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ORIGINAL PAPER

Reproduction of plateau pika (*Ochotona curzoniae*) on the Qinghai–Tibetan plateau

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Abstract The reproduction of the plateau pika (*Ochotona curzoniae*) was investigated in Guoluo District at an elevation of 4,000 m on the Qinghai–Tibetan plateau, China, from April 2007 to August 2008. Reproduction was seasonal, and the breeding season lasted from April to late June/early July. Adults produced two litters in each year, and the mean litter size, estimated by counting the number of embryos in utero, was 3.3±0.1 (n=52) in 2007 and 3.2±0.1 (n=66) in 2008. The timing of reproduction showed high inter-annual variation; lower precipitation and the concomitant delay in spring vegetation phenology may have retarded the onset of the breeding season in 2007 compared with 2008. The most frequent litter sizes were 3 and 4, which together comprised 71.2% and 83.3% of litters in May and June of 2007 and 2008, respectively. Compared with previous studies, reproduction was highly variable between geographic areas. Pikas produced between one and five litters per year in different regions of the plateau over different breeding seasons. This geographic and inter-annual variation appeared to be associated with the duration of plant growth at each site, suggesting that plateau pikas adjust the length of their breeding season to match the period when sufficient energy is available to support the high energy demands of reproduction.

Keywords *Ochotona curzoniae* · Reproduction · Qinghai–Tibetan plateau · Plateau pika

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Introduction

Plateau pikas (*Ochotona curzoniae*) are small, non-hibernating, herbivorous lagomorphs that are distributed widely over the Qinghai–Tibetan plateau from 3,200 to 5,300 m in altitude (Smith and Xie 2008). They inhabit open alpine meadows and typically live in social groups composed of two to six adults and their young that together occupy a family territorial burrow system (Dobson et al. 1998, 2000; Liang 1981; Qu et al. 2008; Smith and Wang 1991). The plateau pika is an endemic species that evolved during the uplift of the Qinghai–Tibetan plateau (Yu et al. 2000), and its life histories and physiology are well adapted to the extreme cold and hypoxic environment of the plateau (Li et al. 2001; Wang et al. 2006; Yang et al. 2006, 2007). Many previous studies have examined the social behavior and reproduction of pikas, but most data to date have been collected from marginal parts of the plateau at altitudes between 3,200 and 3,300 m (Li et al. 1998; Wang and Dai 1991; Yin et al. 2009), with only sporadic reports from higher elevations more characteristic of the plateau as a whole (Shen and Chen

1984). On the Qinghai–Tibetan plateau, the plant growth period and aboveground biomass vary with differences in altitude and ambient temperature (Wang et al. 2004a). At altitudes of 3,200–3,300 m, the plant growth period is about 134–152 days and the maximum aboveground biomass is about 420 g/m^2 (Li et al. 2004; Zhong and Wei 2010); however, at 3,800–4,500 m, the plant growth period is shorter (90–120 days) and the maximum aboveground biomass is correspondingly reduced to only 75–110 g/m^2 (Shen and Chen 1984; Yang et al. 2010). Since reproduction is energetically expensive (Speakman 2008), the availability of plant vegetation and food resources may have dramatic effects on reproductive output (Ylönen et al. 2003). Consequently, reports from lower elevations cannot be easily extrapolated to pikas inhabiting the high plateau. In this paper, our aim was to investigate the reproductive characteristics of plateau pikas at medium elevations on the Qinghai–Tibetan plateau (3,900–4,000 m above sea level) and to compare the reproductive characteristics of this population with data gathered from lower altitudes (3,200–3,500 m).

Material and methods

Study area

This study was carried out on the southeastern flank of the Qinghai–Tibetan plateau, about 15 km east of the small town of Dawu, Guoluo state, Qinghai Province, People's Republic of China (34°25′ N, 100°22′ E, elevation 3,950 m; Fig. 1). The study site (~800 ha) was on a gentle slope. The climate in the area is harsh with an average annual temperature of 0°C. Frost can occur year-round, and soils freeze to more than 2 m deep in the winter. The daily variation in temperature is great (up to about 25°C). Most precipitation falls in the summer between June and August, with the annual mean precipitation being 580 mm. Heavy winter snowfalls are rare. The vegetation at the study site is typical *Kobresia humilis* alpine steppe meadow and is grazed year-round at low density by domestic livestock (yak, *Bos grunniens*, and sheep, *Ovis aries*).

