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Distribution and population status of Przewalski's gazelle, *Procapra przewalskii* (Cetartiodactyla, Bovidae)

Abstract: Przewalski's gazelle (*Procapra przewalskii*) is a rare species endemic to China. Only 200–300 individuals were estimated to survive around the Qinghai Lake by the 1990s. Recent work has revealed that the status of the species is less precarious than indicated by earlier reports; 602 individuals were recorded in 2003. Here, we describe detailed distributions for 9 of the 10 known subpopulations of the gazelle and update its population status. We tallied 1320 individuals, but found that one subpopulation first discovered in 2003 had declined since then and in 2008 was probably close to extirpation. Estimates using distance sampling conducted in a portion of the study area were higher than those that would have resulted from extrapolation of the raw observations underlying them (i.e., unadjusted counts), suggesting that the total population of Przewalski's gazelle was larger than 1320. We conclude that our larger population estimates were mainly due to a more thorough survey protocol and consideration of detection probability, and did not reflect a true population increase.

Keywords: conservation; counts; IUCN Red List; subpopulations; Tibetan Plateau.

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Introduction

Przewalski's gazelle (*Procapra przewalskii* Büchner, 1891), first collected by the Russian explorer Nikolai Przewalski in 1875, is endemic to China. It was once found in parts of Inner Mongolia, Gansu, Ningxia, and Qinghai provinces (Jiang et al. 1995). Surveys during the 1990s revealed surviving populations only in Qinghai Province (Wang and Schaller 1996, Jiang et al. 2003), most of which were located along the margin of the Qinghai Lake Basin (Cai et al. 1990, Jiang et al. 1995). By 1986, fewer than 200 gazelles were thought to survive in several fragmented subpopulations (Cai et al. 1990) and by the 1990s, numerical estimates varied from about 200 (Jiang et al. 1996) to 300 (Wei et al. 1998) animals. Recent demographic analysis suggested that the gazelle population had a genetic bottleneck, probably within a few dozen generations, and the ancestral effective population size had been reduced to <1% of its original size (Yang and Jiang 2011). Concerned about its survival, China listed it as a Class I protected species in 1988 and later in 2001 designated it as one of 15 taxa most urgently in need of protection. The International Union for Conservation of Nature and Natural Resources Species Survival Commission (IUCN/SSC) categorized the species as Critically Endangered (CR) in 1996 and 2003.

More recent work has revealed that the status of the species is less precarious than earlier reports indicated. Surveys have been more extensive and new subpopulations have been discovered: Ye et al. (2006) tallied 602 animals in 2003, Schaller et al. (unpublished data) recorded 471 animals in 2006 in a partial survey, and Zhang Kejia et al. (unpublished data) reported 490 animals in 2007. The gazelle was down-listed to

Endangered [EN, C2a(i)] on the IUCN Red List in October 2008 because the species no longer met the CR criterion of "estimated to have a number of <250 mature individuals and a continuing decline of at least 25% is estimated within three years or one generation" (IUCN 2008).

In collaboration with the Qinghai Forestry Bureau and Conservation International, we began fieldwork in 2007 in order to provide a detailed distribution for each of the known subpopulations and an updated abundance estimate.

Materials and methods

Study area

Our study areas were in the Qinghai Lake Basin and the adjacent Gonghe Basin in the northeast corner of the Tibetan Plateau (36.20–37.60°N, 98.40–100.90°E). Qinghai Lake is the largest salt lake in China, with an area of about 4300 km^2 and elevation of 3200 m. The vicinity of Qinghai Lake has an average annual temperature of about 0°C, and an annual precipitation of 400–500 mm. Gonghe Basin has an average elevation of about 3000 m, with an average annual temperature of about 2°C, and an annual precipitation of about 200 mm (Zhang 2004).

The primary vegetation types in the Qinghai Lake Basin are alpine steppe, alpine meadow, and alpine shrub (Jiang et al. 2000, Zhang 2004). Farms and villages occupy the northern and eastern lake shores, and sand dunes dominate the eastern shore of the lake. In Gonghe, the main vegetation type is desert shrub (Zhang 2004). The topography of our study area is almost flat, except for some sand dunes in the eastern lake area and hills in Tianjun.

The study area occupied portions of four counties (Haiyan, Gangcha, Tianjun, and Gonghe), and encompassed Qinghai Lake Nature Reserve, which was established as a provincial reserve in 1975 and upgraded to a national reserve in 1997. The reserve totals 4952 km^2 (including ~4300 km^2 of open water). Although a national-level reserve, pastoralists continued to live within its boundaries and used its grasslands for their livestock. The boundary of the reserve is formed by four main roads around the lake.

