Current Zoology, 2025, **71**, 124–135
https://doi.org/10.1093/cz/zoae036
Advance access publication 26 June 2024
Original Article

Sexually differentiated decision-making involves faster recruitment in the early stages for the Tibetan antelopes *Pantholops hodgsonii*

Qin Zhu[a,], Jian Guan[b,**], Tianya Lei[a], Kun Xuan[a], Sile Guo[a], Yumeng Zhao[a], Changjian Fu[a], Le Yang[c] and Zhongqiu Li[a,*]**

[a]Lab of Animal Behaviour & Conservation, School of Life Sciences, Nanjing University, Nanjing, Jiangsu 210023, China
[b]School of Electronic and Information Engineering, Jinling Institute of Technology, Nanjing, Jiangsu 211169, China
[c]Department of Zoology, Tibet Plateau Institute of Biology, Lhasa 850000, China

[*]Address correspondence to Zhongqiu Li. E-mail: lizq@nju.edu.cn.
[**]These authors contributed equally to this work.
Handling editor: Janette Boughman

Abstract

Group living is widespread across diverse taxa, and the mechanisms underlying collective decision-making in contexts of variable role division are critical for understanding the dynamics of group stability. While studies on collective behavior in small animals such as fish and insects are well-established, similar research on large wild animals remains challenging due to the limited availability of sufficient and systematic field data. Here, we aimed to explore the collective decision-making pattern and its sexual difference for the dimorphic Tibetan antelopes *Pantholops hodgsonii* (chiru) in Xizang Autonomous Region, China, by analyzing individual leadership distribution, as well as the joining process, considering factors such as calving stages and joining ranks. The distinct correlations of decision participants' ratio with group size and decision duration underscore the trade-off between accuracy and speed in decision-making. Male antelopes display a more democratic decision-making pattern, while females exhibit more prompt responses after calving at an early stage. This study uncovers a partially shared decision-making strategy among Tibetan antelopes, suggesting flexible self-organization in group decision processes aligned with animal life cycle progression.

Key words: calving stage, decision-making, leadership, sexual differences, Tibetan antelopes.

Group living is a widespread phenomenon observed across diverse taxa. The benefits and costs of living in groups have been studied extensively (Krause and Ruxton 2002; Ward and Webster 2016; Ioannou and Laskowski 2023), and variation in these benefits and costs helps explain why there is such diversity in social behavior in the animal kingdom. Avoidance of predation risk is a widespread explanation for group living, while food competition and pathogen transmission are common costs (Ioannou and Laskowski 2023; Yan et al. 2024). To attain the benefits mentioned above, individuals within the group continually adapt their behavior and rhythm, responding to external social cues (Berdahl et al. 2018) based on their accumulated knowledge and experience (Duboscq et al. 2016). Other group members also respond concurrently, thereby facilitating social transmission and collective decision-making (Ioannou and Laskowski 2023). Group members synchronize their activities with those of the collective, thereby maintaining the spatio-temporal dynamics of the group.

Collective decision-making emerges from social feedback networks within a group (Planas-Sitjà et al. 2015). It involves collaborative consultation and response selection among group members (Ward and Webster 2016). However, studying these feedback scenarios in the real world can be difficult because numerous factors interact to shape decision-making process (Watzek et al. 2021). In particular, the ability and the tendency to communicate across the group regulate the dynamics of the decision-making scenarios (Conradt and Roper 2005). Group decision mechanisms can range from completely shared (e.g., consensus), such as in bird flocks (Farine et al. 2014), fish shoals (Ward et al. 2011), and social insect swarms (Carlesso et al. 2023), where most individuals contribute to most decisions, to completely unshared (e.g., leadership), such as those formed by some species of mammals, including primates (Anand and Radhakrishna 2022), cetaceans (Zwamborn et al. 2023), and some ungulates (Yan et al. 2024), where one or a few individuals consistently impose their preferences on other group members, leading to greater possibilities of negotiation or voting and shaping patterns of following and leadership (Krueger et al. 2014; Briard et al. 2015).

The mechanisms by which group-living animals collectively exploit resources, and the role of individuals in group decisions, are central issues for understanding social feedback networks in aggregation. Variation among individuals within social groups is being increasingly recognized as an

Received 17 May 2024; accepted 22 June 2024

important determinant driving group behaviors and shaping collective decisions. Attention has notably been paid to the existence of particular individuals behaving as leaders, or as informed individuals, and to their greater effect on collective decision-making than other group members (Conradt et al. 2009; Michelena et al. 2010). In ungulates, as in many other taxa, the "leaders" always have specific characteristics such as greater age (McComb et al. 2001, 2011), a specific sex (Bourjade and Sueur 2010; Ihl and Bowyer 2011). The leadership can also be influenced by the reproductive status (Sueur 2012), personality (Briard et al. 2015), dominance rank (Krueger et al. 2014), and social relationships between group members (Ramseyer et al. 2009). Thus, in the Plains zebra, *Equus burchellii*, lactating females trigger the harem movement more frequently since their needs are greater than those of their congeners (Fischhoff et al. 2007). While Michelena et al. (2010) demonstrate that in the Scottish blackface sheep, a slight difference in the sensitivity to conspecifics between bold and shy individuals has a strong impact on collective decision-making. Although conflicts of interest tend to disperse individuals (Ramos et al. 2015), ungulates make trade-offs between the motivation to stay within a group of congeners that do not all have the same needs (Rands et al. 2003) and the motivation to move away toward preferred food patches (Yan et al. 2024), thus usually succeed in reaching consensus decisions and traveling together (Conradt and Roper 2005).

The Tibetan antelope *Pantholops hodgsonii* (chiru) is an ungulate species endemic to the Qinghai-Tibet Plateau (QTP) (Schaller 1998). It is listed under first-class protection in China, included in Appendix I of CITES (CITES, 2017), and categorized as Near Threatened on the IUCN Red List (IUCN 2023). Despite the remoteness and vastness of their habitat, the species was at risk of extinction during the 1980s and 1990s as a result of poaching (Hu et al. 2020; Wu et al. 2021). Although the population has steadily increased from 2000 onwards (Schaller 2012), development of animal husbandry, infrastructure development (such as railways and highways), and fencing of pastureland are putting increasing pressure on this species (Xia et al. 2007; Fox et al. 2009). Currently, field studies on Tibetan antelopes are primarily focusing on specific behavioral traits or inter-species comparisons (Schaller et al. 2006; Yu et al. 2008; Luo et al. 2018, 2020; Yang et al. 2018), behavioral rhythms (Lian et al. 2007; Luo et al. 2023), spatial distribution (Hu et al. 2020; Zhang et al. 2021), seasonal migrations (Buho et al. 2011; Manayeva et al. 2011), and associated environmental influencing factors (Yin et al. 2006; Wu 2007; Wei and Xu 2020; Wu et al. 2021). As yet little was known of the collective decision-making pattern or the associated role division (leading and following process) among group members for the Tibetan antelope.

In order to study collective decision-making pattern in animal populations, acquiring high-resolution individual movement data is imperative. In recent years, the rapid advancement of bio-telemetry technologies (Krause et al. 2013; Kays et al. 2015) and remote sensing techniques (Lukeman et al. 2010; Anderson and Gaston 2013; Ling et al. 2019) has made this objective attainable. Presently, animal tracking devices based on the Global Positioning System have exhibited improved performance, facilitating the real-time acquisition of high-frequency, high-precision behavioral data from multiple individuals within a group (Langrock et al. 2013; Farine et al. 2016). However, the success rate of data recovery using such technology depends heavily on factors such as group size, group stability of the target groups, as well as variations in individual responses to the capture and device attachment procedures (Torney et al. 2018). Simultaneously, remote sensing technologies, exemplified by unmanned aerial vehicles (UAVs, drones) (Koh and Wich 2012; Christie et al. 2016), have undergone astonishing development. Leveraging their versatile control platforms, operators can non-intrusively capture animal group behaviors from distances of several kilometers away. And these platforms can adjust camera positions synchronously with changes in the morphology of the subjects, thus enhancing the quality of data acquisition. In addition, the relatively low cost and the increasing maturity of automated computer vision processing (Liu et al. 2014; Torney et al. 2016; Suruliandi et al. 2020) have increasingly endeared UAVs technologies to researchers in the field of animal behavior studies (Hughey et al. 2018).

