding (28). The observed seasonal differences in male and female group sizes further emphasize the role of sex-specific ecological pressures in influencing social organization. Females were consistently found in larger groups than males, a pattern likely attributed to the increased predation risk faced by females and their offspring (35). This finding parallels studies on other ungulate species, where larger female group sizes were linked to enhanced vigilance and predator detection (34).

While the study provides valuable insights into the aggregation patterns of Markhor, several limitations warrant consideration. The absence of data on juvenile group sizes and mixed-sex group dynamics represents a gap in understanding the full spectrum of Markhor social behavior. Future studies could address this limitation by incorporating these variables, thereby providing a more comprehensive perspective on group composition and its ecological determinants. Additionally, the reliance on observational methods may introduce bias due to variability in detection probability across seasons and habitats. Standardized sampling protocols, including the use of remote camera traps, could enhance the accuracy and reliability of future data collection. The lack of significant differences in group sizes across habitat types suggests a degree of ecological plasticity in Markhor, which may enable them to adapt to varying environmental conditions. However, this finding should be interpreted cautiously, as factors such as habitat quality, food availability, and anthropogenic

disturbances were not explicitly quantified. Incorporating these variables into future research could elucidate the nuanced relationships between habitat characteristics and group dynamics.

The study's strengths lie in its robust temporal framework and the use of established statistical methods to analyze seasonal and habitat-based variations. These strengths provide a solid foundation for understanding the ecological and behavioral drivers of Markhor social organization. Nevertheless, the study would benefit from expanding its geographical scope to include other populations of Markhor, as this could reveal regional variations in aggregation patterns and inform broader conservation efforts. This study highlights the critical influence of seasonal factors on Markhor group sizes, particularly during periods of resource scarcity and reproductive activity. The findings underscore the importance of incorporating temporal and ecological variations into conservation planning, while also identifying key areas for future research to enhance the understanding of Markhor behavior and ecology.

CONCLUSION

This study concludes that seasonal variations play a pivotal role in shaping the grouping patterns of Markhor, with larger group sizes observed during winter and rut seasons, driven by resource scarcity and reproductive behaviors. The findings underscore the ecological importance of these adaptive responses, highlighting the interplay between environmental conditions, social dynamics, and survival strategies. Although habitat types showed less influence on group sizes, the study reinforces the necessity of considering seasonal dynamics and habitat preferences in conservation planning. These insights contribute to a deeper understanding of Markhor ecology and provide a foundation for designing targeted conservation efforts that address seasonal resource availability and ecological pressures.

AUTHOR CONTRIBUTIONS

Author	Contribution
Shah Fahad Ali Khan*	Substantial Contribution to study design, analysis, acquisition of Data Manuscript Writing Has given Final Approval of the version to be published
Muhammad Khisroon	Substantial Contribution to study design, acquisition and interpretation of Data Critical Review and Manuscript Writing Has given Final Approval of the version to be published
Mehroon Nisa	Substantial Contribution to acquisition and interpretation of Data Has given Final Approval of the version to be published
Shagufta Naz	Contributed to Data Collection and Analysis Has given Final Approval of the version to be published

REFERENCES

1. Wang, X., Yang, L., Zhao, Y., Yu, C., & Li, Z. (2020). [The group size effect and synchronization of vigilance in the Tibetan wild ass](#). *Current Zoology*, 67(1), 11-16.
2. Lazaro-Perea C. Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defence and assessment of neighbours. *Anim Behav.* 2001;62(1):11–21.
3. Beauchamp, G., & Li, Z. (2021). [A meta-analysis of the group-size effect on vigilance in mammals](#).
4. Herrera EA, Macdonald DW. Resource utilization and territoriality in group-living capybaras (*Hydrochoerus hydrochaeris*). *J Anim Ecol.* 1989;667–79.
5. Crook JH, Ellis JE, Goss-Custard JD. Mammalian social systems: structure and function. *Anim Behav.* 1976;24(2):261–74.
6. Cheng, L., Zhou, L., Bao, Y., & Mahtab, N. (2020). [Effect of conspecific neighbors on the foraging activity levels of the wintering Oriental Storks \(*Ciconia boyciana*\)](#). *Ecology and Evolution*, 10, 10384-10394.
7. van Niekerk, J. H., Forcina, G., & Megía-Palma, R. (2024). [Grouping behaviour and anti-predator responses in the Helmeted Guineafowl](#). *Birds*.
8. Atkins, A., Little, R., Redpath, S., & Amar, A. (2019). [Impact of increased predation risk on vigilance behaviour in a gregarious waterfowl, the Egyptian goose](#). *Journal of Avian Biology*.