Distribution of gazelle subpopulations

From October 2007 to November 2009, we conducted surveys in all known gazelle-occupied areas provided by Ye et al. (2006) and Zhang Kejia et al. (unpublished data), as well as in grassland habitats lying between occupied areas on the northern and eastern shores of Qinghai Lake (Figure 1 and Table 1). To describe the distribution of gazelle subpopulations, we first interviewed local people and reserve staff to obtain information on their approximate geographic range in each area. We then placed parallel transects that overlaid the entire range and extended outward from it toward areas of uncertain distribution. We generated a random starting point in each area, and established an initial transect oriented perpendicular to the nearest road to ease logistics. Additional transects were placed parallel to this transect at 1-km intervals until reaching the estimated boundary of the area. In parts of the northern lake area and Wayu, we placed transects at 2-km intervals because of manpower shortages. We recorded locations of gazelle fecal piles within 2 m on each side of the transect line. If we did not find any fecal pellets on the outermost transect, we walked an additional transect 1 km further from the outermost to confirm that we had reached the end of the gazelle distribution. In the northern and eastern lake areas, we placed secondary transects perpendicular to the primary transects to determine the boundaries on the other dimension (Figure 1).

Gazelle feces were easily identified because our observations indicated that gazelles stand still when defecating so pellets are in piles, whereas domestic sheep and goats usually defecate while walking and thereby scatter the pellets. In addition, gazelle pellets are smaller and more spindly shaped than those of sheep and goats. We did not record fecal pellets when there was uncertainty about the species.

Survey teams (usually three, occasionally one to five), each consisting of at least two observers, walked adjacent transects simultaneously each day from about 10:00 to 16:00. Transects were surveyed in January 1–3, 2009, in Qieji; April 13–June 3, 2009, in gazelle-occupied sites with the exception of Bird Island; and October 3–November 22, 2009, in areas with no gazelle occurrence.

Except for Tianjun, we mapped gazelle distribution from the total accumulation of fecal pellets obtained from transects, as well as from gazelle groups obtained from survey routes (as described in "Abundance"). In Tianjun only, Tibetan gazelles (*Procapra picticaudata* Hodgson, 1846) were sympatric with Przewalski's gazelles. Because we could not discriminate the feces of Tibetan gazelle from those of Przewalski's gazelle, we only used visual locations of Przewalski's gazelle herds to map their distribution. We could visually discriminate the species because Tibetan gazelles are grayer

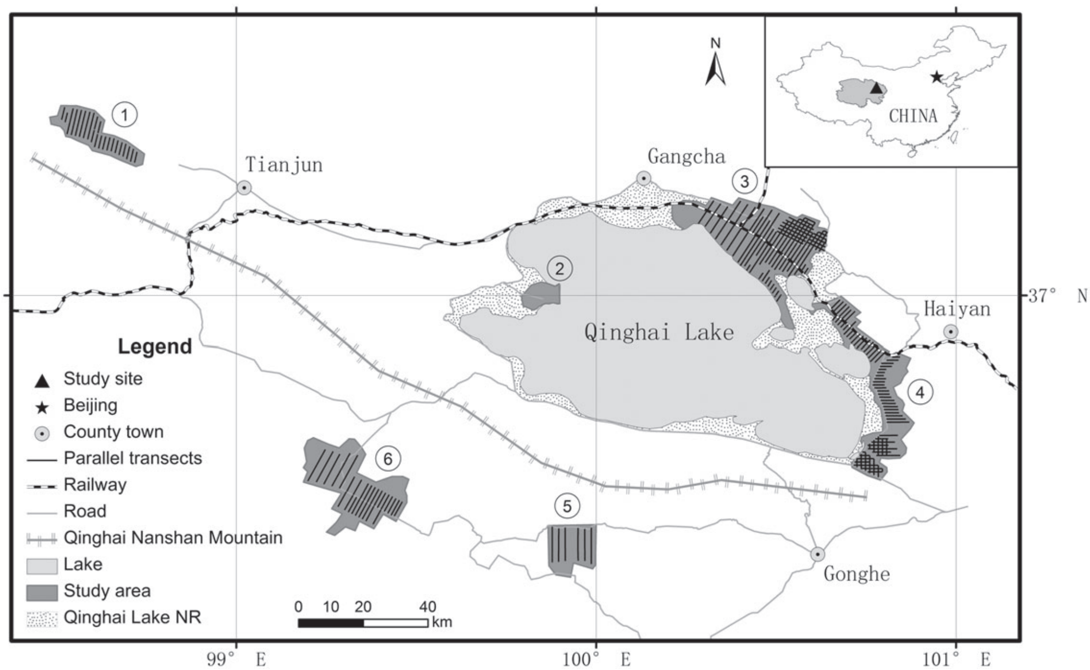

Figure 1 Study areas of Przewalski's gazelle in the northeast corner of the Tibetan Plateau and parallel transects conducted in each area (listed clockwise): 1, Tianjun; 2, Bird Island; 3, northern lake area; 4, eastern lake area; 5, Qieji; 6, Wayu. Basic information for each site can be found in Table 1.