In this study, we investigated the collective decision-making pattern and its associated leadership distribution for the Tibetan antelope, through the combination of field observations, and UAVs technologies. We aim to explore the mysteries of how these antelopes interact and coordinate their behaviors within groups, and the potential differences between male and female groups with regard to their calving stages. Studies have showed that the risk of making a mistake and settling on a bad option often decreases with the number of decision-makers (Sumpter and Pratt 2009; Conradt 2012). In principle, sharing of decisions is more profitable for groups than accepting the unshared decision (Conradt and Roper 2007), which may allow information pooling and, potentially, better decisions (Ward and Webster 2016). In this context, several ungulate species such as the horses (*Equus caballus*, *Euuus ferus przewalskii*), the Tibetan wild ass (*Equus kiang*) collectively revealed a shared decision-making strategy (Yan et al. 2024), and in 7 of the 10 ungulate species Smith et al. (2015) have reviewed, the adult females were responsible for most decision initiation, which highlighted the mechanism of widespread differences in decision-making between sexes.

In dimorphic species such as the Tibetan antelope, the larger size of males compared to females (Luo et al. 2023) results in different energy requirements, food selection, predator avoidance strategies, or activity budgets(Conradt 1998; Ruckstuhl and Neuhaus 2002). Because of these differences, males and females often live in segregated groups (Schaller et al. 2006), except during the breeding season when the energetic imbalance between sexes is reduced due to mating (Wei and Xu 2020). Segregation may also occur according to reproductive status, as pregnant and lactating females are more exposed to predators and have a higher energetic demand than non-pregnant and non-lactating females. Combined with potential kinship associations that exist within a group, these inter-individual differences make some antelopes more likely than others to initiate decision-making and to be followed by their conspecifics. Therefore, we hypothesize that: 1) the Tibetan antelope employs a shared decision-making strategy; 2) leadership distribution is sexually associated, and the decision-making process is related to the calving process.

Materials and Methods

Subjects and study sites

Our study was carried out at Chang Tang Nature Reserve and Siling Co Nature Reserve, Xizang Autonomous Region, China. Both of them are located in the QTP, the highest plateau in the world. The high altitude (above 4,500 m for Chang Tang Nature Reserve, and an average of 4,700 m for Siling Co Nature Reserve), intense solar radiation, low air temperature, and oxygen levels render these 2 reserves a unique environment that shapes animal behaviors.

The Tibetan antelope is exhibiting 2 residency types, migratory and non-migratory. Currently, the population of Tibetan antelopes exceeds 150,000 individuals, with their core habitat situated within the Chang Tang Nature Reserve. Tibetan antelopes residing in the surrounding areas of the Siling Co Nature Reserve in the southern Chang Tang region (Shenzha County and Bangor County) are considered non-migratory, whereas those inhabiting the northern Chang Tang region in Shuanghu County are migratory (Schaller 1998). The Tibetan antelope follows a harem polygyny mating system, wherein a male typically mates with most or all of the females within his harem, which consists of several females during the mating season, occurring from December to January. The calving season takes place from June to July (Luo et al. 2018), prior to which female Tibetan antelopes return to their calving ground and complete childbirth, predominantly from late June to early July, then return to breeding ground in July to August (Schaller et al. 2006; Wei and Xu 2020).

Data collection and extraction

We followed previously planned line transects among the three counties (Shenzha, Shuanghu, Nima) in Nagqu City from June to July 2022 (Supplementary Table S1). Each transect was traversed only once over the entire study. Groups encountered on the return trip would not be sampled. Since the time of data collection was largely restricted around the calving period of the Tibetan antelope, and currently no report has announced the migration pattern of males, we restrain the distance between sampling points on different dates to be more than 30 km to reduce the pseudopositive sampling caused by repeated collection of the same population.

At a certain distance (ranged from 1,000 to 2,500 m) away from the antelopes, drones were controlled by designated operators to fly to a specific altitude and conduct stable behavioral video recording. Before the former recording begins, the drone (Mavic 2 Pro, DJI, China) was initially ascended vertically to an altitude of 200 m above ground level and then maneuvered toward the target group. When antelopes appeared on the monitor, the drone descended gradually to a height of no less than 100 m, at which the study subjects exhibited no signs of distress (Yan et al. 2024). No predators or evident disturbances were observed during the recording. The video recording time was from 08:00 to 19:00 (GMT + 8), and the shooting angle of the camera was 90 °C. Each group was filmed for 10–20 min depending on the battery capacity of the drone.

We selected the segments with relatively stable shooting positions and those that have no repeated entries and exits of antelopes as the target clips for further analysis. Each individual was numbered at the beginning of the segments. We then labeled all individuals in the frame one by one with their types of behavior according to the time. The behavior types were classified into feeding, vigilant, resting, moving, and others as mentioned by Lian et al. (2007). Each member eventually had its identity and a timeline of behavior shifts (Fig. 1). The same process was adopted for 5 h:54 min:21 s of videos from 22 groups. The average group size is 18.083 ± 1.824 for females and 7.700 ± 0.978 for males.

Data analysis

Leadership, followership and decisons

We classified the shooting period into stages before (prior to the 1st of July) and after (1st of July and afterwards) the calving according to our field observation experience. When an individual changes its behavior, we regard the shift as an attempt. An attempt is considered a decision only when it receives responses from at least one other group member (You et al. 2013). The individual who initiates the decision is defined as the leader, while the individuals who respond are referred to as followers (Yan et al. 2024), each with a different order of precedence. The decision requires the follower to shift to the same behavior as the leader (the target behavior) before the leader makes the next shift (Figure 1).

The moment of the leader's behavioral shift is the decision initiation moment. The time from the emergence of the leader to the emergence of the last responder constitutes the decision duration/time during which the initiating behavior leads to a group's decision. Decision latency is the time between the behavior-shift of a follower and the previous follower. Thus, the interval between the behavior-shift moments of the leader's and the first follower is the decision latency of the first follower (Yan et al. 2024). Given the inherent challenge in discerning intentional recruitment in behavioral transitions, attempts without followers are not classified as failures and are excluded from subsequent analyses.

Random behavior shifting

Before proceeding with further analysis, a behavior random permutation model (BRP) was employed to evaluate whether the positioning of specific behavior type (i.e., feeding, vigilant, resting, moving, and others) within the behavioral sequence is random (Luo et al. 2023). The fundamental concept guiding the model implementation entails quantifying the frequency of various behaviors within a sequence and subsequently utilizing an algorithm to randomize these behaviors (i.e., the expected value/times of the co-occurrence of 2 types of behaviors, EV, and its highest probability of occurrence, NHP). The ensuing comparison between the randomized sequence (EV and NHP) and the original sequence (i.e., the observed value/times of the co-occurrence of 2 types of behaviors, OV) was then undertaken to discern potential relationships between any 2 behavior types (Supplementary material for the program code).

We ran 100,000 random permutations of the observed behavior data in each sample/individual. Wilcoxon signed-rank tests were used to compare the differences in mean values of EV-OV (NHP-OV). Instances of behavioral transitions significantly deviating from the expected distribution were categorized as an individual's habitual response (internal-driven action), rather than responses to the initiation of any leaders (external-driven action). Therefore, these highly correlated behavior types were excluded from the corresponding sequences before all subsequent leader–follower analyses.

Leadership distribution

The leadership score (LS_i) of individual i was calculated as:

$$LS_i = \frac{L_i}{D_{\text{group}}},$$

where L_i is the leading times of individual i and D_{group} is the total decision times of the whole group.

