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Nonrandom mixing between groups of Przewalski's gazelle and Tibetan gazelle

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Przewalski's gazelle (*Procapra przewalskii*) and the Tibetan gazelle (*P. picticaudata*) are endemic, closely related, and endangered ungulates of the Qinghai-Tibetan Plateau. The 2 species often occur in mixed-species groups in the upper Buha River of the Plateau. We studied the composition and size of their mixed-species groups over 2 years to determine whether such groups aggregate by chance and to determine a posteriori potential costs and benefits associated with the formation of mixed-species groups. Sex composition and size distribution were similar in single-species groups for both species. Given that population density also was similar for these species, we expected that mixed-species groups that formed by chance would consist of an equal mix of the 2 species. This was true in male and in mixed-sex groups; however, the proportion of female groups composed of Przewalski's gazelles was much larger than expected. In addition, mixed-species groups in winter never included males of both species. The results suggest that these 2 gazelle species do not associate randomly. Mixed-species groups were larger than single-species all-female, all-male, and mixed-sex groups, suggesting that individuals in larger groups may benefit from a reduction in predation risk. The occurrence of mixed-sex, mixed-species groups may increase the risk of crossbreeding and represent a cost to the formation of mixed-species groups in these two gazelle species. DOI: 10.1644/09-MAMM-A-203.1.

Key words: gazelle, mixed-species group, predation risk, Qinghai-Tibetan Plateau, social organization, ungulates

Many groups of animals consist only of conspecifics. However, in sympatric areas groups can comprise more than 1 species. Mixed-species groups have been documented in fishes (Lukoschek and McCormick 2002; Semeniuk and Dill 2006), birds (Morse 1970; Sridhar et al. 2009), and mammals, including ungulates (Fitzgibbon 1990; Keast 1965; Sinclair 1985), dolphins (Querouil et al. 2008), and primates (Gartlan and Struhsaker 1972; Heymann and Buchanan-Smith 2000). The 2 basic questions in research on mixed-species groups are whether such groups arise by chance and what benefits individuals may accrue in such aggregations.

Just as various groups of the same species often encounter each other during movements, mixed-species groups may arise by the chance encounter of groups of different species (Waser 1984). Mixed-species groups also could result from the independent attraction of different species to a particular habitat or site with no derived functional advantages. The role of chance can be examined using data on group composition and habitat use for each species and deriving the expected rate of encounter between groups of different species (Holenweg et al. 1996). Documenting advantages for 1 or more of the species in mixed-species groups provides evidence against the null hypothesis of random grouping. Such advantages have been documented in many mixed-species groups (mammals [Stensland et al. 2003] and birds [Sridhar et al. 2009]).

Functional explanations for why different species mix fall within 3 nonmutually exclusive categories: foraging, antipredation, and social or reproductive advantages (Stensland et al. 2003). Foraging advantages can include cooperation in finding and exploiting resources. Antipredation advantages in mixed-species groups include enhanced detection of predators and dilution of predation risk in larger groups (Stensland et al. 2003). Although such benefits also accrue individuals in single-species groups, mixed-species groups often are larger than single-species groups thus providing extra safety. In addition, it might be worthwhile joining other species that are better able to detect or deter predators or that are more attractive to predators (Fitzgibbon 1990). Finally, individuals of 1 species might be able to enjoy social and reproductive advantages by joining groups of another species. For instance, mixed-species groups can be more successful in defending territories or resources than single-species groups. Joining a mixed-species group also could reduce breeding competition and allow individuals to gain social experience (Stensland et al. 2003).

We examined the random mixing hypothesis in mixed-species groups of 2 endemic ungulate species of the Qinghai-Tibetan Plateau. Przewalski's gazelle (*Procapra przewalskii*) and the Tibetan gazelle (*P. picticaudata*) are closely related, sympatric species that readily form mixed-species groups in the upper Buha River valley, Tianjun County, Qinghai Province, China (Li and Jiang 2006) during the summer and winter. In addition, we addressed indirectly potential costs and benefits of mixed-species groups by documenting the size and composition of mixed-species groups. For instance, a larger size for mixed-species groups relative to single-species groups would be of particular relevance to the antipredation hypothesis. Seasonal changes in group composition as a function of reproductive status would be relevant to the reproductive advantage hypothesis.