and smaller (13–20 kg) than the larger (17–32 kg) and browner Przewalski's gazelle (MacKinnon et al. 2008). Males of the two species also have differently shaped horns. Because 90% of our recorded gazelle herds (n=167) were observed at <1 km, and because we identified species using binoculars and spotting scopes, we are confident in our identification. All areas containing gazelles were examined for potential movement barriers

Area	Area surveyed (km²)	Main vegetation type[a]	Patch[b]	Highest count				95% Volume contours (km²)	Length of routes in Dec 2008 (km)[d]	Number of transects in 2009	Total length of transects (km)
				Jan 2008	Jul 2008	Dec 2008	Aug 2003[c]				
Tianjun	181	AM	TJ	196	193	282	76	108	43	28	112
Bird Island	58	AP and SA	BI	19	24[e]	29[e]	19	–	–	–	–
Northern lake area	657	AP	HGn	173	172	182	190	50	19	31	135
			HGs	89	121	340		155	44	33	154
			TX	31	36	45	62	33	15	29	147
Eastern lake area	436	AP	SD	112	39	113	–	35	9	24	80
			HD	84	56	97	134	58	58	22	71
			YZ	31	46	53[f]	46	32[f]	15	26	114
Qieji	165	DS	QJ	0	–	0	75	–	–	6	63
Wayu	421	DS	WY	90	92	179	–	175	35	27	165
Total	1918			825	779	1320	602	646	238	226	1041

Table 1 Areas surveyed and highest counts in all route surveys conducted in 2008, and length of transects conducted in 2009 for each patch sheltering Przewalski's gazelle, Qinghai Province, China.
[a]Vegetation type: AM, alpine meadow; AP, alpine prairie; SA, saline-alkali; DS, desert shrub. From Zhang (2004). [b]TJ, Tianjun; BI, Bird Island; HGn, Haergai-Ganzihe North; HGs, Haergai-Ganzihe South; TX, Tale Xuanguo; SD, Shadao; HD, Hudong-Ketu; YZ, Yuanzhe; QJ, Qiejie; WY, Wayu. [c]Data from Ye et al. (2006). The number "190" in HGn and HGs also includes gazelles in SD. [d]The total length of routes within 95% volume contours of each patch. [e]Data from Qinghai Lake Nature Reserve. [f]Our survey may not have covered the entire area inhabited by gazelles in YZ, because we found gazelles to the south of the Daotang River (black arrow, Figure 3) in November 2009, the area we had initially considered as non-occupied by gazelles.

such as highways or railway tracks that could function to fragment the area into relatively isolated patches. We estimated the area of gazelle distribution by using the fixed kernel density estimator function in Hawth's analysis tools for ArcGIS (smoothing parameter h=1000 m). We selected 95% volume contours to indicate the distribution range for each patch.

Abundance

We conducted both index counts, in which we attempted to maximize the number of gazelles observed, and distance sampling in which we attempted to estimate population density.

Index counts

A team of two to three observers traveled across study sites to record the sizes of gazelle groups during morning hours (from sunrise to about 11:00). Survey routes were conducted by vehicle where possible (total length 602 km); otherwise, we walked (total length 474 km; Table 2). The routes were placed to detect as many gazelles as possible, according to local guides and our pilot study. We used binoculars and spotting scopes to observe the gazelles. To minimize double counting within any single survey, we did not tally gazelle groups having the same size and structure as one that was previously observed in close proximity. There were few loops in our survey routes, and we ignored those gazelle groups on loops when we head back to roads. If a survey area was too large for a team to finish in a single day, the area was divided into patches and at most four teams, each consisting of two observers, conducted surveys simultaneously to cover the whole area. To minimize the duplicate counts among different teams, we considered gazelle herds with similar size and composition and occurring in proximate area and time as duplicates and recorded only one. We resurveyed each area two to four times (once per day) by traveling along the same route during each of the three survey periods: January 10–25, 2008; July 10–August 5, 2008; and December 4, 2008, to January 4, 2009. Surveys conducted in July and December 2008 covered a larger range than in January 2008 (Table 2).

To assess the effect of survey travel mode on our ability of detecting the animals, we compared encounter rates (number of gazelles detected per kilometer route) on route conducted by vehicle and on foot within the 95% volume contours. For each area, we chose the largest number of gazelle individuals observed in a single day to indicate a minimum population count.

Distance sampling

In the northern lake area, we also estimated gazelle density using distance sampling in April 23–27 and May 20–28, 2009, using the transect procedures detailed above (see "Distribution of gazelle subpopulations"). We recorded the location on the transect line where we observed gazelles (using a hand-held GPS), estimated sighting angles and distances to the general areas where each gazelle group was initially seen, and calculated the perpendicular distances from gazelle groups to the transect line. Distances and sizes of gazelle groups formed the input for the Conventional Distance Sampling analysis engine of DISTANCE 6.0 (Thomas et al. 2009). We truncated observations beyond 600 m from transects, which accounted for 8% of the observations. Because in the field we estimated sighting distances to the nearest 50 m (e.g., 50, 100, and 150 m), we grouped observations into six 100-m intervals (0–100, 100–200, 200–300, 300–400, 400–500, and 500–600 m) to reduce the impact of imprecision in distance estimation. For density estimation, we regressed ln (group size) on detection probability and used the size-bias regression method if regression was significant at α=0.15; otherwise, we used the mean group size. We tested all models suggested by Buckland et al. (1993) based on criteria of robustness, desired shape, and efficiency. Because the corrected Akaike's Information Criterion adjusted for small sample size (AIC_c) (Burnham and Anderson 2002) and χ^2 goodness-of-fit tests indicated that those candidate models