9. Lung MA, Childress MJ. The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. *Behavioral Ecology*. 2007;18(1):12–20.
10. Jędrzejewski W, Jędrzejewska B, Okarma H, Ruprecht AL. Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieża National Park, Poland. *Oecologia*. 1992;90(1):27–36.
11. Takada H, Minami M. Do differences in ecological conditions influence grouping behaviour in a solitary ungulate, the Japanese serow? *Behaviour*. 2019;156(3–4):245–64.
12. Cherry MJ, Conner LM, Warren RJ. Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. *Behavioral Ecology*. 2015;26(4):1091–9.
13. Ping X, Li C, Jiang Z, Liu W, Zhu H. Interference competition and group size effect in sika deer (*Cervus nippon*) at salt licks. *Acta Ethol*. 2011;14(1):43–9.
14. Ramesh T, Sankar K, Qureshi Q, Kalle R. Group size, sex and age composition of chital (*Axis axis*) and sambar (*Rusa unicolor*) in a deciduous habitat of Western Ghats. *Mammalian Biology*. 2012;77(1):53–9.
15. Proffitt KM, Gude JA, Shamhart J, King F. Variations in elk aggregation patterns across a range of elk population sizes at Wall Creek, Montana. *J Wildl Manage*. 2012;76(4):847–56.
16. Ahmad S, Rehman EU, Ali H, Din N, Haider J, Din JU, et al. Density Pattern of Flare-Horned Markhor (*Capra falconeri*) in Northern Pakistan. *Sustainability*. 2022;14(15):9567.
17. Bashir M, Fazili MF, Ahmad F, Ahmad J. Dietary ecology of Markhor (*Capra falconeri cashmiriensis*) in winter range of Kazinag National Park, Kashmir, J&K, India. *Indian J Sci Technol*. 2020;13(24):2463–74.
18. Arshad M, Malik RN, Saqib Z. Assessing potential habitats of Kashmir Markhor in Chitral Gol National Park, Khyber Pakhtunkhwa, Pakistan. *Pak J Bot*. 2013;45(S1):561–70.
19. Qamar FM, Ali H, Ashraf S, Daud A, Gillani H, Mirza H, et al. Distribution and habitat mapping of key fauna species in selected areas of western Himalaya, Pakistan. *The Journal of Animal and Plant Sciences*. 2011;21(2):396–9.
20. Arshad M, Qamer FM, Saleem R, Malik RN. Prediction of Kashmir markhor habitat suitability in Chitral Gol National Park, Pakistan. *Biodiversity*. 2012;13(2):78–87.
21. Beauchamp G. Exploring the role of vision in social foraging: what happens to group size, vigilance, spacing, aggression and habitat use in birds and mammals that forage at night? *Biological Reviews*. 2007;82(3):511–25.
22. Bowyer RT, McCullough DR, Rachlow JL, Ciuti S, Whiting JC. Evolution of ungulate mating systems: Integrating social and environmental factors. *Ecology and evolution*. 2020;10(11):5160–78.
23. Raman TRS. Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India. *Journal of Biosciences*. 1997;22(2):203–18.
24. Wood E. Spatial Ecology and Resource Selection of Bighorn Sheep (*Ovis canadensis*) Ewes in a Prairie Badlands Population. 2020;
25. Sorato E, Gullett PR, Griffith SC, Russell AF. Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Animal Behaviour*. 2012;84(4):823–34.
26. Gower CN. Behavioral responses of elk to winter wolf predation risk in the Madison Headwaters Area, Yellowstone National Park. Montana State University; 2009.
27. Tettamanti F, Viblanc VA. Influences of mating group composition on the behavioral time-budget of male and female alpine ibex (*Capra ibex*) during the rut. *PLoS One*. 2014;9(1):e86004.
28. Creel S, Winnie Jr JA. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Anim Behav*. 2005;69(5):1181–9.
29. White PJ, Proffitt KM, Lemke TO. Changes in elk distribution and group sizes after wolf restoration. *The American Midland Naturalist*. 2012;167(1):174–87.
30. Brennan A, Cross PC, Creel S. Managing more than the mean: using quantile regression to identify factors related to large elk groups. *Journal of Applied Ecology*. 2015;52(6):1656–64.
31. Cotterill GG, Cross PC, Cole EK, Fuda RK, Rogerson JD, Scurlock BM, et al. Winter feeding of elk in the Greater Yellowstone Ecosystem and its effects on disease dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2018;373(1745):20170093.
32. Peterson LM, Weckerly FW. Male group size, female distribution and changes in sexual segregation by Roosevelt elk. *PLoS One*. 2017;12(11):e0187829.

33. Kie JG, Johnson BK, Noyes JH, Williams CL, Dick BL, Rhodes OE, et al. Reproduction in North American elk *Cervus elaphus*: paternity of calves sired by males of mixed age classes. *Wildlife Biol.* 2013;19(3):302–10.
34. Vander Wal E, Van Beest FM, Brook RK. Density-dependent effects on group size are sex-specific in a gregarious ungulate. *PLoS One.* 2013;8(1):e53777.
35. Vander Wal E, Yip H, McLoughlin PD. Sex-based differences in density-dependent sociality: an experiment with a gregarious ungulate. *Ecology.* 2012;93(1):206–12.