Materials and Methods

Study site and species.—We conducted our study in the Upper Buha River valley, Tianjun County, Qinghai Province, China (36°53′30″−48°39′12″N, 96°49′42″−99°41′48″E), located in the northwestern part of the Qinghai Lake watershed area and south of the Qilian Mountains (Li et al. 2008). Elevations range from 2,850 to 5,826 m, with average elevation of 3,800 m. Local climate is characterized by dry, cold, and long winters, strong winds, high levels of solar radiation, and a short frost-free period. Mean annual temperature is −1.5°C with an extreme recorded low temperature of −40°C. Annual precipitation varies from 330 to 412 mm, and most rain falls between June and September. The main vegetation type in the study area consists of alpine meadow. Shrubs are found along the Buha River valley, which is the largest river flowing into Qinghai Lake. Four seasons are not distinguished clearly in the study area; however, the period from June to September is the plant-growing period and October to May is the plant-withering period.

Przewalski's gazelles occur only around Qinghai Lake, and population size is estimated to be only a few hundred individuals (Jiang et al. 1995, 2000). Przewalski's gazelle has been classified as Critically Endangered by the Species Survival Commission of the International Union for the Conservation of Nature (IUCN) from 1996 to 2008 and Endangered after 2008 (IUCN 2009) and is a Category I (Endangered in China) National Protected Wild Animal Species in China since 1989 (Wang and Xie 2004). The Tibetan gazelle (*P. picticaudata*) resides in fragmented habitat patches on the Qinghai-Tibetan Plateau; however, the population is decreasing sharply, and its range is shrinking rapidly (Schaller 1998; Zhang and Jiang 2006). Although it is listed as Low Risk in the IUCN *Red List of Threatened Species* (IUCN 2009), the Tibetan gazelle is a Category II (Threatened) National Protected Wild Animal Species in China (Wang and Xie 2004). Both gazelles rut from December to January and lamb from July to August, although Tibetan gazelles usually lag 1–2 weeks behind Przewalski's gazelles (Li and Jiang 2006; Lu and Wang 2004; You and Jiang 2005). Population size for both gazelles has been estimated at 100 in the study area. Gray wolves (*Canis lupus*) and Tibetan sand foxes (*Vulpes ferrilata*) are predators in the area (Li et al. 2008).

The 2 species of gazelle can be distinguished using morphological traits. Horns are backward-curving and tenuous in male Tibetan gazelles but backward-inward-curving and strong in male Przewalski's gazelles. Przewalski's gazelles usually have brownish yellow pelage whereas Tibetan gazelles have grayish pelage. Przewalski's gazelles usually weigh >25 kg and are larger and heavier than Tibetan gazelles, which usually weigh <20 kg (Jiang 2004). Subadult males can be distinguished in each species by their different pelages.

Censuses.—Data on group size and composition were recorded from route surveys during summer (June–September 2005, June–July 2006), when lambing occurs, and winter (December 2005–January 2006, January 2007) when rutting occurs. Transect routes traversed all habitat types, including river valley, flat terrain, and mountain slopes, so that all individuals in the study area would be recorded. Observations were carried out using binoculars (8 × 42) or a telescope (20 × 60–63). The total route length was approximately 20 km. A transect was walked once every 3 days, and a daily survey took 6–8 h. Because groups usually remained together for a few hours, it was therefore unlikely that the same group was counted twice.

A group was defined as an aggregation of individuals that were separated by no more than 50 m (Clutton-Brock et al. 1982), and usually interindividual distances in groups were <5 m. For each group we recorded group size, species composition, and the sex of each group member.

For single-species groups of each species we recognized 3 different types of groups: female groups, which included ≥1 female and no males; male groups, which included ≥1 adult or subadult male and no females; and mixed-sex groups, which included ≥1 female and ≥1 adult male. It was not possible to distinguish between adult and subadult females in the present study. Similarly, we recognized 3 different types of mixed-species groups: female groups, which included ≥1 female of each species and no males of either species; male groups, which included ≥1 adult or subadult male of each species and no females of either species; and mixed-sex groups, which included ≥1 adult or subadult male of 1 species and ≥1 female of the other species.

Data analysis.—Data for group size were $\log_{10}$-transformed before analysis to normalize the distribution. In all analyses we fitted models separately for the summer and the winter.