Survey	Route length (km)	Route within 95% volume contours (km)	Route on foot (km)	Route by vehicle (km)	No. of gazelle groups	Mean group size±SD
Jan 2008	274	155	86	69	59	12.4±17.9
Jul 2008	320	244	113	131	225	6.6±9.0
Dec 2008	481	238	111	127	191	11.1±23.1

Table 2 Survey efforts and encounter rates on routes of the three surveys conducted from January to December 2008. All figures were calculated from records within the 95% volume contours, except for the first column.

had similar level of support, we produced an AIC-weighted average of alternative models in DISTANCE.

Results

Distribution of Przewalski's gazelle

We recorded 1254 locations of gazelle groups and 2449 locations of gazelle fecal piles in our total combined surveys. Gazelles were found in five surveyed areas: (1) Tianjun; (2) Bird Island; (3) northern lake area; (4) eastern lake area; and (5) Wayu (Figures 2–5). We found no evidence of Przewalski's gazelle in the Qieji area.

Abundance

The median encounter rate on all survey routes conducted on foot (3.1 gazelles/km, n=63) was similar to that on routes conducted by vehicle (3.4 gazelles/km, n=79; Mann-Whitney U=2388, p=0.68), suggesting that the mode of survey did not significantly affect our ability of detecting the animals. The numbers of gazelles we tallied differed considerably among the surveys, with certain amount of relative survey effort (Table 2). We considered the 1320 gazelles tallied in December 2008 the most appropriate to consider a minimum population count (Table 1).

We recorded 1072 gazelles in 65 groups on ca. 460 km of distance sampling transects in the northern lake area (including patches of Tale Xuanguo, Haergai-Ganzihe North, and Haergai-Ganzihe South) in April 23–27 and May 20–28, 2009. These transects were completed by three survey teams during this relatively long period, such that some gazelles were recorded more than once and this number did not represent a minimum population count. In comparison, we had visually tallied 567 gazelles on survey routes in the same area during December 2008. Truncation of 600 m perpendicular distance to 92% of observations reduced sample size from 65 to 60. The mean gazelle group size was 16.4 animals (95% CI, 11.3–23.9).