Data collection

The total vegetation cover, the green vegetation cover, and the area of bare ground within the study site were measured monthly from April to August in both 2007 and 2008. Ten 50×50-cm quadrats were chosen randomly near the core area of the study site. Local climate data, including monthly precipitation and temperature, were obtained from the Qinghai Provincial Meteorological Bureau 15 km from the study site.

Pikas were captured using the string noose method (Dobson et al. 1998). The gestation period of plateau pikas is about 21 days, so the work schedule was divided to cover two to three sample periods per month to obtain sufficiently fine-grained data. We distinguished the adults from the young by body mass and color of fur, as well as the hardness and length of toes. About 20 adult males and 20 adult females were captured during each sampling period and killed and dissected. In total, 186 males and 181 females were dissected in 2007, and 157 males and 220 females were dissected in 2008. Once a pika was captured, it was immediately placed into a plastic cage measuring 0.4×0.2×0.2 m. Two to three pikas were placed in each cage and dry grasses were added to the cage to reduce fighting. Vegetables such as fresh carrots were provided as food. After pikas were taken back to the laboratory in 2 h, body mass and gender were recorded. Pikas were anesthetized and killed by cervical dislocation. The animals were then dissected and tissue samples were obtained. Testes and the left epididymal tail of males, as well as the uterus and ovaries of females, were weighed with an electronic balance (nearest to 0.001 g). If placental scars and embryos were

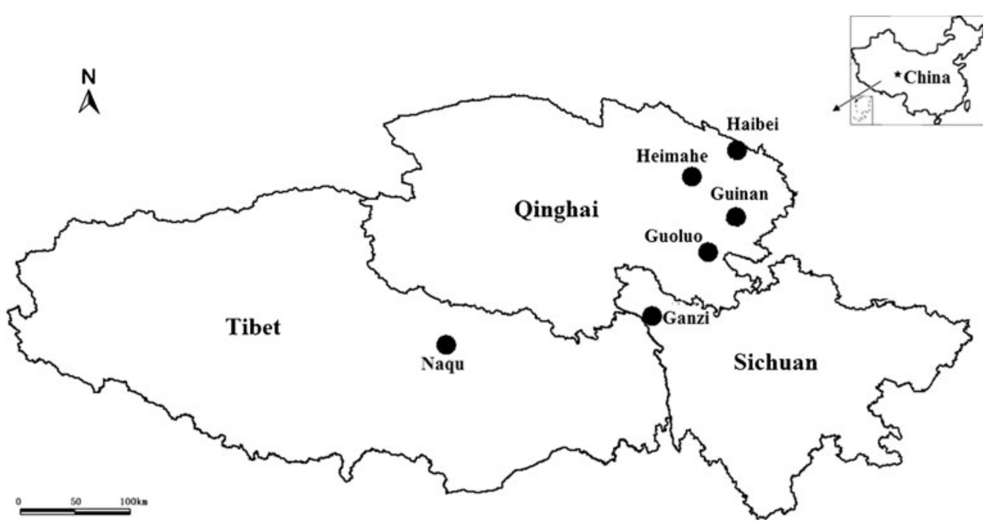

Fig. 1 Map of the study area in the Qinghai–Tibetan plateau

detected in a female simultaneously, we concluded that the individual had two or more litters. Litter size was determined by counting viable embryos in utero. All the procedures were reviewed and approved by the ethical review board of the Northwest Institute of Plateau Biology, Xining, Qinghai Province, China.

Statistical analysis

To test for significant differences in vegetation coverage, adult body mass, reproductive organ mass, and litter size between months and years, we used ANOVA and LSD tests. Independent samples *t* tests were used to analyze the differences in body mass and reproductive organ masses in the same study area between years. Occurrences of scrotal testes in males and pregnancy in females in different months were analyzed using one-sample *t* tests. Differences with a *P* value of 0.05 or less were considered significant. All values are expressed as the mean±SE. All the statistical procedures were performed using SPSS (version 16.0, SPSS Inc., Chicago, IL, USA).

