Sexual segregation in goitered gazelles (*Gazella subgutturosa*)

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Abstract: Sexual segregation (by habitat or socially) is found in many species, and is especially well described for gregarious ruminants, particularly Cervinae and Caprinae, while less is known about Antilopinae. In this study, we investigated the degree of sexual segregation and social organization of goitered gazelles (*Gazella subgutturosa* (Güldenstädt, 1780)), which have a quite distinctive (up to 30%) body size dimorphism between sexes. We used three indices for measuring the degree of sexual segregation: proportion of mixed-sex groups among all groups, proportion of adult females and males in mixed-sex compared with unisex groups, and Conradt's segregation coefficient (SC). All these measures confirmed that goitered gazelles had very high levels of segregation all year: the proportion of mixed-sex groups was very low (4.6%) compared with unisex herds (95.4%); the proportion of adult males and females in mixed-sex groups was also low (<13%) compared with those in unisex groups; and the SC was very high (0.80–0.98), indicating that considerable segregation occurred. Although SC decreased to some extent during the rut (November–December), as expected, female groups stayed segregated from males (SC = 0.81–0.86) and formed mixed-sex herds only for very short time periods during mating. Surprisingly, the SC dropped to its lowest values during spring (April) and autumn (October) migration periods (0.71 and 0.67, respectively). Our results will contribute to better understanding the behavioural adaptations of goitered gazelle to the arid environment and help in the species conservation and management.

Key words: body dimorphism, goitered gazelle, *Gazella subgutturosa*, segregation coefficient, sexual segregation.

Résumé : La ségrégation sexuelle (au niveau de l'habitat ou socialement) est observée chez de nombreuses espèces et a été particulièrement bien décrite chez des ruminants grégaires, notamment des cervinés et des caprinés, alors que pour les antilopinés, les connaissances à cet égard sont plus limitées. Dans la présente étude, nous avons examiné le degré de ségrégation sexuelle et d'organisation sociale des gazelles à goitre (*Gazella subgutturosa* (Güldenstädt, 1780)), qui présentent un dimorphisme sexuel marqué (jusqu'à 30 %) en ce qui concerne la taille du corps. Nous avons utilisé trois indices pour mesurer le degré de ségrégation sexuelle : proportion des groupes de sexes mixtes parmi tous les groupes, proportion de femelles et de mâles adultes dans les groupes mixtes comparativement aux groupes unisexes et coefficient de ségrégation de Conradt (SC). Toutes ces mesures ont confirmé que les gazelles à goitre présentent un degré élevé de ségrégation tout au long de l'année : la proportion de groupes mixtes était très faible (4,6 %) comparativement à celle des groupes unisexes (95,4 %), la proportion des mâles et des femelles adultes dans les groupes mixtes était également faible (<13 %) comparativement à la proportion observée pour les groupes unisexes, et le SC était très élevé (0,80–0,98), indiquant une importante ségrégation. Bien que le SC ait diminué dans une certaine mesure durant le rut (novembre–décembre), comme prévu, les groupes de femelles sont demeurés séparés des mâles (SC = 0,81–0,86), ne formant des troupeaux mixtes que pour de courtes périodes durant l'accouplement. Fait surprenant, le coefficient de ségrégation a atteint ses valeurs les plus faibles durant les périodes de migration printanière (avril) et automnale (octobre) (0,71 et 0,67, respectivement). Ces résultats contribueront à une meilleure compréhension des adaptations comportementales de la gazelle à goitre à un environnement aride et aux efforts de conservation et de gestion de l'espèce.

Mots-clés : dimorphisme corporel, gazelle à goitre, *Gazella subgutturosa*, coefficient de ségrégation, ségrégation sexuelle.