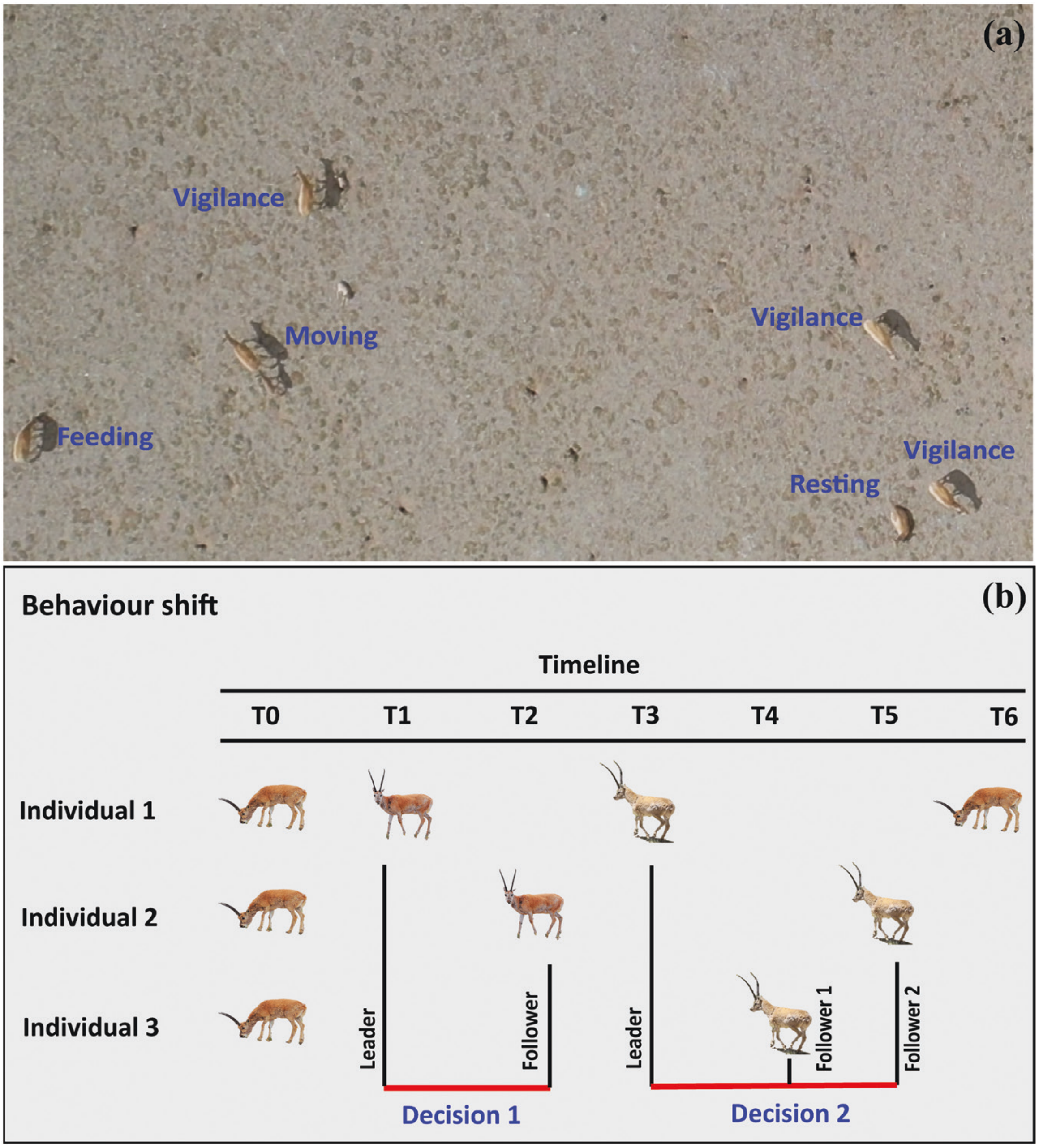

Figure 1. A schematic illustration of behavioral transitions and the decision-making process for Tibetan antelopes.

Leading probability (L_p) focused only on individual performance and was represented by leading times (L_i) divided by the sum of an individual's leading times and following times (F_i):

$$L_p = \frac{L_i}{L_i + F_i}.$$

The mean value of L_p for each sex was then served as thresholds to differentiate habitual leaders from others. Those members who never lead nor follow were regarded as "non-joiner" ($L_i = F_i = 0$). Individuals whose L_p surpass the mean value of the same sex ($L_{p_i} > L_{p_{male}}$ or $L_{p_i} > L_{p_{female}}$, where L_{p_i} is the leading probability of individual i, $L_{p_{male}}$, and $L_{p_{female}}$ were mean values of L_p for each sex) were regarded as "habitual leaders," while those below were classified into "habitual followers."

We used the Gini coefficient (G), which is commonly used to evaluate income inequality in economics, to quantify the degree of inequality of leadership distribution among the Tibetan antelopes. G was originally applied to evaluate wealth distribution, but in biology and sociology, it has been increasingly used to measure the degree of inequality in animal behavior. For example, the flight activity among the foraging honeybee *Apis mellifera* (Tenczar et al. 2014; Klein et al. 2019), the leadership distribution among the Tibetan wild ass *Equus kiang* (Yan et al. 2024), and the contributions of helpers in wild Kalahari meerkats *Suricata suricatta* (Rotics and Clutton-Brock 2021).

Following Yan et al. (2024), we evaluated the degree of inequality of leadership distribution among the Tibetan antelopes by examining the skew of leadership scores for all antelopes by computing an adjusted Gini index (G_a), which corrects small group size bias (Banerjee et al. 2021) with values comprised between 0 (if all individuals contributed equally) and 1 (if only one individual performed, that is, completely unequal):

$$G_a = \frac{\sum_i^n \sum_j^n \left|LS_i - LS_j\right|}{2\,(n-1)},$$

where LS_i and LS_j are leadership scores of individual i and j which belong to the group with n individuals.

We evaluated the effects of group size, sex, calving stage, and their interactions (fixed factors) on both decision times and Gini coefficient (response variables) by utilizing GLMM analysis with the *lmerTest* R package (Kuznetsova et al. 2017). We included group identity as a random factor to account for the interdependencies among data derived from the same group. By employing correlation analysis, we explored the potential impact of both group size and the proportion of participants on the duration of decision-making processes.

Joining process of the decision-making

Moreover, we studied individual latencies for joining group behavior-shift decisions (i.e., the latency of a follower j is the time between the behavior-shift of follower j and the previous follower $j-1$) by performing survival analysis and curve estimation. A linear distribution of the survival curve reveals that the probability of an antelope joining the decision is dependent on time, while a power or exponential distribution means that this probability is not dependent on time but rather on the number of individuals that have already joined the movement (Sueur et al. 2009; Ramos et al. 2015; Yan et al. 2024). In addition, we used curve estimation to assess the relation between the distribution of average latencies and the joining rank of followers. If this distribution follows a non-linear function, the joining process can be inferred to be a mimetic phenomenon (Ramos et al. 2015).

A comparative analysis of the decision latency as well as for the decision duration on male and female groups before and after the calving were conducted for the first 3 joining steps (the joining latency for the 1st, 2nd, and 3rd followers) given that only 8.48% of all decision events had more than three followers. We applied nonparametric Kruskal–Wallis analyses of variance to decision latency and decision duration given their abnormal distributions. Subsequently, Dunn's test was conducted to assess the post hoc pairwise differences among the testing groups.

In order to explore the potential trade-offs Tibetan antelopes exhibited between decision-making efficiency and accuracy, the proportion of participants was ascertained by dividing the total number of leaders and followers actively involved in each decision-making event by the group size. Thereafter, any correlations among the proportion of participants, the decision duration, and the group size were examined with the psych R package (William 2024). The "holm" correction was performed to adjust the probabilities for multiple tests.

The BRP analysis was conducted with MATLAB (R2023b). All other statistical analyses were performed in the R statistical computing environment v4.0.5. The level of statistical significance was set as $P = 0.05$. All data were reported as mean ± *SE*.

Results

Among the 1,383 times of potential leading-following events (Supplementary Table S3), we identified 330 times of decisions (Supplementary Table S4) for 22 groups (131 and 199 times for female and male groups, respectively) after RBP analysis (Supplementary Table S2). Most of the highly correlated transition sequences are linked to movement behavior, such as the mutual transition between movement and foraging, as well as vigilance. The G_a of leadership disrtibution ranges from 0.197 to 0.802, with a mean of 0.403 (SE = 0.166), and G_a for female groups is marginally significantly higher than that of males (0.455 ± 0.157 vs 0.341 ± 0.161; Wilcoxon rank sum test, $W = 89$, $P = 0.059$). Decision times are interactively affected by group size, sex, and calving stage (Table 1). As group size increases, there is a significant decrease in the proportion of participants involved in decision-making ($r = -0.765$, $P < 0.001$), while the proportion of participants is positively correlated with the decision duration simultaneously ($r = 0.397$, $P < 0.001$; Figure 2).