Results

Climate and vegetation

The monthly temperature ranged from −12.7°C to 11.4°C over the two study years, and the total annual precipitation was 584.5 mm in 2007 and 581 mm in 2008. There were no dramatic differences in average monthly temperatures between early spring in 2007 and 2008. From February to April, the mean temperature was −3.3°C in 2007 and −4.5°C in 2008; in April, the average temperature was 1.7°C in 2007 and 1.9°C in 2008. However, there was a difference in spring precipitation between the 2 years. In spring 2007, total precipitation was only 14.2 mm, and just 2.3 mm of rainfall fell in April, while 22.1 mm of rain was recorded during spring 2008, with 12.5 mm in April.

Predictably, there was also a significant difference in green vegetation cover between the 2 years in May, June, and August—May, $F_{1,18}$=84.827, P<0.001; June, $F_{1,18}$=15.420, P=0.001; August, $F_{1,18}$=5.399, P=0.032—but the differences in April and July were not significant: April, $F_{1,18}$=0.037, P=0.850; July, $F_{1,18}$=0.343, P=0.565 (Fig. 2). However, the total vegetation coverage was not significantly different between years, except in June and August when there was greater total vegetation in 2008 (April: $F_{1,18}$=1.027, P=0.324; May: $F_{1,18}$=3.057, P=0.097; June: $F_{1,18}$=15.420, P=0.001; July: $F_{1,18}$=1.986, P=0.176; August: $F_{1,18}$=5.399, P=0.032).

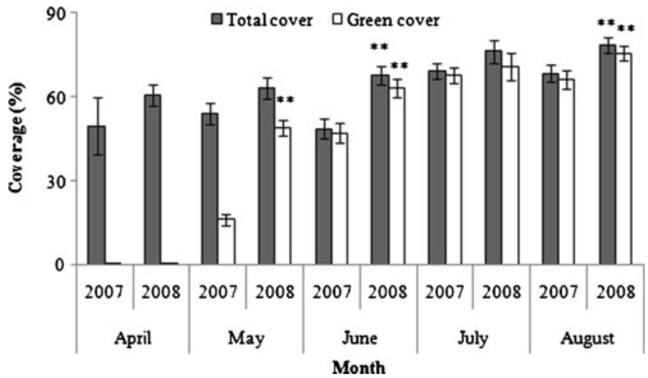

Fig. 2 Total vegetation coverage and coverage by green vegetation from April to August within the study site in 2007 and 2008. *Asterisks above bars* denote significant annual differences in the same month. **P<0.01

Pika body mass

During both 2007 and 2008, significant differences in male body mass were detected between sampling periods (2007: $F_{10,176}$=3.341, P=0.001; 2008: $F_{10,146}$=5.573, P<0.001; Fig. 3). In 2007, body masses from late May to June as well as from mid-July to late August were significantly higher than between late April to mid-May and early July (Fig. 3). In 2008, body masses from late April to early July and late August were significantly higher than between mid-July to mid-August. Body masses of females also showed significant differences among sampling periods in both 2007 and 2008 (2007: $F_{10,193}$=11.326, P<0.001; 2008: $F_{10,199}$=14.388, P<0.001; Fig. 3). In 2007, body masses in late May and early June were significantly higher than in other periods; in late August, adult female body masses recovered and were significantly higher than in July and early or mid-August. In 2008, body masses from late April to early June were significantly higher than between mid-June and August. Between years, the body masses of both sexes were significantly lower from April to mid-May in 2007

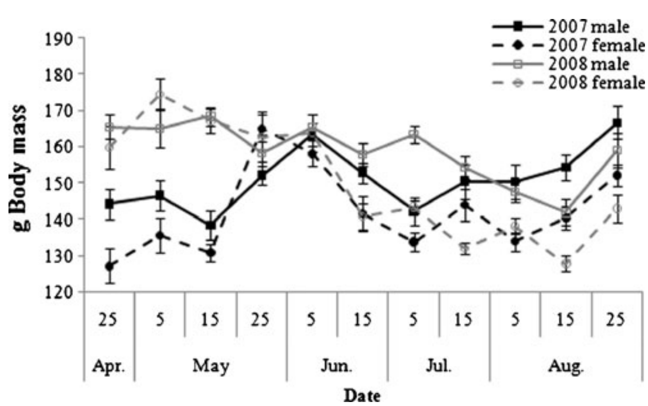

Fig. 3 Body mass (in grams, means±SE) of plateau pikas over the summers of 2007 and 2008 in Guoluo, Qinghai, China. Body mass data were pooled two or three times monthly

compared with 2008 ($P<0.01$), while no significant differences between years were detected from late May to August ($P>0.05$).