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Introduction

Most studies on sexual segregation (by habitat or socially) have focused on ruminants (Clutton-Brock et al. 1987; Conradt and Roper 2000; Ruckstuhl and Neuhaus 2002; Bowyer 2004), although it is also common in nonruminants, and has been reported across a wide range of taxonomic groups such as some plants, some invertebrates, and many vertebrate taxa, including fishes, reptiles, birds, kangaroos, bats, rodents, carnivores, cetaceans, primates, and humans (Ruckstuhl and Neuhaus 2005). Among ruminants, sexual segregation is most common in social species with a high degree of sexual size dimorphism, seasonal mating, and in populations in which both males and females can roam about freely (absence of any kind of individual male territories that give them possibility to monopolize females and exclude other males) (Ruckstuhl and Neuhaus 2000). In many ruminant species, males are larger in body size than females, and the sexes stay in separate unisex groups outside the rutting period (Miquelle et al. 1992; Main et al. 1996; Bleich et al. 1997). Ruckstuhl and Neuhaus (2002) reported that sexual segregation is the rule in ruminant species in which males are at least 20% larger than females.

Apparently, sexual segregation seems less common in the Antilopinae, which are also ruminants, and this phenomenon was only reported in impala (*Aepyceros melampus* (Lichtenstein, 1812)), springbok (*Antidorcas marsupialis* (Zimmermann, 1780)), gerenuk (*Litocranius walleri* (Brooke, 1879)), and Thomson's gazelle (*Gazella thomsoni* Günther, 1884) (Ruckstuhl and Neuhaus 2002; Yearsley and Pérez-Barbería 2005). Many antelope species do not have a distinctive sexual dimorphism in body size, in contrast to extremely dimorphic Caprinae (wild sheep and ibex) and Cervinae (deer) (Ruckstuhl and Neuhaus 2002). Many of the Antilopinae have males with permanent individual territories, which are particularly characteristic for relic dwarf antelopes from the tribe Neotragini (Giotto and Gerard 2010). Therefore two conditions, namely sexual size dimorphism and the absence of permanent individual territories in males, implicated in sexual segregation are not met for some antelopes. However, many antelope species have not been tested yet for sexual segregation.

Goitered gazelles (*Gazella subgutturosa* (Güldenstädt, 1780)) do not have a very pronounced sexual dimorphism in body size (Zhevnerov et al. 1983), but the maximum mass of males and females in goitered gazelles is 43 and 33 kg, respectively, which leads to up to a 30.3% difference in body mass (Heptner et al. 1961), and thus exceeds the 20% threshold reported for segregating species (following the formula in Ruckstuhl and Neuhaus 2002). Furthermore, male goitered gazelles are territorial during the rut (November–December), but roam freely within their home range for the rest of the year (Blank 1986, 1998). This indicates that sexual segregation should be found in goitered gazelles. As sexual segregation has never been examined for goitered gazelles, the aim of our study is to report on the degree of sexual segregation in this species and how the degree of segregation changes according to season and reproductive activities.

Given the biology of the species and their sexual size dimorphism, we thus expect goitered gazelles to segregate outside the rutting period and predict that (*i*) the proportion of

mixed-sex groups and number of individuals inside of these groups will be very low compared with all other type of groups and number of individuals inside of them, (*ii*) the proportion of adult males and females in mixed-sex herds will be significantly lower than those in unisex groups for most seasons, and (*iii*) Conradt's segregation coefficient will be high (above 0.5 range, where 0 is no segregation and 1 is complete segregation) all year, except during the rutting period, when this value should decrease because of mating events.

Materials and methods

We carried out our observations in the Ili depression (for further details on the study site see Blank 1998) during 1981–1987 and used two methods to sample groups of goitered gazelles: (1) counting gazelles along pedestrian transects (total of 2 000 km) and car routes (10 000 km) and (2) observing them from a vantage point (for focal animal sampling) with binoculars (magnification 8×) and telescopes (magnification 30× to 60×). We counted gazelles once every month at least (3.81 ± 0.17 weeks (mean ± SE), $n = 30$). To avoid resampling the same individual during a census, we used the following method. We followed south–north parallel transects every 5 km, which covered the entire study area. We started counts from the west and moved along transects to the east, stopping every 3 km for the focal sampling and counted gazelles along transects from each side forward, but we did not count any on the way back when crossing an already sampled area. During focal sampling, we moved the telescope always clockwise and registered antelopes within distances of 0.5 km. During constant focal animal sampling, we kept gazelles under continuous visual observation for long periods of time (4.20 ± 0.32 h per day (mean ± SE), range 0.5–9 h per day, $n = 417$) using binoculars and telescopes of same magnification as described above. Any detected group was included only once during the continuous observation period if it did not change its composition. In the majority of the cases, groups were stable and did not change their composition during observation hours, with the exception of most mixed-sex groups during the rut, when female groups crossed the net of individual male territories and formed short-lived herds with territorial male. If such groups stayed together less than half an hour, then they were recorded as a separate female group and a single male. If they stayed together for longer than half an hour, then they were noted as a mixed-sex group.