Decision-making pattern

In Tibetan antelope, individuals take different roles in leading behavior-shift decisions. In each group, 1–9 antelopes were identified as habitual leaders. Among 86% (19/22) of the groups, the proportion of habitual leaders did not exceed half. The mean leadership probabilities were comparable between males and females, yet there was a statistically significant difference in their variances (Figure 3; Bartlett test, Bartlett's *K*-squared = 8.738, $P = 0.003$). Females exhibited higher variance, indicating less homogeneity in role division (A subset of individuals excels in initiation, while another subset demonstrates a preference for following) while making decisions compared to males. Virtually all female habitual leaders exhibited decision-leading frequencies above the mean, while the decision-leading frequencies of male habitual leaders were randomly distributed on both sides of the evenly shared leadership line (Figure 3), elucidating that the role division within the male group exhibits a more democratic distribution while making decisions.

Joining process of the decision-making

Survival analysis and curve estimation showed that the decision latency follows a exponential distribution for males in both before- ($R^2 = 0.934$, $F_{1,420} = 7047.11$, $P < 0.001$, $y = 1.053 \times {}^{-0.031}$, $R^2_{\text{exponential}} > R^2_{\text{power}} > R^2_{\text{linear}}$) and after- ($R^2 = 0.939$, $F_{1,125} = 3478.284$, $P < 0.001$, $y = 0.839 \times {}^{-0.013}$, $R^2_{\text{exponential}} > R^2_{\text{power}} > R^2_{\text{linear}}$) the calving, for females before the calving ($R^2 = 0.953$, $F_{1,551} = 1764.89$, $P < 0.001$, $y = 0.852 \times {}^{-0.01}$, $R^2_{\text{exponential}} > R^2_{\text{power}} > R^2_{\text{linear}}$). While for the female groups after the calving, the fitting of the power function was better ($R^2 = 0.923$, $F_{1,265} = 2309.895$, $P < 0.001$, $R^2_{\text{power}} > R^2_{\text{exponential}} > R^2_{\text{linear}}$) (Figure 4). All these indicating that the joining process of the Tibetan antelopes depends on the number of antelopes that have already joined the decision. The distribution of mean latency according to the joining rank of followers did not follow any obvious pattern for both sexes (Supplementary Table S5).

Owing to the fact that in the vast majority (125/131) of decision-making processes among females, the number of participants did not exceed 3, we conducted sex comparisons for the first, second, and third joining latency, as well as the decision duration. We found decision-joining differentiation between sexes occurred for the first joining latency. The first decision latency among females after the calving is smaller

Table 1. Results of GLMMs evaluating the effect of group size, sex, calving stage on the Gini index and decision times of the Tibetan antelopes.

	Estimates	Std. error	*t* value	*P* value
Gini Index				
Intercept	0.919	0.638	1.440	0.172
Group size	−0.023	0.030	−0.783	0.447
Sex	−0.587	0.690	−0.851	0.409
Stage	−0.656	0.655	−1.001	0.334
Group size × Sex	0.015	0.049	0.309	0.761
Group size × Stage	0.035	0.031	1.143	0.272
Sex × Stage	0.970	0.730	1.329	0.205
Group size × Sex × Stage	−0.058	0.053	−1.085	0.296
Decision times				
Intercept	−1.256	38.373	−0.033	0.974
Group size	0.965	1.780	0.542	0.596
Sex	−8.274	41.485	−0.199	0.845
Stage	4.147	39.420	0.105	0.918
Group size × Sex	2.270	2.918	0.778	0.450
Group size × Stage	−0.658	1.848	−0.356	0.727
Sex × Stage	−59.617	43.908	−1.358	0.196
Group size × Sex × Stage	***8.070***	***3.207***	***2.516***	***0.025***

Significant *P* values are in bold.

Figure 2. Correlation analysis of the proportion of decision participants, decision duration, and group size. Asterisks are labeled as indicators for statistical significance (* represents for $P \leq 0.05$, ** represents for $P \leq 0.01$, *** represents for $P \leq 0.001$).

than that of males after the calving, as well as of females before the calving. It is notable that, unlike males whose decision duration lengthens after the calving stage, female antelopes appear to abbreviate their decision duration postpartum. Furthermore, the decision duration for females is significantly lower than that of males (Figure 5).

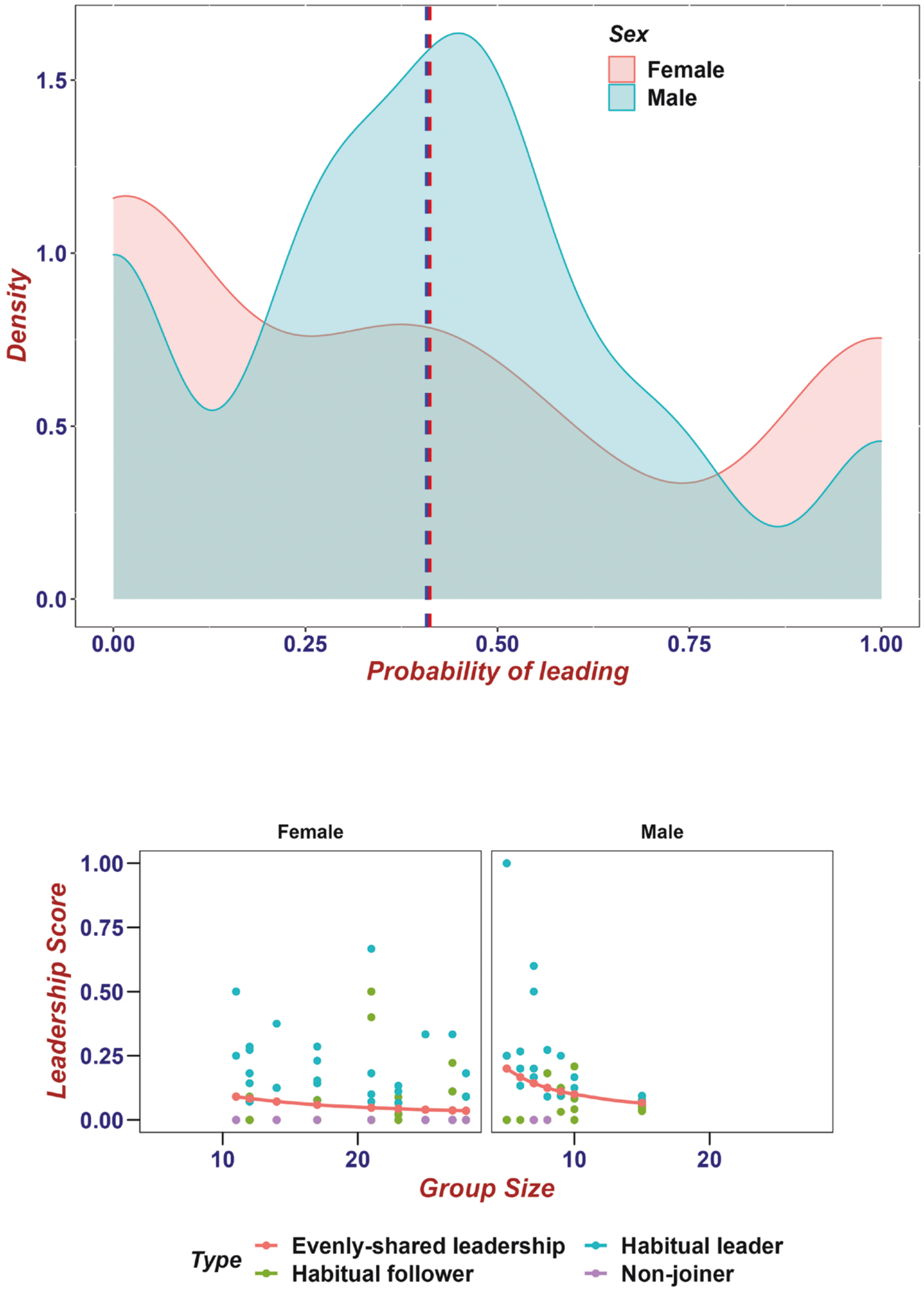

Figure 3. The density of leading probability (the upper panel) for all antelopes and their leadership score distribution with regard to their role categorization (panel at the bottom; habitual leaders, habitual followers, and non-joiner). The dashed lines in red and blue represent the mean value of leading probability for female and male respectively. The red solid line represents leadership score when leadership was evenly shared among group members (1/*n*).