The proportions of each group type in single-species groups of each species and in mixed-species groups were compared with chi-square tests. We compared group sizes in single-species groups using a linear model, with year, sex, species, and the interaction between sex and species as factors. Excluding group sizes of 1, we compared group sizes of single- and mixed-species groups using a linear model with year, sex, species composition (3 levels: Przewalski's gazelles alone, Tibetan gazelles alone, and mixed-species groups), and the interaction between sex and species (Kim and Timm 2006). The proportion of Przewalski's gazelles in each mixed-species group was investigated in a linear model using mixed-species groups larger than 2 individuals with year, sex, group size, and the interaction between sex and group size as factors. Mixed-species groups with only 2 gazelles were excluded given that the proportion of Przewalski's gazelles could be only 0.5. All post hoc tests were carried out with the sequential Bonferroni P-value adjustment (Rice 1989). The analyses were carried out using SAS version 9.1 (SAS Institute Inc., Cary, North Carolina) and the overall level of statistical significance was set at $\alpha = 0.05$ throughout.

Results

Group composition.—Over the 2 years of study we encountered 528 groups in summer and 249 groups in winter and an almost equal number of groups of the 2 species (319 Przewalski's gazelle groups and 327 Tibetan gazelle groups). Group sizes ranged from 1 to 36 for Przewalski's gazelle, 1 to 31 for the Tibetan gazelle, and 2 to 62 for mixed-species groups. The total number of mixed-species groups was 131.

The proportion of female, male, and mixed-sex groups varied significantly with species composition of the groups during the summer (Fig. 1A; $\chi_2^2 = 20.81$, $P < 0.01$). Post hoc tests revealed that the proportions of female groups ($P = 0.29$), male groups ($P = 0.06$), and mixed-sex groups ($P = 0.10$) did not differ between single-species groups of the 2 species. Female groups were less common in mixed-species groups than in single-species groups of the 2 species combined ($P < 0.01$), and male groups ($P < 0.01$) and mixed-sex groups ($P < 0.01$) were more common.

The proportions of female, male, and mixed-sex groups varied significantly with species composition of the groups during the winter also (Fig. 1B; $\chi_2^2 = 105.63$, $P < 0.01$). Post-hoc tests revealed that in single-species groups female groups were more common in the Tibetan gazelle than in Przewalski's gazelle ($P < 0.01$), but male groups ($P < 0.01$) and mixed-sex groups ($P = 0.03$) were less common. Mixed-sex groups were more common in mixed-species groups than in single-species groups of the 2 species combined ($P < 0.01$), and male groups ($P < 0.01$) and female groups ($P = 0.03$) were less common. No mixed-species groups ever contained males of both species during winter, although this occurred to some extent during summer.

Group size.—In summer, in single-species groups, mean group size did not vary over the 2 years of study ($F_{1,431} = 0.01$, $P = 0.94$) and between the 2 species ($F_{1,431} = 0.17$, $P = 0.68$; Fig. 2A). Mean group size varied significantly with sex composition of the groups ($F_{2,431} = 31.74$, $P < 0.01$), but the effect of sex was similar in the 2 species as revealed by the nonsignificant interaction between sex and species ($F_{2,431} = 0.62$, $P = 0.54$). Post hoc tests revealed that mean group size was larger in mixed-sex groups than in single-sex groups and larger in female groups than in male groups.

In winter, in single-species groups, mean group size did not vary over the 2 years of study ($F_{1,201} = 0.49$, $P = 0.48$). Mean group size varied significantly with sex composition of the groups ($F_{2,201} = 201.00$, $P < 0.01$; Fig. 2B) but was similar between the 2 species ($F_{1,201} = 0.05$, $P = 0.83$; Fig. 2B). Post hoc tests revealed that mean group size was smaller in male groups than in either female or mixed-sex groups, but no difference was observed between female or mixed-sex groups. Mean group size in female groups ($P = 0.18$) and in mixed-species groups ($P = 0.53$) did not differ between the 2 species, but male groups were somewhat smaller in Przewalski's