Masses of reproductive organs

For males, the testes became much larger from April to June, but the average testis mass dropped to <0.1 g in August (Fig. 4a). There were significant differences in the mean masses of testis over the sampling periods (2007: $F_{10,346}=100.138$, $P<0.001$; 2008: $F_{10,288}=122.658$, $P<0.001$). On average, testis mass in April and May was significantly higher than in June for both years, and the average testis mass in June was also significantly higher than in July and August. The average testis mass in late April was slightly higher in 2008 compared with 2007 ($F_{1,70}=5.850$, $P=0.018$); however, the average testis mass from late May to early July was significantly lower in 2008 compared with the same period in 2007 (late May: $F_{1,49}=28.494$, $P<0.001$; early June: $F_{1,52}=15.596$, $P<0.001$; mid-June: $F_{1,54}=13.837$, $P<0.001$; early July: $F_{1,63}=18.859$, $P<0.001$). The seasonal variation in the average mass of the left epididymal tail mirrored the results for testes (Fig. 4b). There were significant differences in the mean mass of the left epididymal tail over the sampling periods (2007: $F_{10,167}=23.433$, $P<0.001$; 2008: $F_{10,117}=21.598$, $P<0.001$). The average mass of the left epididymal tail from April to early June was significantly higher than in July and August in both years. Overall, the mean mass of the left epididymal tail was slightly lower from April to May in 2007 compared with 2008 (late April: $F_{1,34}=1.343$, $P=0.255$; early May: $F_{1,31}=2.509$, $P=0.123$; mid-May: $F_{1,27}=0.897$, $P=0.352$; late May: $F_{1,23}=1.162$, $P=0.292$), but was significantly higher from June to early July 2007 compared with 2008 (early June: $F_{1,25}=5.720$, $P=0.025$; mid-June: $F_{1,26}=4.153$, $P=0.05$; early July: $F_{1,31}=4.717$, $P=0.038$).

There was also seasonal variation in the average masses of the uterus and ovary. Significant differences in average uterus mass were detected over the sampling periods in both years (2007: $F_{10,138}=16.636$, $P<0.001$; 2008: $F_{10,138}=34.858$, $P<0.001$). The mean uterus mass from April to June was significantly higher than between July and August (Fig. 4c).The mean uterus mass peaked at