Discussion

This study first investigated the collective decision-making pattern and its potential sexes difference for the Tibetan antelopes, by analyzing individual leadership scores and exploring their within-group distribution, as well as correlating the joining latency of decision-making with sexes, calving stages, and the joining ranks. We conducted behavior-shifting data analysis and found that the joining process depends on the number of antelopes that have already joined the decision. Tibetan antelopes demonstrate a partially shared decision-making mechanism, with males exhibiting a more democratic distribution of leadership. The decision-making

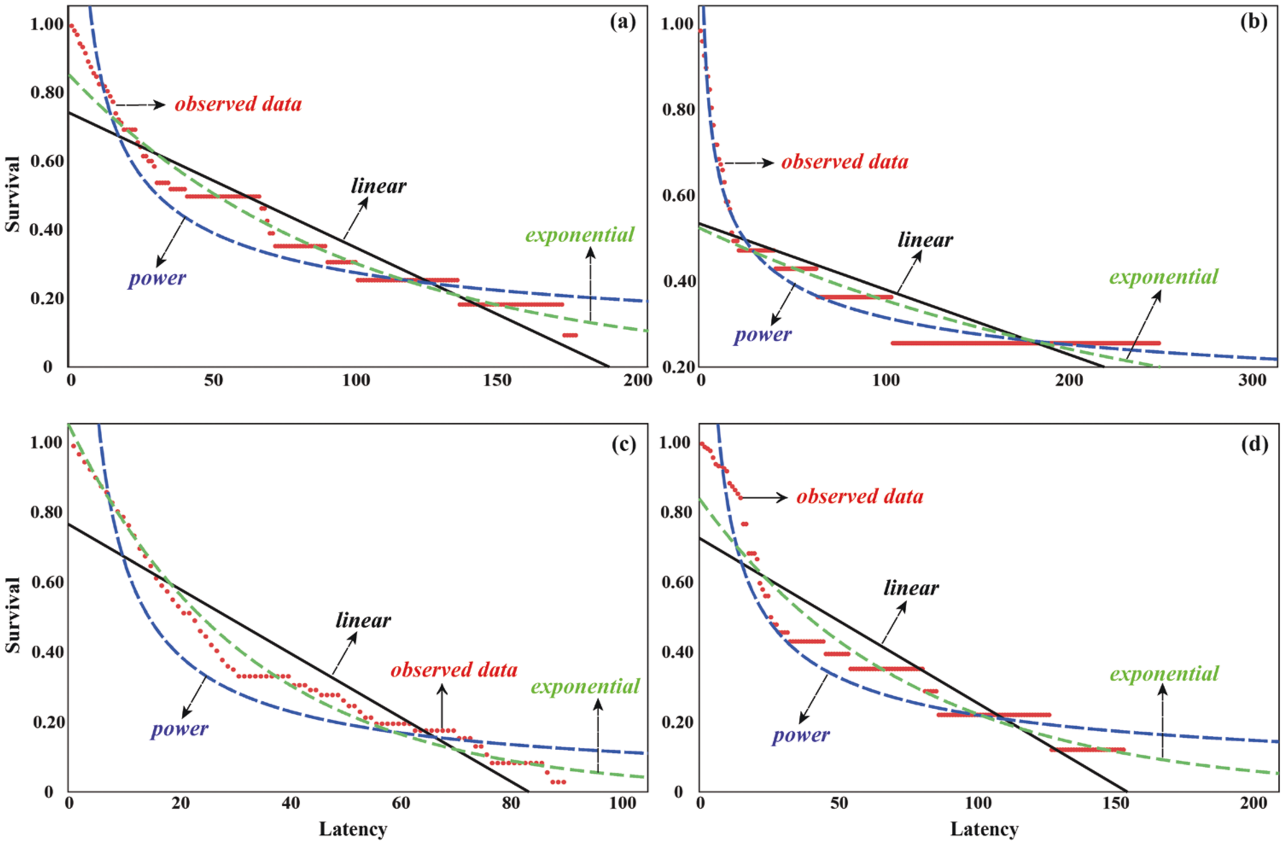

Figure 4. Distribution of decision latency for the Tibetan antelope. English letters on the top-right corner of each panel (a, b, c, d) represent for female group before the calving, female group after the calving, male group before the calving, male group after the calving respectively. The relationship between the two variables were indicated with dashed arrows in each panel.

process involves a trade-off between decision speed and accuracy, with females displaying significantly shorter decision duration and faster decision response rates at early stage, particularly post-calving.

Unequally shared decision-making strategy

Generally, the Tibetan antelopes use partially shared decision-making mechanisms in their behavior-shifting decisions. Decisions in group-living animals are usually made under uncertainty, which means individuals lack certain information about at least some aspects of the matter under consideration (Couzin et al. 2005; Sumpter and Pratt 2009). As a consequence, game theory suggests sharing decision-making is more beneficial for the majority of group members given its advantage of helping eliminate individual errors through pooling personal information from several decision-makers (Conradt and Roper 2007; Ward et al. 2011; Conradt 2012). This may be the case for the Tibetan antelopes, as they live in highlands where food resources are relatively scarce (Schaller 1998; Lian et al. 2007) and are being increasingly affected by infrastructure development (Wu et al. 2021), competition from domestic animals, and so on (Hu et al. 2020), making it particularly important to utilize information aggregation and collective intelligence beyond the wisdom of crowds (Sasha and Johnstone 2002; Kameda et al. 2022).

Tibetan antelope shows uneven leadership distribution, with only partial members taking charge of the decision initiation (Figure 3). Generally, the unequally shared decision-making strategy is believed to be related to sex, age, experience, personality, and energy level, which affect the decision system and how individuals react to the environment (Ramos et al. 2015; Yan et al. 2024). The observed differences in role division between sexes in decision-making further substantiate this assertion. As the last migratory ungulate in China, the female Tibetan antelope has the perilous mating/calving migrations and a high energy-consuming calving period in its annual life cycle. Compared to their male congeners, female antelopes may face higher survival threats throughout the year. Therefore, females exhibiting a propensity for decision initiation rather than following may be indicative of those possessing extensive survival experience (Ramos et al. 2021), particularly among the older cohort like other ungulate species (Briard et al. 2015). Conversely, females consistently adopting a follower role without initiating decisions likely encompass a subset of sub-adult females cohabiting with adult females but characterized by relatively limited survival experience (Fischhoff et al. 2007; Bourjade et al. 2009; Smith et al. 2015).

Behavioral syndromes may also be involved in leading to inter-individual variation in behavioral tendencies across contexts (Sih 2013) for Tibetan antelopes. A syndrome involving exploratory behavior, fearfulness, and response to environmental change (i.e., antipredator activity) has been identified in a number of ungulates and termed the "proactive-reactive axis" (Réale and Festa-Bianchet 2003; Sih et al. 2004; Found and Clair 2016). Proactive elk (*Cervus canadensis*) were characterized by greater exploration of novel objects, increased vigilance, and a greater frequency of leading other elks to new habitats (Found and Clair 2016); while a study of sheep,