We recorded detailed descriptions of horns (for males only), muzzle, and neck coloration for ageing. An exact age determination of gazelles was impossible under field conditions, and we thus divided them into three age groups: (1) young (up to 7 months) with body size noticeably less than an adult's, a bright dark spot on the muzzle above the nose, and males having crooked horns up to half the length of the ears; (2) subadults or yearlings (up to 20 months) with body size slightly less than an adult's, a grey spot on the muzzle, and males having crooked horns equal to ear length; and (3) adult gazelles (more than 20 months) without spots on the muzzle above the nose, and males having lyrate horns 1.5–3 times longer than their ears (Zhevnerov et al. 1983).

We distinguished four kinds of groups: female, male, mixed-sex, and subadult. Herds of subadults were uncommon, and thus were merged with adult groups according to sex for analyses (yearling-female groups typically merged with female groups, yearling-male groups with male-only groups, and very rare yearling groups of both sexes joined mixed-sex groups). Female groups contained one or more adult females plus young or (and) subadult females (yearlings). Male groups contained one or more adult males plus subadult males (yearlings). Mixed groups consisted of one or more adult males and one or more adult females plus subadults (yearlings of both sexes) or (and) young. We recorded gazelles as member of a group if they were <50 m from each other, moved in the same direction, and stayed together longer than half an hour (these are measures commonly used in defining groups of ungulates) (Ruckstuhl 1998). Territorial males during rut and female groups that just crossed individual male ranges and stayed with a male only 10–30 min quite often were considered a single male and a separate female group.

We pooled our results for different years, and our values for each month are based on the cumulative data across all 6 years. Pooling data seemed necessary because sampling was done unevenly across years and months and some months did not have sufficient data for a given year to be presented and analyzed separately. Moreover, preliminary tests for separate months confirmed that they did not significantly vary across years.

Three indices were used to evaluate the degree of sexual segregation in goitered gazelles (Shi et al. 2005). First, the percentage of mixed-sex groups from all observed social groups; here, we calculated two proportions: (1) the number of mixed-sex groups versus all observed gazelle groups and (2) the number of individuals inside of these groups versus all observed gazelle individuals. Second, the proportion of adult males and females in mixed-sex groups versus the number of adult males and females in unisex groups (Hillman 1987; Owen-Smith 1993). And three, the segregation coefficient first proposed by Conradt (1998).

The first index mentioned above is too indiscriminate because any mixed-sex group would be labelled as such as soon as one individual of the opposite sex was present in the group. For a refined measure, we used the second index, which took into consideration the number of adult gazelles in mixed-sex and unisex groups. The third index or Condradt's segregation coefficient (SC) yields the degree of sexual segregation. However, we included singletons for our calculations of SC values, as suggested by Bonenfant et al. (2007). This is important because singletons are very commonly observed in goitered gazelle and omitting those individuals would considerably bias the segregation index.

Conradt's SC (Conradt 1998) was calculated according to the following formula:

$$\mathrm{SC}_{\mathrm{social}} = 1 - [(N - 1)/X \cdot Y] \cdot \sum [x_i \cdot y_i/(n_i - 1)]$$

where x_i is the number of adult males in ith group, y_i is the number of adult females in ith group, n_i is the number of adults in ith group ($n_i = x_i + y_i$), X is the total number of adult males sampled, Y is the total number of adult females sampled, N is the total number of adults sampled ($N =$

$X + Y$). SC ranges from 0 (no segregation) to 1 (complete segregation) (Conradt 1998).