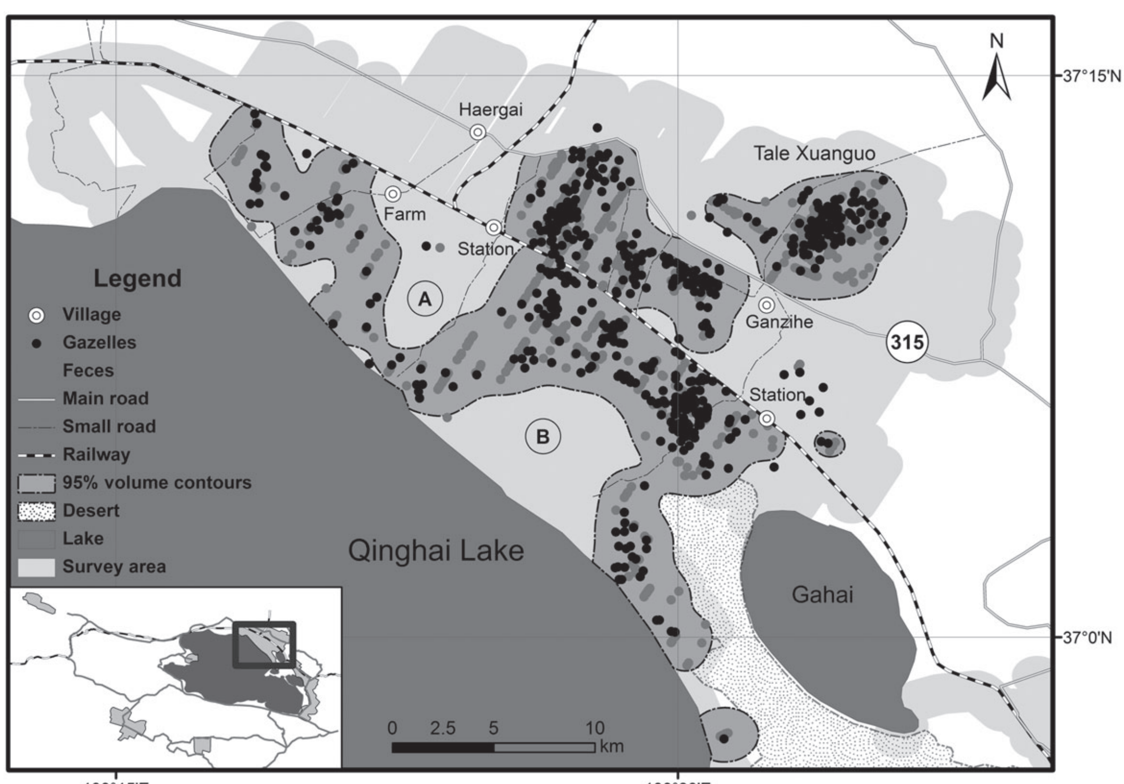

Figure 2 Gazelle herd locations and fecal piles recorded in all the surveys conducted from January 2008 to November 2009 in the northern lake area. The area was composed of three patches: Tale Xuanguo (to the north of Highway 315), Haergai-Ganzihe North (in between Highway 315 and the railway), and Haergai-Ganzihe South (to the south of the railway). The light gray area was buffered from transects and survey routes (1 km each side), indicating the area surveyed.

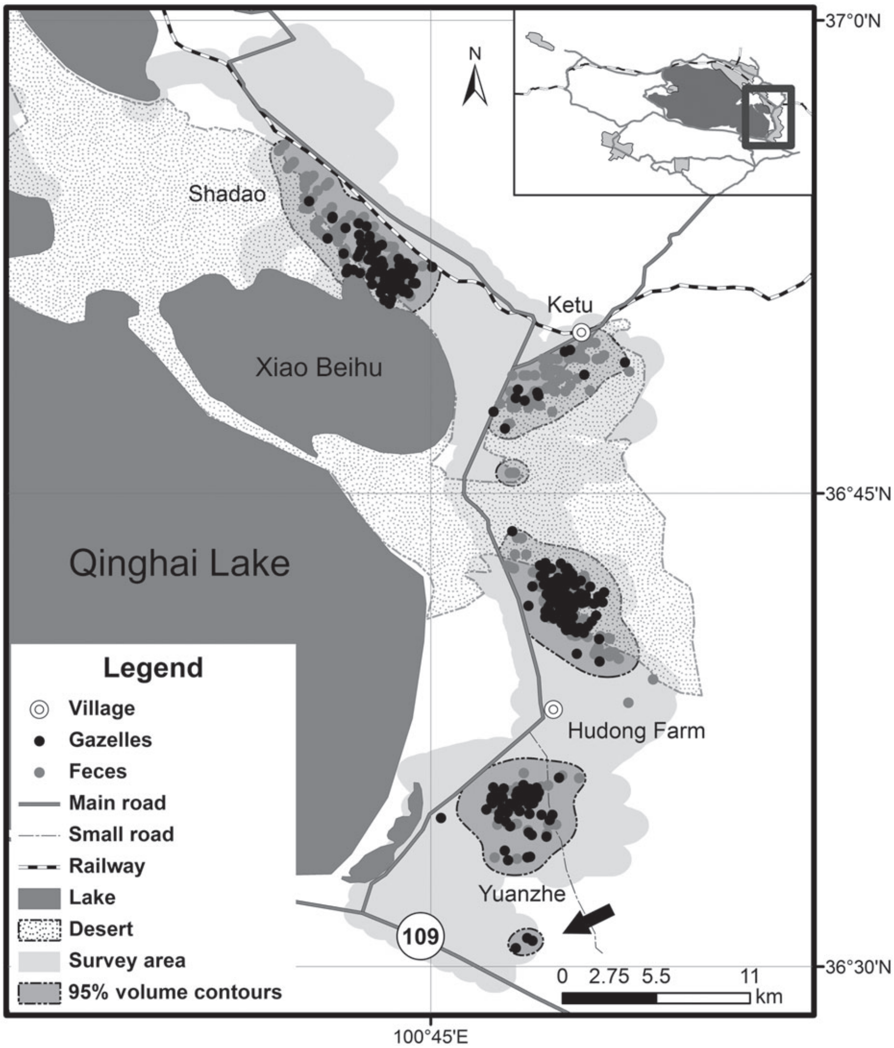

Figure 3 Gazelle herd locations and fecal piles recorded in all the surveys conducted from January 2008 to November 2009 in the eastern lake area (see Figure 2 for legend). The area was divided into three relatively separated patches: Shadao, Ketu-Hudong, and Yuanzhe, by a road and a large farm (Hudong Farm) and local communities around it.

Histograms of groups detected on distance provided no evidence of evasive movement on the part of gazelles. The four detection functions we considered had similar AIC_c scores (Table 3). Because we considered models with $\Delta AIC_c<2$ as having similar support, we produced an AIC-weighted average of these models through bootstrapping (n=999). Because the regression of group size on distance was not significant (for the uniform cosines model: slope=-0.247, t=-0.041, p=0.378; similar results for the other models), we used mean group size (rather than a distance-adjusted group size) for estimating gazelle density. The density of gazelle groups was estimated as 0.31/km^2 (95% CI, 0.16–0.57), and the density of gazelle individuals was estimated as 4.71 gazelle/km^2 (95% CI, 1.99–7.87). Our transects covered an area of 357 km^2; thus, the abundance within the northern lake area was estimated as 1653 (95% CI, 712–2810).