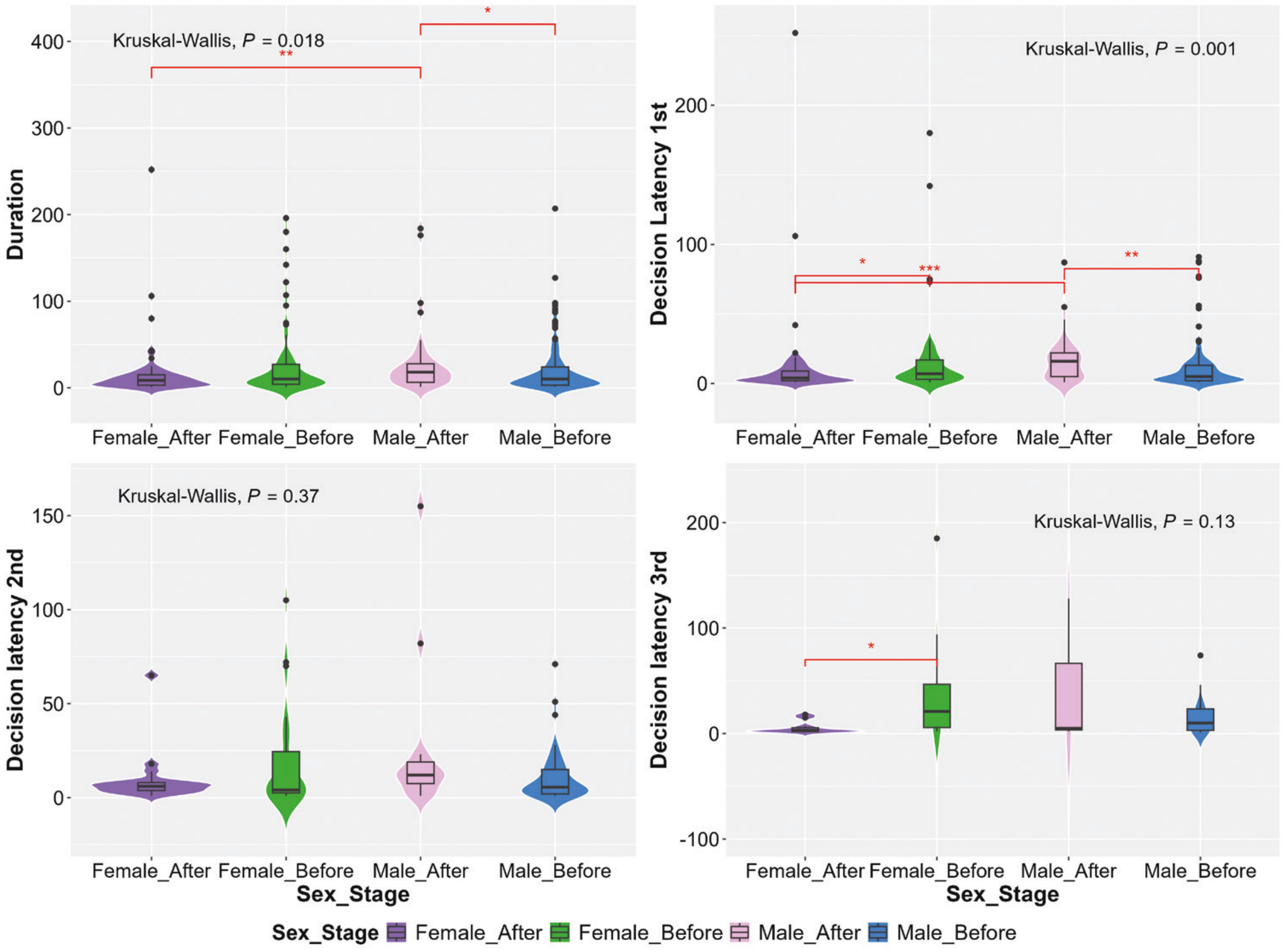

Figure 5. Comparisons of the decision duration and the first, second, and third joining latency for female and male groups before and after the calving stage. Asterisks are labeled as indicators for statistical significance (* represents for $P \le 0.05$, ** represents for $P \le 0.01$, *** represents for $P \le 0.001$).

Ovis aries, found that stress responses were related to lower willingness to eat novel foods (Villalba et al. 2009). For the Tibetan antelope, inhabiting an environment characterized by insufficient food resources, the variations in their capacity to differentially respond to conspecific competition, plant defenses, and fluctuating environmental conditions, alongside individual differences in personality and food preference, as well as social hierarchy, may influence the intensity of their behavioral tendencies. Consequently, this may result in more frequent decision-making by certain individuals. For example, antelopes exhibiting more selective feeding habits are more likely to explore various habitat patches, thereby initiating movement and foraging decisions more frequently. While individuals with lower social status may predominantly engage in alert-related decision-making in most scenarios.

Trade-off between decision accuracy and speed

The progression of decision-making in Tibetan antelopes depends on how many individuals have already joined the decision, and this process is flexibly regulated by the size of the group and the ratio of decision-making participants. The markedly distinct correlations observed between the proportion of participants and group size, as well as between group size and decision duration (with one being positive and the other negative), suggest a counterintuitive relationship. Specifically, as group size escalates, there is a corresponding constriction in the breadth of decision-making information spreading. This discovery further corroborates the notion posited in previous research that an increase in group size does not invariably enhance member engagement (Dyer and Chittka 2004; You et al. 2013). These results highlight the trade-off between accuracy and speed in Tibetan antelope during decision-making, which underscore the inherent complexity within group dynamics and offer novel insights into the collective behavior of social groups.

The involvement of fewer individuals in decision-making may help prevent the introduction of erroneous information associated with excessive participants as well as lead to a faster rate of information transmission (Ward et al. 2008). This strategy is crucial for the survival of Tibetan antelopes. The harsh conditions on the Qiangtang Plateau, which are typical of limited aboveground biomass resources and a widespread presence of medium- and large-sized wild predators (the Wolf *Canis lupus*, the Tibetan blue bear *Ursus arctos pruinosus* as well as the Snow leopard *Panthera uncia*), all exerting pressure on Tibetan antelopes. Under such background, Tibetan antelopes must make precise decisions without expending too much energy to sustain their survival and reproductive needs.

Sexually differentiated decision-making involves faster recruitment in the early stages

Female groups exhibited significantly shorter joining latency of the first follower after calving when compared to most other sex-calving stage categories (Figure 5). Despite the absence of brood-rearing behavior in these female groups during the data collection period, our result indicates a divergence in decision-making patterns between sexes following calving. One plausible reason is the variation in the interaction among individuals arising from differing levels of predation risk before and after the calving, which has long been recognized as a lethal threat factor for female ungulates during lactating (Lian et al. 2007; Berg et al. 2021). For our case, female and brood-rearing groups remain within the same calving ground in each county, where the number of predators such as the Common raven *Corvus corax* and the Wolf increases with the number of newborn lambs. Concurrently, the males disperse to other areas characterized by lower predation risk. The higher tightness in the female individuals after the calving made them respond quicker to group members (Lian et al. 2007). Another probable reason is the more intense resource competition on the calving ground following parturition, as opposed to the pre-calving period. This competition likely facilitates quicker feedback from the followers.

While this study has yielded significant findings, it is essential to acknowledge its limitations. First, the inherent challenges in conducting continuous follow-up studies on stationary field populations restricted our access to complete behavioral data for specific populations throughout their entire experimental cycles. This limitation prevented us from fully elucidating potential changes in decision-making patterns within fixed groups. Second, we currently lack data on the relative spatial distribution of individuals within the groups and have not yet detailed the relative positional associations based on behavioral shifts. These aspects are crucial for understanding the differentiated behavioral change strategies exhibited by group-living individuals. Finally, it will be imperative to include the nursery group in future analyses and thoroughly explore decision-making patterns across a wider range of group categories, with a particular focus on understanding the impact of the offspring proportion on the collective decision-making for the Tibetan antelopes. Therefore, we advocate the more comprehensive combined use of field validation and high-precision technologies in future research to effectively investigate collective decision-making patterns and their sexual differentiation in Tibetan antelopes.

Acknowledgment

We would like to thank Qiong Wu, Andi, and Shiqi for conducting fieldwork. We are grateful to Shiping Mao from the Forestry and Grassland Bureau of Nagqu City, Xizang Autonomous Region, to Taqing from the Bureau of Natural Resources of Shenzha County, to Gesang Lunzhu from the Bureau of Natural Resources of Nima County, for their help on the fieldwork preparing.

Funding

This study was financially supported by the National Natural Science Foundation of China (Grant no. 32101237), the China Postdoctoral Science Foundation (Grant no. 2021M691522), the National Key Research and Development Program (Grant no. 2022YFC3202104), and the Tibet Major Science and Technology Project (Grant no. XZ201901-GA-06). The funders had no role in study design, data collection, and analysis, decision to publish, or preparation of the manuscript.

Conflict of Interest

All authors declared no conflict of interests.

Authors' Contributions

Q.Z., J.G., and Z.Q.L. conceived and designed the study. Q.Z., Z.Q.L., and L.Y. provided funding support. S.L.G., Y.M.Z., and C.J.F conducted fieldwork for collecting data. Q.Z., J.G., T.Y.L., and K.X. processed, and analyzed the data. Q.Z. wrote the first manuscript and J.G. and Z.Q.L. reviewed and edited the draft. All authors read the draft and contributed to the discussion and completion of the final manuscript.

Data Availability

All original data that support the findings of this study are available in the supplementary material.

Ethics Statement

Our study entailed noninvasive behavioral observation for wild Tibetan antelopes without any manipulation experiments. Our data were collected through permission of the Forestry and Grassland Bureau of Nagqu City, Xizang Autonomous Region in accordance with Chinese wildlife laws. All the observational protocols in this study were approved by the Chinese Wildlife Management Authority.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

References

Anand S, Radhakrishna S, 2022. Collective movement decision-making in primates in crop-raiding contexts. *Behav Processes* **196**:104604.