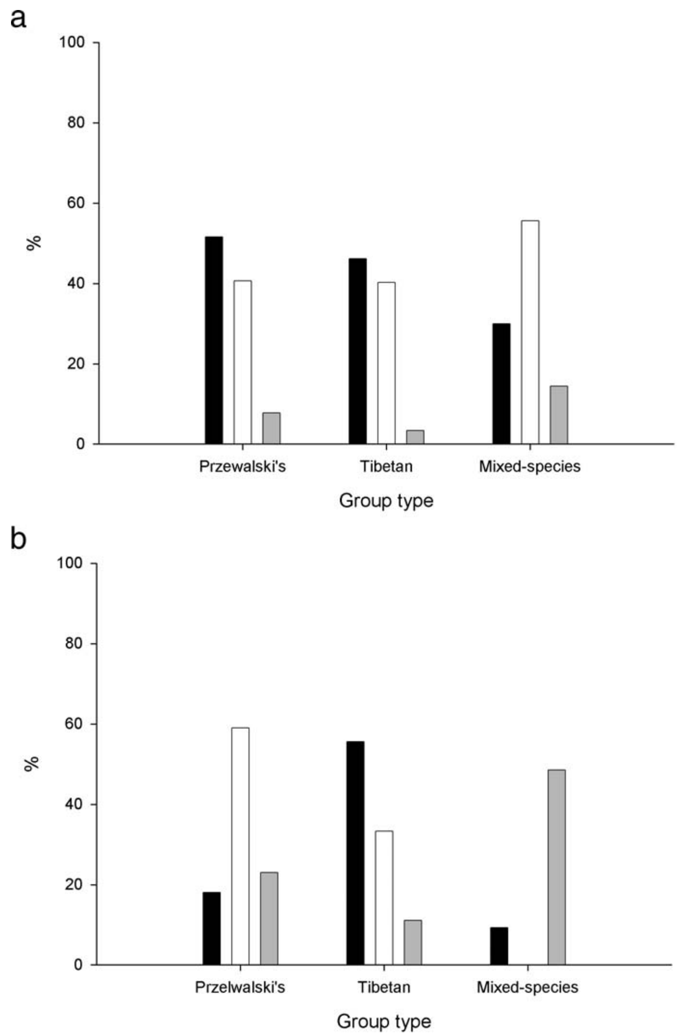

FIG. 1.—Percentage of different group types (black = female, white = male, gray = mixed sex) in single-species groups of Przewalski's gazelles and Tibetan gazelles and in mixed-species groups during the a) summer and b) winter.