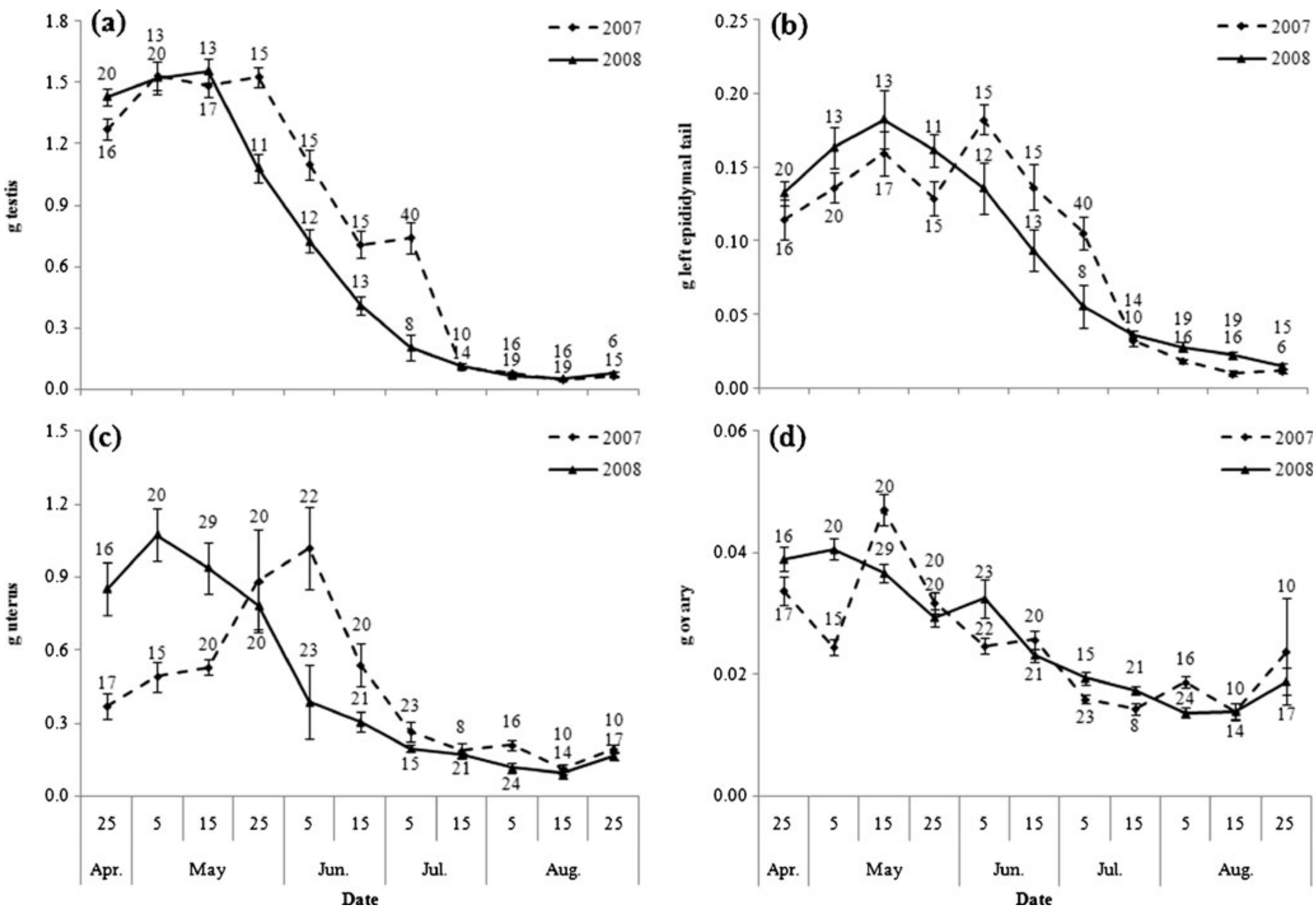

Fig. 4 Average masses of testis (**a**), left epididymal tail (**b**), uterus (**c**), and ovary (**d**) from April to August. Statistical comparisons are given in the text

1.02±0.17 g (n=6) in early June 2007 and at 1.07±0.11 g (n=6) in early May 2008. The average uterus mass from April to mid-May was significantly lower in 2007 compared with 2008 (late April: $F_{1,20}$=20.076, P<0.001; early May: $F_{1,16}$=25.754, P<0.001; mid-May: $F_{1,28}$=20.864, P<0.001), but significantly higher in June 2007 than in June 2008 (early June: $F_{1,11}$=7.818, P=0.017; mid-June: $F_{1,33}$=7.397, P=0.01). Significant differences in the average ovary masses were also apparent over the sampling periods in both years (2007: $F_{10,383}$=22.045, P<0.001; 2008: $F_{10,409}$=35.677, P< 0.001). The mean mass of a single ovary from late April to June was significantly higher than from July to mid-August in both years (Fig. 4d). The average ovary mass from late April to early May 2008 was significantly higher than in 2007 (late April: $F_{1,22}$=148.176, P<0.001; early May: $F_{1,19}$=263.622, P<0.001).

Fertility level

Fertility varied over the summer breeding period. Fluctuations in the proportion of males with scrotal testes matched the proportion of females pregnant. From late April to early June, the proportion of males with scrotal testes was significantly higher than in July and August (2007: t_{10}= 4.030, P=0.002; 2008: t_{10}=3.182, P=0.01; Fig. 5a). The pregnancy rate of adult females also showed significant changes over the summer (2007: t_{10}=2.592, P=0.027; 2008: t_{10}=2.819, P=0.018; Fig. 5b). In 2007, the pregnancy rate was 5.9% in April and peaked at 90% in late May. In June, the pregnancy rate was 60% and then declined in July and August to 8.7% and 0%, respectively. In April 2008, all captured females were pregnant, and pregnancy rates remained high (40–100%) until early June, while no adult females were caught that were pregnant in July and August.