Anderson K, Gaston KJ, 2013. Lightweight unmanned aerial vehicles will revolutionize spatial ecology. *Front Ecol Environ* **11**:138–146.

Banerjee I, Warnier M, Brazier FMT, Helbing D, 2021. Introducing participatory fairness in emergency communication can support self-organization for survival. *Sci Rep* **11**:7209.

Berdahl AM, Kao AB, Flack A, Westley PAH, Codling EA et al., 2018. Collective animal navigation and migratory culture: From theoretical models to empirical evidence. *Philos Trans R Soc London Ser B* **373**:20170009.

Berg JE, Reimer J, Smolko P, Bohm H, Hebblewhite M et al., 2021. Mothers' movements: Shifts in calving area selection by partially migratory elk. *J Wildl Manage* **85**:1476–1489.

Bourjade M, Sueur C, 2010. Shared or unshared consensus for collective movement? Towards methodological concerns. *Behav Processes* **84**:648–652.

Bourjade M, Thierry B, Maumy M, Petit O, 2009. Decision-making in Przewalski horses (*Equus ferus przewalskii*) is driven by the ecological contexts of collective movements. *Ethology* **115**:321–330.

Briard L, Dorn C, Petit O, 2015. Personality and affinities play a key role in the organisation of collective movements in a group of domestic horses. *Ethology* **121**:888–902.

Buho H, Jiang Z, Liu C, Yoshida T, Masuda R, 2011. Preliminary study on migration pattern of the Tibetan antelope (*Pantholops hodgsonii*) based on satellite tracking. *Adv Space Res* **48**:43–48.

Carlesso D, McNab JM, Lustri CJ, Garnier S, Reid CR, 2023. A simple mechanism for collective decision-making in the absence of payoff information. *Proc Natl Acad Sci USA* **120**:e2216217120.

Christie KS, Gilbert SL, Brown CL, Hatfield M, Hanson L, 2016. Unmanned aircraft systems in wildlife research: Current and future applications of a transformative technology. *Front Ecol Environ* **14**:241–251.

CITES, 2017. Convention on International Trade in Endangered Species of Wild Fauna and Flora. Appendices I, II and III [cited 2023 September 07]. Available from: https://cites.org/sites/default/files/eng/app/2017/E-Appendices-2017-10-04.pdf.

Conradt L, 1998. Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proc Biol Sci* **265**:1359–1363.

Conradt L, 2012. Models in animal collective decision-making: Information uncertainty and conflicting preferences. *Interface Focus* **2**:226–240.

Conradt L, Krause J, Couzin ID, Roper TJ, 2009. "Leading according to need" in self-organizing groups. *Am Nat* **173**:304–312.

Conradt L, Roper TJ, 2005. Consensus decision making in animals. *Trends Ecol Evol* **20**:449–456.

Conradt L, Roper TJ, 2007. Democracy in animals: The evolution of shared group decisions. *Proc Biol Sci* **274**:2317–2326.

Couzin ID, Krause J, Franks NR, Levin SA, 2005. Effective leadership and decision-making in animal groups on the move. *Nature* **433**:513–516.

Duboscq J, Romano V, MacIntosh A, Sueur C, 2016. Social information transmission in animals: Lessons from studies of diffusion. *Front Psychol* **7**:1147.

Dyer AG, Chittka L, 2004. Bumblebees (*Bombus terrestris*) sacrifice foraging speed to solve difficult colour discrimination tasks. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* **190**:759–763.

Farine DR, Aplin LM, Garroway CJ, Mann RP, Sheldon BC, 2014. Collective decision making and social interaction rules in mixed-species flocks of songbirds. *Anim Behav* **95**:173–182.

Farine DR, Strandburg-Peshkin A, Berger-Wolf T, Ziebart B, Brugere I et al., 2016. Both nearest neighbours and long-term affiliates predict individual locations during collective movement in Wild baboons. *Sci Rep* **6**:27704.

Fischhoff IR, Sundaresan SR, Cordingley J, Larkin HM, Sellier M-J et al., 2007. Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Anim Behav* **73**:825–831.

Found R, Clair CS, 2016. Behavioural syndromes predict loss of migration in wild elk. *Anim Behav* **115**:35–46.

Fox J, Dhondup K, Dorji T, 2009. Tibetan antelope *Pantholops hodgsonii* conservation and new rangeland management policies in the western Chang Tang Nature Reserve, Tibet: Is fencing creating an impasse? *Oryx* **43**:183–190.

Hu J, Wu X, Dai M, 2020. Estimating the population size of migrating Tibetan antelopes *Pantholops hodgsonii* with unmanned aerial vehicles. *Oryx* **54**:101–109.

Hughey LF, Hein AM, Strandburg-Peshkin A, Jensen FH, 2018. Challenges and solutions for studying collective animal behaviour in the wild. *Philos Trans R Soc London Ser B* **373**:20170005.

Ihl C, Bowyer RT, 2011. Leadership in mixed-sex groups of muskoxen during the snow-free season. *J Mammal* **92**:819–827.

Ioannou CC, Laskowski KL, 2023. A multi-scale review of the dynamics of collective behaviour: From rapid responses to ontogeny and evolution. *Philos Trans R Soc London Ser B* **378**:20220059.

IUCN. (2023). The IUCN Red List of Threatened Species. Version 2022-2. [cited 2023 September 7]. Available from: https://www.iucnredlist.org

Kameda T, Toyokawa W, Tindale RS, 2022. Information aggregation and collective intelligence beyond the wisdom of crowds. *Nat Rev Psychol* **1**:345–357.

Kays R, Crofoot MC, Jetz W, Wikelski M, 2015. Terrestrial animal tracking as an eye on life and planet. *Science* **348**:aaa2478.

Klein S, Pasquaretta C, He XJ, Perry C, Søvik E et al., 2019. Honey bees increase their foraging performance and frequency of pollen trips through experience. *Sci Rep* **9**:6778.

Koh LP, Wich SA, 2012. Dawn of drone ecology: Low-cost autonomous aerial vehicles for conservation. *Trop Conserv Sci* **5**:121–132.

Krause J, Krause S, Arlinghaus R, Psorakis I, Rutz C, 2013. Reality mining of animal social systems. *Trends Ecol Evol* **28**:541–551.

Krause J, Ruxton GD, 2002. The benefits of group formation. In: *Living in Groups*. Oxford: Oxford Academic, 6–40.

Krueger K, Flauger B, Farmer K, Hemelrijk C, 2014. Movement initiation in groups of feral horses. *Behav Processes* **103**:91–101.

Kuznetsova A, Brockhoff PB, Christensen RHB, 2017. *lmerTest Package: Tests in Linear Mixed Effects Models*. *J Stat Softw* **82**:1–26.

Langrock R, Hopcraft JGC, Blackwell PG, Goodall V, King R et al., 2013. Modelling group dynamic animal movement. *Methods Ecol Evol* **5**:190–199.

Lian XM, Zhang TZ, Cao YF, Cai ZY, Su JP, 2007. Diurnal behavioral time budgets and activity rhythm of the female Tibetan antelope (*Pantholops hodgsoni*) in summer. *Acta Theriol Sin* **27**:53–57. In Chinese.

Ling HJ, McLvor GE, Westley J, van der Vaart K, Vaughan RT et al., 2019. Behavioural plasticity and the transition to order in jackdaw flocks. *Nat Commun* **10**: 5174.

Liu K, Skibbe H, Schmidt T, Blein T, Palme K et al., 2014. Rotation-invariant HOG descriptors using Fourier analysis in polar and spherical coordinates. *Int J Comput Vision* **106**:342–364.

Lukeman R, Li YX, Edelstein-Keshet L, 2010. Inferring individual rules from collective behavior. *Proc Natl Acad Sci USA* **107**:12576–12580.

Luo YC, Wang L, Yang L, Li XF, Anselme P et al., 2023. Using a behavior random permutation model to identify displacement grooming in ungulates. *Curr Zool* **69**:200–207.

Luo YC, Wang L, Yang L, Tan M, Wu YQ et al., 2018. Puppet resting behavior in the Tibetan antelope (*Pantholops hodgsonii*). *PLoS One* **13**:e0204379.

Luo YC, Wang L, Yang L, Wang XX, Tian XJ et al., 2020. Unpredictability of vigilance in two sympatric Tibetan ungulates. *Ethology* **126**:883–889.