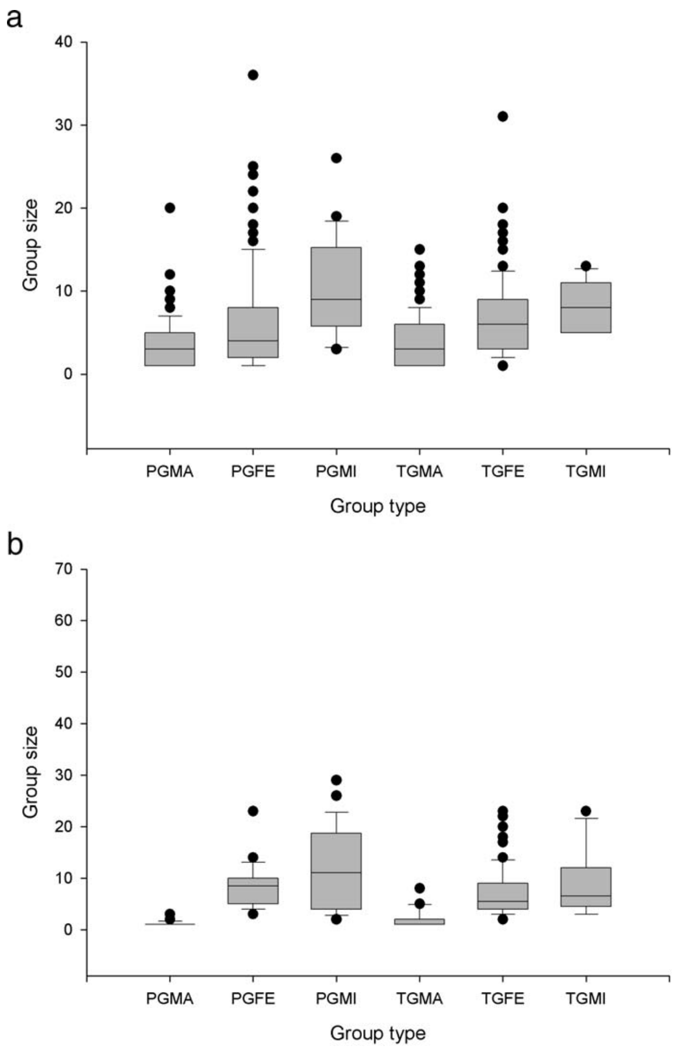

FIG. 2.—Box plot of group sizes in single-species groups of Przewalski's gazelles and Tibetan gazelles during the a) summer and b) winter. Group types are codes with 4 letters: the first 2 letters correspond to species composition (PG = Przelwalski's gazelles, TG = Tibetan gazelles), and the last 2 letters correspond to sexual composition of the groups (MA = male groups, FE = female groups, MI = mixed-sex groups). The line in each box corresponds to the median, and the box extends from the 25th to the 75th percentiles. Whiskers reach 1.5 times the interquartile range, and dots correspond to data outside this range.

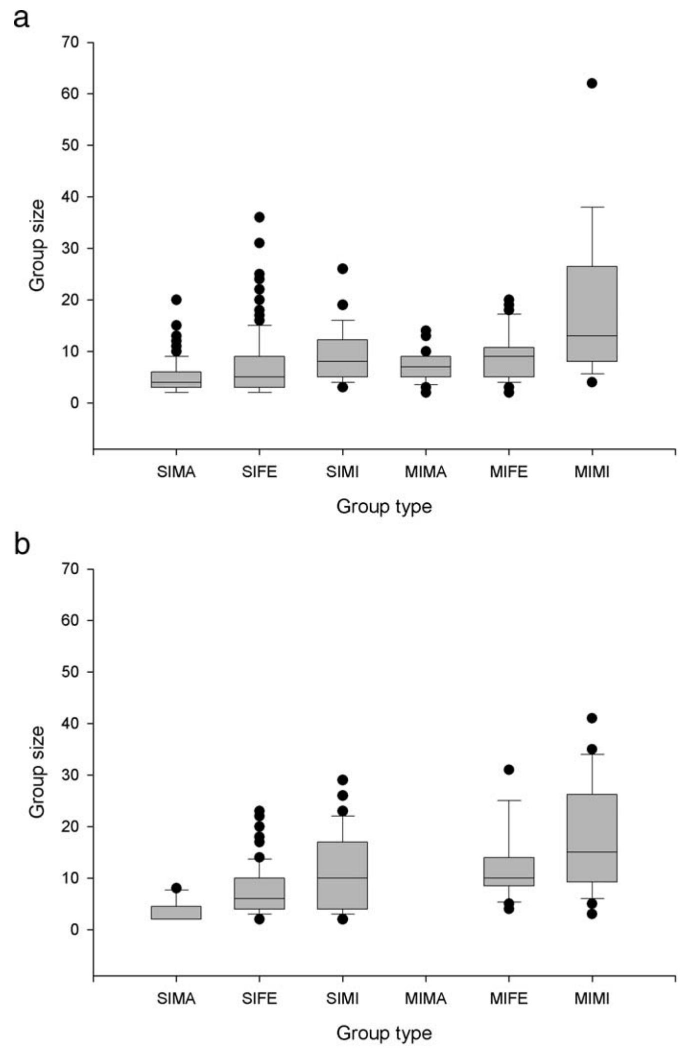

FIG. 3.—Box plot of group sizes in single-species groups of the 2 gazelles combined and in mixed-species groups during the a) summer and b) winter. Groups of size 1 are excluded. Group types are codes with 4 letters: the first 2 letters correspond to species composition (SI = single-species, MI = mixed-species), and the last 2 letters correspond to sexual composition of the groups (MA = male groups, FE = female groups, MI = mixed-sex groups). The line in each box corresponds to the median, and the box extends from the 25th to the 75th percentiles. Whiskers reach 1.5 times the interquartile range, and dots correspond to data outside this range.

gazelle than in the Tibetan gazelle ($P = 0.02$; not significant using Bonferroni correction).

For the comparison of group sizes in single- and in mixed-species groups we excluded solitary groups and combined data for the 2 species given that group sizes were quite similar between the 2 species. In summer (Fig. 3A) mean group size did not differ between the 2 years of study ($F_{1,432} = 0.62$, $P = 0.43$) but varied significantly according to species composition ($F_{1,432} = 12.53$, $P < 0.01$) and sex composition ($F_{2,432} = 18.60$, $P < 0.01$). We observed no interaction between species and sex composition ($F_{2,432} = 0.43$, $P = 0.65$). Mixed-species groups were larger than single-species groups. Post hoc tests revealed that mean group size was larger in mixed-sex groups than in either male or female groups ($P < 0.01$) and larger in female than in male groups ($P = 0.04$).