Discussion

Distribution of gazelle subpopulations

We documented nine patches occupied by Przewalski's gazelles (Table 1). Except the Qieji area, we found gazelles living in all patches documented as occupied in 2003 by Ye et al. (2006). The Qieji subpopulation was first described in 2003 when 75 gazelles were recorded (Ye et al. 2006). However, we found no gazelles there in

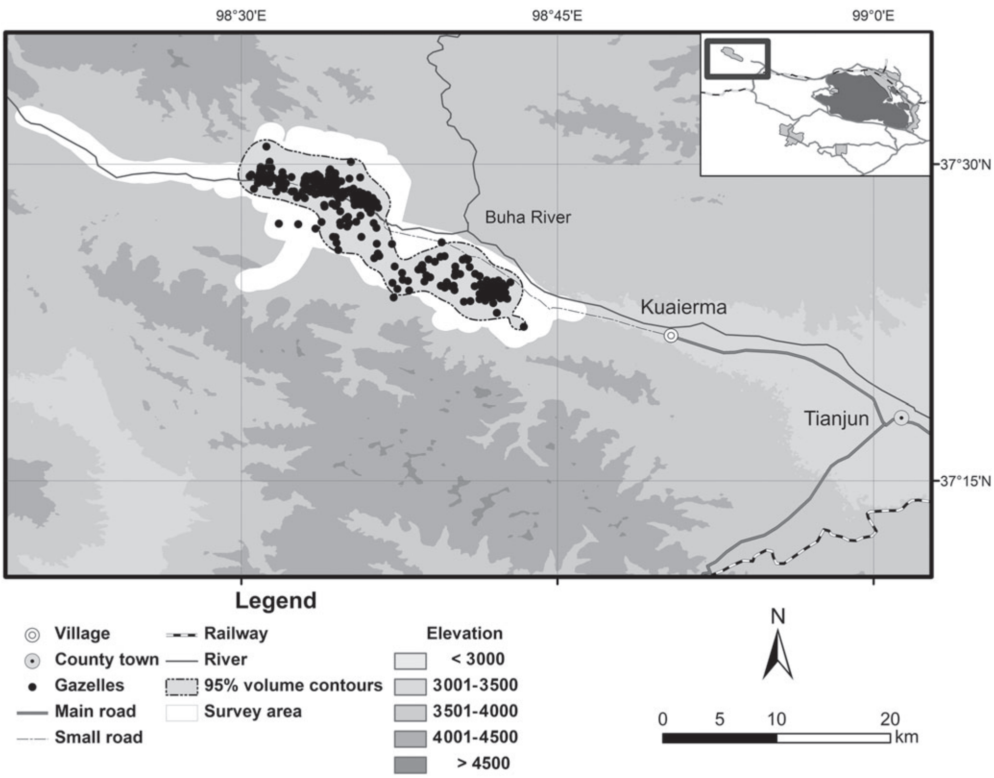

Figure 4 Gazelle herd locations recorded in all the surveys conducted from January 2008 to November 2009 in Tianjun (see Figure 2 for legend).

our route survey in January 2008. In December 2008, we walked 63.5 km of transect line, covering the central part of the area surveyed by Ye et al. (2006), but found no evidence of gazelles. Thus we considered Qieji as non-occupied by gazelles.

Our transects and survey routes covered the entire known geographic distribution of Przewalski's gazelles in the northern and eastern lake areas, with the exception of two sites: (1) We found gazelles to the south of the Daotang River (Figure 3) in November 2009, an area we had initially considered as non-occupied. More surveys are needed to verify the southeast boundary of gazelle distribution range in Yuanzhe. (2) We expended little survey effort in the large area of sand dunes between Haergai-Ganzihe South and Shadao (Figure 3). We are unsure whether gazelles in these two areas use this desert habitat as a corridor, i.e., whether there is connectivity between these two areas.

In the northern lake area, we recorded few gazelle groups or fecal piles around areas of high human density such as villages and railway stations, suggesting that gazelles may be avoiding using areas with intensive human activities. Meanwhile, we also found no gazelle or fecal piles on large farmlands (A, Figure 2), and a seasonal wetland – dry in winter, but wet in summer (B, Figure 2) – in this area, indicating the two types of vegetation were not preferred habitat by gazelles.

In Tianjun, gazelles occurred in the valley of the Buha River on both sides of the river (Figure 4). Our transects and survey routes in this area may have lacked sufficient coverage to map the southern boundary of gazelle habitat. Because there are mountains on both sides of the river, and Przewalski's gazelles use relatively low elevation and relatively flat terrain (Leslie et al. 2010), we believe gazelles did not occur further south of our survey area, although it would be worthwhile to survey nearby valleys to confirm their absence.