Twelve of 16 females captured in mid-June in 2007 and 2008 were pregnant while still suckling young. Only 2 of 23 lactating females were pregnant in July. In 2007, pregnancies occurred from late April to early July and peaked between early May and mid-June, while in 2008 they occurred between late April and mid-June (Fig. 5b). We estimated that the breeding season of plateau pikas in Guoluo lasts about 50–70 days. The uterus of some females we dissected during the late breeding season consisted secondary uterus spots. Tertiary uterus spot has not been recorded in this population. Therefore, we concluded that the plateau pika produced up to two litters annually at our study site in Guoluo.

Litter size

The mean litter size was 3.3±0.1 (n=52) in 2007 and 3.2± 0.1 (n=66) in 2008 (Fig. 5c). It peaked in early May at a value of 4 (n=3) in 2007 and 3.39 (n=18) in 2008 and peaked again in mid-June with 3.75 (n=12) in 2007 and 3.33 (n=3) in 2008. The litters conceived were first observed in late April of both years, and the last were found in early July 2007 and mid-July 2008. Since there were relatively few samples in late April and early July, we only compared litter sizes in May and June. Significant differences were detected among periods in 2007 ($F_{4,47}$= 3.405, P=0.016), with the mean litter size from mid-May to early June being significantly smaller than in early May and mid-June. However, no significant difference in litter size was detected in 2008 ($F_{4,61}$=1.313, P=0.275). The most common litter sizes were 3 and 4, which together accounted for 71.2% of all litters in 2007 and 83.4% in 2008 (Fig. 6).

Discussion

Reproduction in mammals is costly (Speakman 2008). Its process, including onset of breeding, litter size, and number of litters in a breeding season, is thus likely affected by the resources available in its habitat to sustain the energy demands of reproduction. Plateau pika is a native herbivorous species of lagomorphs inhabiting the Qinghai–Tibetan plateau (Smith and Xie 2008). They have short spring–summer breeding seasons typical to herbivorous small mammals inhabiting alpine environments (Smith and Ivins 1983). Early breeding is advantageous for increasing the time available for both offspring and parents to prepare for the coming winter (Millar 1973). However, the breeding cannot commence until resources are adequate to support the reproductive attempt. Our data showed that the onset of breeding in a pika population in Guoluo Region is earlier in 2008 than in 2007. This annual variation may be due to the annual change of climate. In the alpine meadow ecosystem of the Qinghai–Tibetan plateau, temperature and precipitation are the two main factors that influence plant phenology. Increasing temperature and precipitation in spring can advance the start of the plant growth period, resulting in increased aboveground biomass on the plateau (Yang and Piao 2006). In the Guoluo region where our study site was located, there were no significant differences in temperature during spring and summer between 2007 and 2008. Yet, early spring precipitation in 2008 was twice that in 2007 on average. The highest precipitation was recorded in April 2008, when the rainfall was 5.5 times that in April 2007. This increased rainfall was correlated with improved coverage of green vegetation in early summer 2008. Early commencement of pika breeding may be a response to the earlier availability of food resources. These data were consistent with previous suggestions that reproduction of plateau pikas in Guoluo regions is energy-limited (Shen and Chen 1984; Smith 1988).