In spite of the three indices being calculated in different ways, all of them fluctuated over the months in the same way and demonstrated the same regularity. So, the pooled data did not differ based on the index used. We applied a χ^2 goodness-of-fit test to check for significant differences in the proportions of sightings of mixed-sex and unisex groups and Mann–Whitney U test for post hoc paired comparisons. In addition, we used a Kruskal–Wallis test to compare monthly differences in the occurrence of the different group types. Proportion data were arcsine-transformed. The effect of month on the percentage of adult males and females in mixed-sex groups versus those in unisex groups was tested using one-way ANOVAs. Fisher's least significant differences (LSD) post hoc comparisons were then used to compare means between separate pairs of values (subgroups). SC values were compared between months using one-sample Student's t tests, provided tests for normality were satisfied. As we used Student's t tests eight times for the same data set, we applied the Bonferroni correction to our P value and our new threshold for significance thus was $P < 0.008$.

Results

The total time of observation was approximately 1750 h, which included 38.3 h in March, 191.7 h in April, 469.8 h in May, 374.0 h in June, 173.3 in July, 51.0 h in August, 29.9 h in September, 50.2 h in October, 224.1 h in November, and 147.7 in December.

Proportion of mixed-sex groups among all observed social groups

During our observations, we indentified 14 345 gazelles from 6 017 groups, including 2 482 solitary individuals, according to sex and age. Among them, we found 3127 female groups (52.0% from all herds), which contained 7505 gazelles (52.3% of all indentified individuals). We found 2280 male groups, which made up 37.9% of all groups, and contained 4879 gazelles or 34.0% of all individuals. We also observed 277 incidences of mixed-sex groups, which were rare compared with female and male groups, and represented only 4.6% of all herds (they contained 1465 gazelles or 10.2% of all individuals). We noted 333 yearling groups (5.5%), which included 496 individuals (3.5%). The χ^2 goodness-of-fit tests demonstrated significant differences between these occurrences (groups: $\chi^2_{[3]} = 39.5$, $P < 0.001$; number of individuals within them: $\chi^2_{[3]} = 27.7$, $P < 0.001$).

Considering monthly fluctuations, the proportion of mixed-sex groups and individuals within them were at a maximum in April (Mann–Whitney test; groups: $Z = -5.719$, $P = 0.000$; individuals: $Z = -9.817$, $P = 0.000$) and October (groups: $Z = -6.557$, $P = 0.000$; individuals: $Z = -3.707$, $P = 0.000$), and minimal in August (groups: $Z = -1.735$, $P = 0.034$; individuals: $Z = -2.452$, $P = 0.014$) and September (groups: $Z = -2.953$, $P = 0.003$; $Z = -3.832$, $P = 0.000$). Mixed-sex groups were more common in November (the rut) compared with most other months (groups: $Z = -4.465$, $P = 0.000$; individuals: $Z = -7.072$, $P = 0.000$), but this value was lower than that noted in April and October (groups: $Z = -4.460$, $P = 0.000$; individuals: $Z = -7.318$,