Manayeva K, Hoshino B, Igota H, Nakazawa T, Sumiya G, 2011. Seasonal migration and home ranges of Tibetan antelopes (*Pantholops hodgsonii*) based on satellite tracking. *Int J Zool Res* **13**:26–37.

McComb K, Moss C, Durant SM, Baker L, Sayialel S, 2001. Matriarchs as repositories of social knowledge in African elephants. *Science* **292**:491–494.

McComb K, Shannon G, Durant SM, Sayialel K, Slotow R et al., 2011. Leadership in elephants: The adaptive value of age. *Proc Biol Sci* **278**:3270–3276.

Michelena P, Jeanson R, Deneubourg J-L, Sibbald AM, 2010. Personality and collective decision-making in foraging herbivores. *Proc Biol Sci* **277**:1093–1099.

Planas-Sitjà I, Deneubourg J-L, Gibon C, Sempo G, 2015. Group personality during collective decision-making: A multi-level approach. *Proc Biol Sci* **282**:20142515.

Ramos A, Bousquet CAH, Sueur C, 2021. How leadership could be used to manage domestic and wild ungulate herds. *Appl Anim Behav Sci* **239**:105326.

Ramos A, Petit O, Longour P, Pasquaretta C, Sueur C, 2015. Collective decision making during group movements in European bison, Bison bonasus. *Anim Behav* **109**:149–160.

Ramseyer A, Boissy A, Thierry B, Dumont B, 2009. Individual and social determinants of spontaneous group movements in cattle and sheep. *Animal* **3**:1319–1326.

Rands SA, Cowlishaw G, Pettifor RA, Rowcliffe JM, Johnstone RA, 2003. Spontaneous emergence of leaders and followers in foraging pairs. *Nature* **423**:432–434.

Réale D, Festa-Bianchet M, 2003. Predator-induced natural selection on temperament in bighorn ewes. *Anim Behav* **65**:463–470.

Rotics S, Clutton-Brock T, 2021. Group size increases inequality in cooperative behaviour. *Proc Biol Sci* **288**:20202104.

Ruckstuhl KE, Neuhaus P, 2002. Sexual segregation in ungulates: A comparative test of three hypotheses. *Biol Rev Camb Philos Soc* **77**:77–96.

Sasha RXD, Johnstone RA, 2002. Managing uncertainty: Information and insurance under the risk of starvation. *Philos T R Soc B* **357**:1519–1526.

Schaller GB, 1998. Chiru (Tibetan Antelope). In: ShallerGB, editor. *Wildlife of the Tibetan Steppe*. Chicago: University of Chicago Press, 41–79.

Schaller GB, 2012. Riddle of the calving ground. In: Sifton E, editor. *Tibet Wild: A Naturalist's Journeys on the Roof of the World*. WA, DC: Island Press, 29–42.

Schaller GB, Kang A, Cai X, Liu Y, 2006. Migratory and calving behavior of Tibetan antelope population. *Acta Theriol Sin* **2**:105–113. In Chinese.

Sih A, 2013. A behavioral ecology view of decision making: Something old, something borrowed, something new. In: Zentall TR Crowley PH, editors. *Comparative Decision Making*. Oxford, UK: Oxford University Press, 243–270.

Sih A, Bell AM, Johnson JC, Ziemba RE, 2004. Behavioral syndromes: An intergrative overiew. *Q Rev Biol* **79**:241–277.

Smith JE, Estrada JR, Richards HR, Dawes SE, Mitsos K et al., 2015. Collective movements, leadership and consensus costs at reunions in spotted hyaenas. *Anim Behav* **105**:187–200.

Sueur C, 2012. Viability of decision-making systems in human and animal groups. *J Theor Biol* **306**:93–103.

Sueur C, Petit O, Deneubourg JL, 2009. Selective mimetism at departure in collective movements of Macaca tonkeana: An experimental and theoretical approach. *Anim Behav* **78**:1087–1095.

Sumpter DJT, Pratt SC, 2009. Quorum responses and consensus decision making. *Philos Trans R Soc London Ser B* **364**:743–753.

Suruliandi A, Kavitha J, Nagarajan D, 2020. An empirical evaluation of recent texture features for the classification of natural images. *Int J Comput* **42**:164–173.

Tenczar P, Lutz CC, Rao VD, Goldenfeld N, Robinson GE, 2014. Automated monitoring reveals extreme interindividual variation and plasticity in honeybee foraging activity levels. *Anim Behav* **95**:41–48.

Torney CJ, Dobson AP, Borner F, Lloyd-Jones DJ, Moyer D et al., 2016. Assessing rotation-invariant feature classification for automated wildebeest population counts. *PLoS One* **11**:e0156342.

Torney CJ, Lamont M, Debell L, Angohiatok RJ, Berdahl AM, 2018. Inferring the rules of social interaction in migrating caribou. *Philos T R Soc B* **373**:20170385.

Villalba JJ, Manteca X, Provenza FD, 2009. Relationship between reluctance to eat novel foods and open-field behavior in sheep. *Physiol Behav* **96**:276–281.

Ward AJW, Herbert-Read JE, Sumpter DJT, Krause J, 2011. Fast and accurate decisions through collective vigilance in fish shoals. *Proc Natl Acad Sci USA* **108**:2312–2315.

Ward AJW, Sumpter DJT, Couzin ID, Hart PJB, Krause J, 2008. Quorum decision-making facilitates information transfer in fish shoals. *Proc Natl Acad Sci USA* **105**:6948–6953.

Ward AJW, Webster MM, 2016. *Sociality: The Behaviour of Group-Living Animals*. Berlin: Springer Cham.

Watzek J, Hauber ME, Jack KM, Murrell JR, Tecot SR et al., 2021. Modelling collective decision-making: Insights into collective anti-predator behaviors from an agent-based approach. *Behav Processes* **193**:104530.

Wei ZQ, Xu ZR, 2020. Habitat distribution of Tibetan antelope in the Chang Tang plateau and influential factors. *Acta Ecol Sin* **40**:8763–8772. In Chinese.

William R, 2024. *psych: Procedures for Psychological, Psychometric, and Personality Research*. R package version 2.4.3. Available from: https://CRAN.R-project.org/package=psych.

Wu T, Lian XM, Li HQ, Wang D, Chen JP et al., 2021. Adaptation of migratory Tibetan antelope to infrastructure development. *Ecosyst Health Sust* **7**:1910077.

Wu YH, 2007. Adaptation of migration of femaIe Tibetan antelope for precipitation distribution on the Qinghai-Tibet Plateau. *Acta Theriol Sin* **27**:298–307. In Chinese.

Xia L, Yang QS, Li ZC, Wu YH, Feng ZJ, 2007. The effect of the Qinghai-Tibet railway on the migration of Tibetan antelope *Pantholops hodgsonii* in Hoh-xil National Nature Reserve, China. *Oryx* **41**:352–357.

Yan XT, Wang X, Zhao YM, Zhu Q, Yang L et al., 2024. Collective decision-making and spatial patterns in orientation of an endemic ungulate on the Tibetan Plateau. *Curr Zool* **70**:45–58.

Yang L, Luo YC, Tan M, Jiang ZG, Li ZQ et al., 2018. Tick-defense grooming patterns of two sympatric Tibetan ungulates. *J Zool* **307**:242–248.

Yin BF, Huai HY, Zhang YL, Zhou L, Wei WH, 2006. Influence of Qinghai-Tibetan railway and highway on wild animal's activity. *Acta Ecol Sin* **26**:3917–3923. In Chinese.

You WY, Shi JB, Lu FY, Dong SK, Li XW et al., 2013. Traits and process of group decision-making in Przewalski's gazelle (*Procapra przewalskii*). *Acta Theriol Sin* **33**:293–299. In Chinese.

Yu ZY, Yang L, Lv SJ, Yin BF, Liu YQ et al., 2008. Behavioral comparison of Tibetan antelope (*Pantholops hodgsoni*), Kiang (*Equus kiang*), Tibetan gazelle (*Procapra picticaudata*) along Qinghai-Tibetan highway. *J Yangzhou Univ* **29**:10–13. In Chinese.

Zhang JJ, Jiang F, Li GY, Qin W, Wu T et al., 2021. The four antelope species on the Qinghai-Tibet plateau face habitat loss and redistribution to higher latitudes under climate change. *Ecol Indic* **123**:107337.

Zwamborn E, Boon N, Whitehead H, 2023. Collective decision-making in aquatic mammals. *Mamm Rev* **53**:238–253.