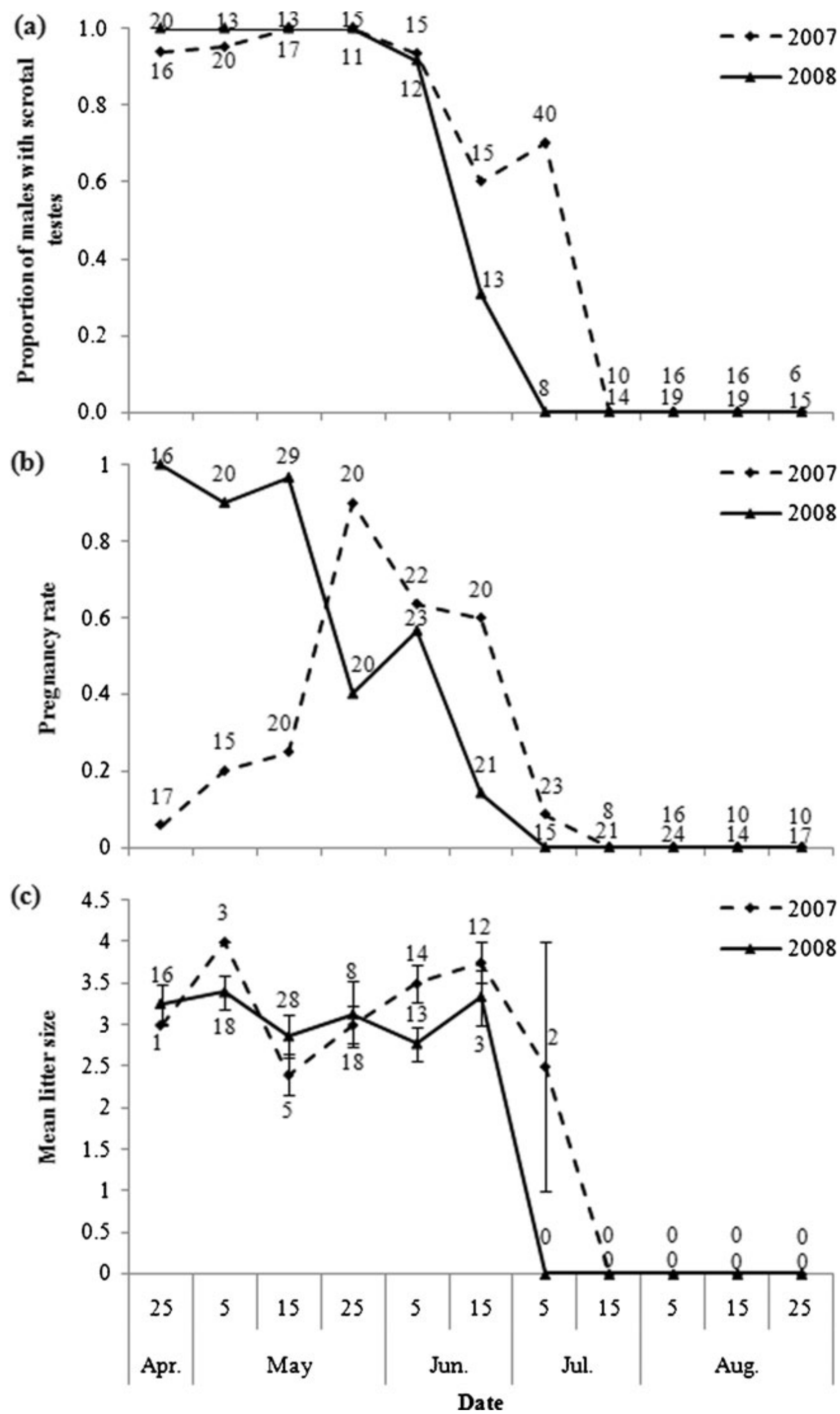

Fig. 5 Fertility levels of adult pikas from April to August. **a** Proportion of males with scrotal testes. **b** Pregnancy rate. **c** Mean litter size of pregnant females by counting viable embryos in utero

Early onset of breeding may have important fitness implications for herbivorous animals inhabiting the alpine ecosystem where the plant growing season is short; early breeding can increase the time available for both offspring and parents to prepare for the coming winter (Millar 1973; Smith and Ivins 1983). However, the breeding cannot commence until resources are adequate to support the reproductive attempt. Small mammals usually meet energy demands for reproduction by increasing food intake (Degen et al. 2004; Johnson et al. 2001; Liu et al. 2003), meaning that food availability has a major effect on the rate and timing of reproduction in herbivorous small mammals (Santos et al. 2006; Ylönen et al. 2003). Precipitation can therefore be a key driver for mammalian reproduction (Krebs et al. 2004; Masters 1993) by increasing the food resources available (Singleton et al. 2001) in the early breeding season. The increased precipitation in spring 2008 was correlated with advanced plant growth, improved