Gazelles in Wayu were first described by Zhang Kejia et al. (unpublished data). Our transects and survey routes covered the area of known distribution near the village (Figure 5); however, we were unable to determine the boundaries of gazelle habitat on the open and flat grassland that lacked mountains or rivers. A newly built road (almost finished in August 2009), from Dashuiqiao to Wayu extends to the Gonghe County town, dissecting the habitat of this gazelle subpopulation (Figure 5). This road will be the new Qinghai-Tibet highway, supporting heavy traffic; it may have an impact on the survival of this subpopulation.

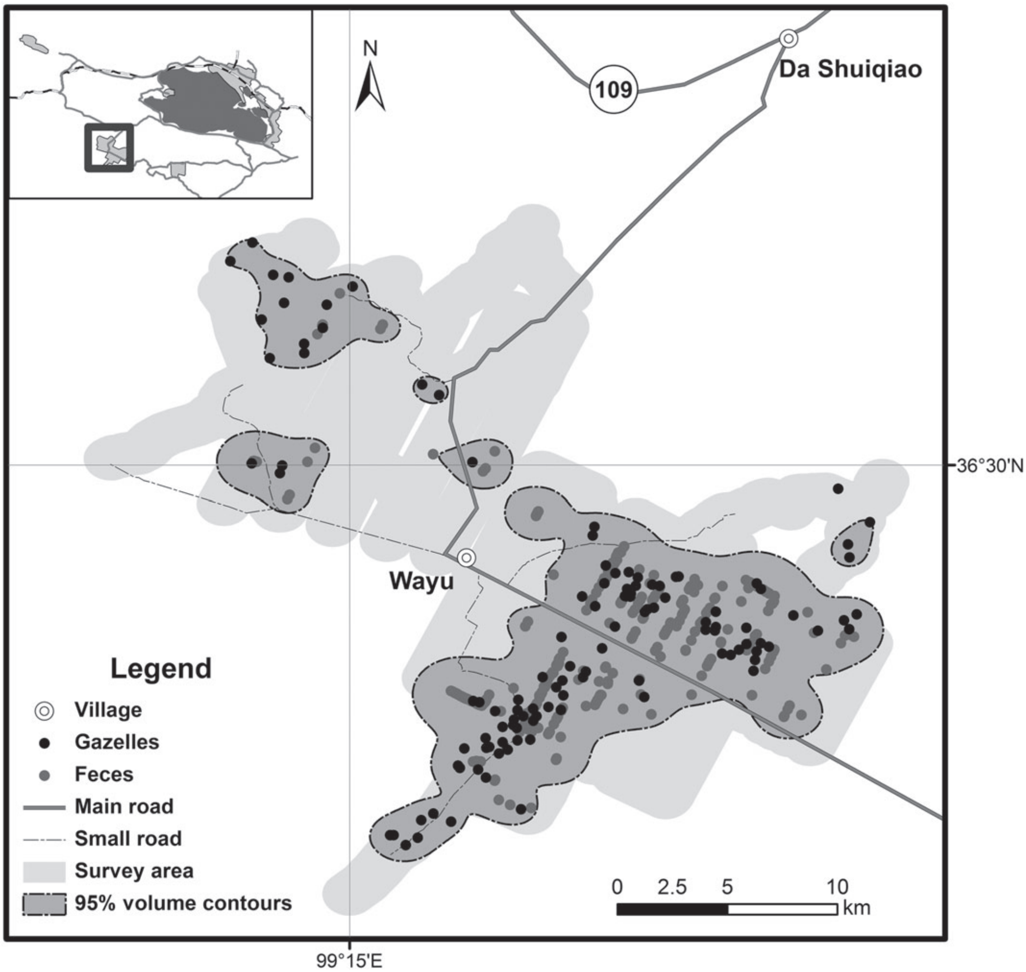

Figure 5 Gazelle herd locations and fecal piles recorded in all the surveys conducted from January 2008 to November 2009 in Wayu (see Figure 2 for legend).

Abundance

We do not interpret the gazelle numbers documented in December 2008 as representing a true increase over our earlier surveys. Rather, we consider the counts of January and July 2008 as biased low because (1) the total length of survey routes in January 2008 was much shorter than in the other two surveys, and (2) the group size was smaller in July than in December 2008 as gazelles tend to form larger groups during winter (Li et al. 1999, Lei et al. 2001), although the lengths of survey routes and the numbers of gazelles groups recorded in the two surveys were similar. Additionally, July is probably too early in the year to count neonates. Parturition has generally been considered as occurring from May to mid-June (Leslie et al. 2010). However, reserve staff and local pastoralists consistently told us that the calving season of Przewalski's gazelles begins at the end of June, although their opinions differed about when it ends. Mongolian gazelle (*Procapra gutturosa* Pallas, 1777) calves adopt a hiding strategy during their first 2–3 weeks of life (Odonkhuu et al. 2009), and neonates of Tibetan gazelle hide for up to 2 weeks (Schaller 2003). Similarly, we found calves of Przewalski's gazelle hiding alone several times in July; however, no hiding calf was found after August 1. For those reasons, we suggest it is more efficient to conduct index counts in winter than in summer.