In winter (Fig. 3B) mean group size did not differ between the 2 years of study ($F_{1,165} = 0.53$, $P = 0.47$) but varied significantly according to species composition ($F_{1,165} = 14.28$, $P < 0.01$) and sex composition ($F_{2,165} = 14.11$, $P < 0.01$). The interaction between species and sex composition could not be analyzed because we observed no male mixed-species groups. Mixed-species groups were larger than single-species groups. Post hoc tests revealed that mean group size was larger in mixed-sex groups than in either male or female groups ($P < 0.01$) and larger in female than in male groups ($P = 0.02$).

Proportion of Przewalski's gazelles in mixed-species groups.—In summer the overall proportion of Przewalski's gazelles in mixed-species groups, as given by the intercept of the model, was 0.54 ($SE = 0.11$). This proportion did not vary between years of study ($F_{1,83} = 2.88$, $P = 0.09$) and tended to increase slightly with group size (β or slope = 0.79, SE = 0.39; $F_{1,83} = 4.07$, $P = 0.04$). The proportion varied significantly with sex composition ($F_{1,83} = 10.51$, $P < 0.01$). Post hoc tests revealed that the least squares mean (± SE) proportion (controlling for group size) was significantly higher in female groups (0.80 ± 0.05) than in either male groups (0.54 ± 0.04) or mixed-sex groups (0.57 ± 0.08; $P < 0.0001$), but no difference was found between male and mixed-species groups ($P = 0.71$). The interaction between sex and group size was not significant and was removed from the final model.

In winter the overall proportion of Przewalski's gazelles in mixed-species groups was 0.54 ($SE = 0.15$). This proportion did not vary between years of study ($F_{1,37} = 0.03$, $P = 0.86$) and with group size (β or slope = −0.81, $SE = 0.60$; $F_{1,37} = 1.82$, $P = 0.18$). The proportion varied significantly with sex composition ($F_{1,37} = 8.78$, $P < 0.01$). The least squares mean (± SE) proportion (controlling for group size) was significantly higher in females groups (0.84 ± 0.13) than in mixed-sex groups (0.41 ± 0.07). The interaction between sex and group size was not significant and was removed from the final model.

Discussion

Mixed-species groups were a common occurrence in Przewalski's gazelle and Tibetan gazelle of the plateau during the summer and winter. In some sex categories mixed-species groups were more frequent than single-species groups.

In general, mixed-species groups are more likely to occur when the species have similar feeding habits or habitat requirements (Heymann 1997; Stensland et al. 2003). For the species involved, niche separation should not be too small, because interspecific competition may become too intense, or too large, ensuring that the species can coexist. A recent study on diet indicated that both species of gazelles on the plateau fed on similar plant types but that the Tibetan gazelle fed more on Leguminosae whereas Przewalski's gazelle fed more on Gramineae (Li et al. 2008). Both gazelles showed a similar behavioral rhythm including feeding peaks at dawn and dusk (Liu and Jiang 2004; Lu and Wang 2004). Both gazelles occur in the same habitat and also share the same predators (Li et al. 2008; Liu and Jiang 2002; Zhang and Hu 2002).

Body size also plays an important role in the formation of mixed-species groups. Heymann (1997) analyzed body size (head–body length) data of tamarins (*Saguinus* spp.) and found that divergence in body size ranged between 8% and 17% for associated species and 1% and 4% for nonassociated species. Head–body length ranges from 105 to 110 cm in adult Przewalski's gazelles and 80 to 90 cm in Tibetan gazelles, with a body-size divergence of about 20% (Jiang 2004). The difference in body size, with the associated niche divergence observed in food type, might have been sufficient to allow the formation of mixed-species groups in the 2 gazelle species.

The type and size of groups can be another factor limiting the formation of mixed-species groups (Fitzgibbon 1990). Species with more similar grouping patterns may mix more easily. As discussed below, the sex combination and sizes are very similar in groups of the 2 gazelle species. For all the above reasons the formation of mixed-species groups in the 2 gazelle species apparently faced few constraints.