Fig. 1. Proportion (box plots with confidence intervals) of adult female and male goitered gazelles (*Gazella subgutturosa*) found in mixed-sex groups from March to December 1981–1987 in Ili depression, southeastern Kazakhstan. Means and standard errors are shown. Different letters above each box plot indicate significant differences in values, whereas both letters above the one box plot indicate partial significance, based on an one-way ANOVA followed by a Fisher's least significant differences (LSD) post hoc test.. *, $P < 0.05$; **, $P < 0.001$.
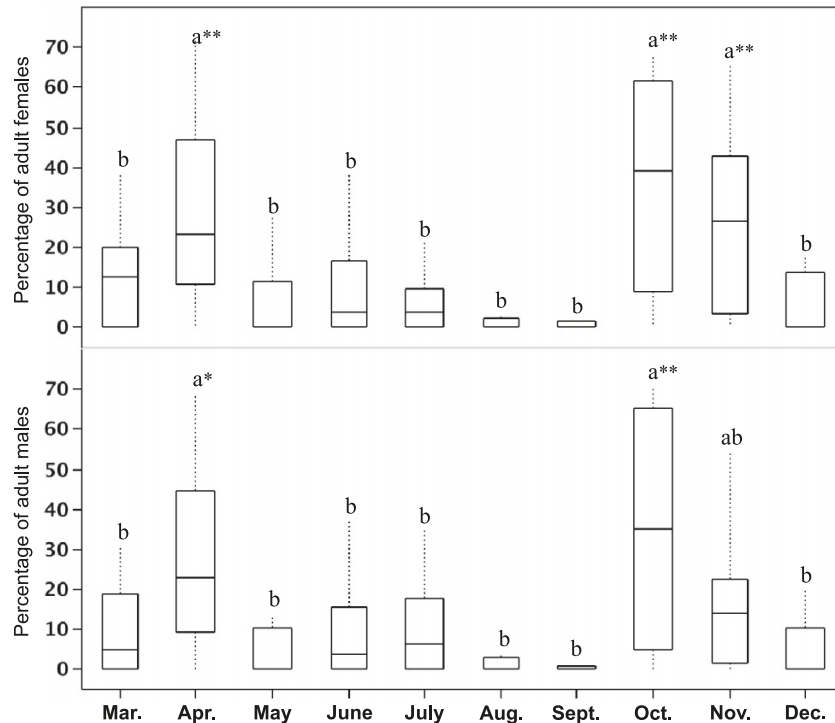
$P = 0.000$). Moreover, the proportion of mixed-sex groups decreased abruptly again during December (end of rut). The proportion of mixed-sex groups observed changed significantly over the months (χ^2 goodness-of-fit test, $\chi^2_{[7]} = 25.5$, $P = 0.001$). The number of mixed-sex groups was considerably lower compared with female groups (Kruskal–Wallis test, $\chi^2_{[1]} = 9.6$, $P < 0.005$) or male groups (Kruskal–Wallis test, $\chi^2_{[1]} = 5.5$, $P < 0.05$) throughout the year (Fig. 1). Differences were not as pronounced for the number of individuals within various groups: the proportion of mixed-sex groups was still significantly lower compared with female groups (Kruskal–Wallis test, $\chi^2_{[1]} = 6.2$, $P < 0.05$), while the proportion was not different from male groups (Kruskal–Wallis test, $\chi^2_{[1]} = 1.1$, $P = 0.29$).

Proportion of all adult males and females in mixed-sex versus unisex groups

This value fluctuated significantly over the different months for females (ANOVA, $F_{[9,3125]} = 7.63$, $P < 0.001$) and for males ($F_{[9,2228]} = 4.15$, $P < 0.001$). A maximal proportion of adult gazelles formed mixed-sex groups in April and October (Fig. 1). The lowest proportion of adult gazelles in mixed-sex groups were recorded in August and September, although they were not significantly differed from other months. In November (the rut), the proportion was significantly higher compared with most months for females except for April and October, but the proportion was significant for males only partially (for 4 out of 10 months) (Fig. 1). In December (end of rut), the proportion of adult females and males in mixed-sex groups compared with unisex groups

was considerably lower compared with November and maximum values in April and October, whereas the proportion was insignificant when compared with the rest of the months. In most months, the proportion of females and males in mixed-sex groups compared with unisex groups was lower than 13%. And only in April, October, and November did this proportion exceed 13% (Fig. 1).

The segregation coefficient (SC)

The SC value was highest during August (0.98) and September (0.94) (Student's *t* test, $t_{[8]} = -4.859$, $P = 0.001$ and $t_{[8]} = -3.156$, $P < 0.05$, respectively, compared with the mean of all other months), when gazelles were almost completely segregated. During the rutting period in November (0.80), this coefficient was lower ($t_{[6]} = 5.684$, $P = 0.001$ compared with other months with the exception of April and October), though at the end of the breeding period (December), the SC value increased again (0.86) and was not significantly different from other months ($t_{[6]} = 2.274$, $P > 0.05$) with the exception of April and October. Minimum SC values were noted in April and October, when they dropped down to 0.71 ($t_{[8]} = 5.151$, $P = 0.001$) and 0.67 ($t_{[8]} = 7.524$, $P < 0.001$ compared with other months). During the rest of the year, SC had intermediate but high values, which fluctuated between 0.86 and 0.91.

Discussion

As would be predicted by their sexual size dimorphism (Ruckstuhl and Neuhaus 2002), goitered gazelles are sexually segregated for most of the year. Surprisingly, the proportion

of mixed-sex groups (4.6%) and the proportion of adult males or females in mixed-sex groups was very low (<13%) compared with unisex groups, and the SC value was very high outside the rutting period (0.86–0.98) except for April and October. And even during the rutting period in November and December, the SC value remained between 0.80 and 0.86. That the degree of sexual segregation remained high during the rutting season is an unusual finding for ruminants.