In the northern lake area, the 1653 (95% CI, 712–2810) estimate from distance sampling was much higher than the 567 gazelles obtained from the index count, which confirmed that the index counts were biased low. Thus, we urge caution when using direct counts as indices of population abundance. On the other hand, the point estimate from distance sampling was accompanied by a wide confidence interval. The observed sizes of gazelle groups varied from 1 to 99 animals ($\bar{X} \pm SD$=16.4±24.1, n=60), which contributed to this wide confidence interval, although we conducted the transect survey when

Detection key functions	Uniform	Uniform	Half-normal	Hazard rate
Terms	Cosine	Simple polynomial		
AIC_c	208.45	209.42	208.69	209.85
χ^2(df)	1.34 (4)	2.33 (4)	1.57 (4)	0.68 (3)
Chi-p	0.85	0.67	0.81	0.88
f (0)	0.0025	0.0023	0.0025	0.0030
p	0.66	0.73	0.67	0.56
DS (SE)	0.29 (0.05)	0.26 (0.04)	0.28 (0.05)	0.34 (0.11)
D (SE)	4.72 (1.22)	4.25 (1.06)	4.61 (1.22)	5.51 (2.15)
n (SE)	1686 (437)	1516 (380)	1645 (434)	1966 (768)

Table 3 Models used to estimate the density of Przewalski's gazelle in the northern lake area of Qinghai Lake, Qinghai Province, China, April–May 2009, using the program DISTANCE.
Because these models provided similar support, we used an AIC-weighted average of models to estimate gazelle density.
χ^2 (df), Chi-square goodness-of-fit test (degree of freedom); Chi-p, probability of a greater χ^2 value; f (0), value of the probability density function at zero for line transects; p, probability of detecting a gazelle group; DS (SE), estimate of the density of gazelle groups (standard error); D (SE), estimate of the density of gazelle individuals (standard error); n (SE), estimate of number of gazelles in specified area (standard error).

groups are generally the smallest (Lei et al. 2001). Additionally, assemblages of Przewalski's gazelle are more like loose and temporal aggregations than tight knit groups. We considered that individual gazelles acted together as a group, but one group can be divided into smaller and relatively separated aggregations, although an aggregation should be well defined. Thus, the variance of group size may be reduced, and precision of estimates from distance sampling can be improved. Increasing sample sizes will improve future precision of estimates, although it will incur costs in both time and effort.

Difference in counts of gazelle populations and conservation implications

The difference in counts from the 1990s to 2008 was probably due to the larger range covered by the later surveys. Ye et al. (2006) surveyed the Tianjun, Tale Xuanguo, and Qieji areas where gazelles had been assumed absent during the 1990s, and we included Wayu as a newly found subpopulation. The relatively extensive survey conducted in 2003 by Ye et al. (2006) was used in the more recent IUCN/SSC Red List evaluation of the status of Przewalski's gazelle. Although Ye et al. (2006) did not report specific methods (e.g., length of survey routes, total area covered), we interpret their numbers as uncalibrated index counts. Thus, with the exception of the subpopulation in Qieji, we cannot compare their counts directly with ours. We found no gazelles in Qieji, whereas Ye et al. (2006) recorded 75 individuals, suggesting a marked decrease from 2003 to 2008. The local pastoralists we interviewed believed that gazelles in this area had declined owing to recent poaching.

Przewalski's gazelles face challenges other than poaching. In 2003, the central government of China initiated grassland restoration programs throughout the country, and wildlife conservation is also better acknowledged and enforced than earlier. However, the intensity and speed of development in the Qinghai Lake region has been remarkable. The remaining distribution of Przewalski's gazelle occupies a narrow space between sand dunes and human settlements, and available grasslands are also heavily grazed by livestock. The total number of livestock in the four counties around Qinghai Lake was recently estimated at 2.9 million (Qi 2009). There is a high dietary overlap of gazelles and sheep, which indicates potential competition between the two, especially when vegetation is senescent (Li et al. 2008). Meanwhile, habitat fragmentation has been intensified by rangeland fencing (Liu and Jiang 2002, Yu 2008). Fragmented small populations are highly vulnerable, and evaluations based on status of the species as a whole may obscure the vulnerability of these small subpopulations. The majority (63%) of local people around the Qinghai Lake have a positive attitude toward Przewalski's gazelle, although no more than half of them are aware that grassland fences, livestock, roads, and wolves (*Canis lupus* Linnaeus, 1758) may negatively affect the gazelles (Hu et al. 2009). Despite the encouraging indications that the total number of Przewalski's gazelles was larger than earlier estimates, the remaining subpopulations still require concerted efforts to reduce poaching, restore grassland habitats, and reduce obstructions that preclude movements among them.

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