Single-species groups of the 2 species of gazelles were very similar in size and structure. The proportions of mono- and heterosexual groups were similar in single-species groups of the 2 gazelles during the summer. In the winter the proportion of female groups was higher in the Tibetan gazelle. In addition, mixed-sex groups also were more common in both species during winter, as would be expected during the reproductive season. Mixed-species groups consisted primarily of male groups during the summer and of mixed-sex groups in the winter.

In single-species groups group sizes did not differ between the 2 species in the summer or winter for any of the possible sex combinations. Generally, male groups were the smallest. Mixed-species groups were larger than single-species groups for any of the possible sex combinations, and the largest mixed-species groups consisted of heterosexual groups.

Given that the density of the 2 species was the same in the study area, the number of groups of the 2 species encountered during observations also was the same, and size and structure of the groups are similar in the 2 species, especially during the summer, one would expect that mixed-species groups should be an equal mix of the 2 species under the null hypothesis of random arrival and departure of individuals in mixed-species groups. Results indicate that although the prevalence of Przewalski's gazelles in mixed-species groups was about 50% overall, the prevalence was much higher in female groups and also tended to increase with group size, thus indicating nonrandom mixing. In addition, the absence of mixed-species groups with males of the 2 species during winter suggests that mixing was not random. The null hypothesis of random mixing rarely has been examined (Holenweg et al. 1996; Waser 1984; Whitesides 1989). Although specific details about the rate of encounter between groups of different species are needed to test the hypothesis statistically, we offer circumstantial evidence against the hypothesis based on mixed-species group composition assuming equal group-size distributions in the 2 species.

We offer broad lines of inquiries on the potential advantages of mixed-species groups in gazelles, based on the size and composition of mixed-species groups of the 2 gazelles. Further empirical research is needed to test these hypotheses more thoroughly. We believe that foraging advantages are probably unimportant in the study area because cooperation in food acquisition is not needed for grazers, and detection of food is probably not an issue with a large and evenly distributed food supply such as vegetation. Antipredation advantages are more likely given that mixed-species groups were larger than single-species groups in the 2 species. The formation of larger groups would be beneficial for both gazelle species to detect predators more easily and dilute predation risk. Recent studies on antipredator vigilance in the 2 species showed that individuals in larger groups spent less time vigilant (Li and Jiang 2008; Li et al. 2009). It is not clear whether individuals of 1 gazelle species would be able to decrease vigilance to a larger extent in mixed-species groups than by associating with the same number of conspecifics, but at the very least joining groups of another species can increase group size effectively. Mixed-species groups offer other antipredation advantages for individuals, such as joining a more vulnerable or a more alert species (Fitzgibbon 1990; Goodale and Kotagama 2008). Future work could determine whether 1 gazelle species is more vulnerable or more alert than the other.

The higher prevalence of Przewalski's gazelles in mixed-species female groups could indicate that either female Tibetan gazelles are less likely to join female groups of the other species or are less likely to persist in these groups once formed, or both. That such a high prevalence was observed both during the summer and winter suggests that intersexual competition likely does not explain why female Tibetan gazelles often were found with male Przewalski's gazelles rather than males of their own species. The results may indicate that disbanding of groups containing the 2 species is more likely in female groups, perhaps indicating some incompatibility between the 2 species in their foraging together.

Heterosexual mixed-species groups consisted of a male and several females in both gazelle species. The formation of mixed-sex groups in ungulates was more common during winter and probably served a mating function (Walther et al. 1983). Competition among males for mates was usually strong, leading to the absence of mixed-species male groups. Fighting between or among males of the 2 species does occur (Z. Li, pers. obs.), perhaps explaining why males of the 2 species avoided one another. We also witnessed mating behavior between male Przewalski's gazelles and female Tibetan gazelles during winter 2005. The formation of mixed-sex, mixed-species groups implies a risk of crossbreeding. We have observed mating behavior between the 2 gazelles and even found possible hybrids. However, we lack more detailed molecular evidence. Nevertheless, the possible crossbreeding would constitute a cost to the formation of mixed-species groups assuming that the offspring are infertile.

In conclusion, we found that mixed-species groups of Przewalski's and Tibetan gazelles are common and do not represent a random mix. Given that mixed-species groups are larger than single-species groups, a probable benefit of belonging to a mixed-species group is a reduction in predation risk; however, we also noted the risk for crossbreeding in mixed-sex, mixed-species groups. Future studies could examine whether detection of predators is more efficient in mixed-species groups than in single-species groups and determine the extent to which the 2 species crossbreed.

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