A possible explanation for high degrees of sexual segregation during the breeding season can be found in the peculiarities of the social and spatial organization of goitered gazelles, which might distinguish it from other gazelle species. The most intensive rutting courtships of goitered gazelles are observed from early November to early December (Blank 1998). Males create a net of individual ranges on a communal display area where each male marks and defends quite a small mating territory against neighbouring bucks and outsiders. This net of territories is situated along the daily movement corridors of female groups of goitered gazelles. Females roam freely within their home range, including individual territories of males inside their ranges, but pass across a net of individual territories to reach their diurnal resting and nocturnal foraging areas. In contrast, every territorial male tries to detain female groups as long as possible, though females always successfully leave territories within 10–30 min of their arrival. Female groups just cross individual male territories during the entire rutting season, but only at the end of the breeding period (from late November to early December) will they stay inside of a chosen male's territory for 1–3 days during which mating occurs almost simultaneously for all females. After that, the rutting season finishes very abruptly (Blank 1998). As a result, December had a lower SC value than November, but it was still higher than during migrations in April and October.

From the behaviour of females, it is evident that they stay segregated from males most of the time, even during the rutting period, and only form mixed-sex groups for a very limited mating period. So, the surprising high degree of sexual segregation in these gazelles, even during the breeding period, seems to be a consequence of the seasonal short breeding period and the high level of mating synchrony, which could be an adaption to the severe arid conditions of northern deserts (Zhevnerov et al. 1983; Blank 1992).

Another explanation for the high SC values lies in our data collection protocol: much of our data during the rut was collected during long continued visual observations and herds of females with territorial males were noted as separate groups (and not as mixed-sex groups), because such mixed-sex groups existed for a very short time only, between 10 and 30 min. Consequently, only groups in which females and a male stayed together longer than half an hour were noted as mixed-sex groups.

Goitered gazelles in our study area migrate seasonally in April and October (Sludskiy 1956; Blank 1990). During early April, gazelles formed a maximum number of mixed-sex groups and gathered into large herds and moved to the west part of Ili Hallow, where the vegetation start-up occurs earlier than on the wintering grounds (Zhevnerov et al. 1983; Blank 1990). Migration of goitered gazelles is much shorter nowadays than previously recorded (Dereviagin 1947), as human settlements have reduced their former migrations routes.

Spring migration typically lasts a week and autumn migration occurs in October, when gazelles move back to their wintering ranges (Blank 1990). Accordingly, the proportion of mixed-sex groups in April and October was larger (25% and 35%, respectively) and SC values were smaller (0.71 and 0.67, respectively) than during the rutting period, or any other times of the year.

Although sexual segregation is common among ruminants (Bon and Campan 1996; Bon et al. 2001; Ruckstuhl and Neuhaus 2002; Bowyer 2004), they typically are found in mixed-sex groups during the rut. This is markedly different from goitered gazelles, because they are also segregated during the rut. We do not know if this is a trait typical for other gazelles and antelopes, which is something that needs further investigation. In this study, we demonstrated that goitered gazelles have a distinctive social organization, which is likely a behavioural adaptation of this species to the arid environment. A better understanding of the social organization and behaviour of goitered gazelles is important also for the conservation and management of this species. Numbers of goitered gazelles in Central Asia have declined in the last 100 years, and the former continuous natural habitat is now heavily fragmented because of habitat loss (Kingswood and Blank 1996). The inadequate management of remaining populations was noted by IUCN as the most important negative factors for the conservation efforts of the world's goitered gazelle population at present (Mallon and Kingswood 2001). Furthermore, there are a number of specific organizations for breeding of goitered gazelles in semicaptive conditions (i.e., in Uzbekistan, Saudi Arabia, and Turkey) and numerous zoos that keep this species in captivity (Mallon and Kingswood 2001; Kasparek 1986). For adequate management and conservation of the species, it is imperative that managers provide goitered gazelles with the social structure and sexual segregation that they evolved in their natural environment.

Acknowledgements

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