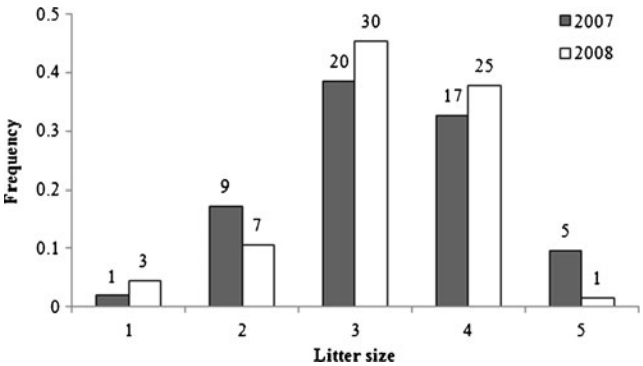

Fig. 6 Frequency distribution of the number of embryos in utero of pregnant females in May and June of 2007 and 2008

vegetation coverage, and increased food supply. Compared with the body masses from April to mid-May 2007, the body masses of adults from April to mid-May 2008 were higher, indicating that at this stage the grasslands provided enough food to meet the energy needs of pikas, including that required for reproduction. The pattern of variation in mass of the reproductive organs, the proportion of scrotal testes, and pregnancy rates measured in 2007 were time-lagged (later) compared with 2008, suggesting that the reproduction of plateau pika shows inter-annual plasticity. That is, pikas adjusted the onset of the breeding season according to the annual variation of food resources.

Since larger body mass can increase the winter survival of small, non-hibernating mammals (Schorr et al. 2009), the increase in body mass in late August may have been a preparation for the harsh winter season. Wang et al. (2006) compared the body mass of plateau pikas in April, July, October, and January and suggested that body mass was constant throughout the year. However, the cold season of alpine meadow starts in late August, and the lack of data at the beginning of cold season cannot accurately represent the annual variation of plateau pika body mass. Smith (1978) found an increase of 11–17 g in body mass during August, which is of obvious benefit against the cold and as a guard against winter food shortages, but did not influence their ability to avoid predators.

Maximizing reproductive fitness is the obvious outcome of mammalian evolution (Harshman and Zera 2007); however, reproduction will generally be less than the maximum litter size due to a variety of physiological and behavioral constraints as well as opposing selection pressures (e.g., environment, resources; Barnes and Partridge 2003; Both 1998; Frick et al. 2010; Morris 1992). In our study, the most common litter sizes were 3 and 4. Compared with other studies in lower altitude regions where the maximum litter size was 8 or 9 (Table 1), the maximum litter size was only 5 in Guoluo. Parents should produce a litter size which maximizes their lifetime reproductive success, including offspring recruitment and

Table 1 Geographic variation in reproduction of plateau pikas on Qinghai–Tibetan plateau

Study site	Guoluo	Haibei	Heimahe	Guinan	Ganzi	Naqu
Altitude (m)	3,830	3,220	3,200	3,500	4,200	4,507
Annual temp. (°C)	−3.9	−1.6	−0.7	0	−1.6	−2.8
Jan. mean temp. (°C)	−12.6	−15	−13.7	−11.3	−12.8	−12.8
Jul. mean temp. (°C)	9.7	10.1	10.6	13.9	8.7	8.9
Precipitation (mm)	528	560	402.65	414.8	596	440
Humidity (%)	43	67	54	51	64	57
Evaporation (mm)	2,472	1,238	1,446.6	1,378.6	1,230	1,810
Illumination time (h)	2,260	2,467.7	2,920	2,783.4	2,318	2,550
Max aboveground biomass (g/m^2)	112	418.5	235.2	279.5	428.4	74.97
Vegetation period (days)	110	134–152	120–162	120	125	90–100
Breeding season	April–June	April–September	March–August	April–July	March–July	April–June
Litters per year	1–2	2–4	3–5[a]	2–3	2–3[a]	1–2
Mean litter size (range)	3.6±0.9 (1–6) 3.3±0.81 (1–5)	3.8±0.1 (1–5) 4.6±0.2 (1–9)	5.5±0.3 3.9±0.4 (1–8)	–	2.9±0.3 (1–6) 3.2±0.3 (1–6)	4.6 (1–8)
References	Shen and Chen (1984); Present study	Liang (1981); Nie (2005); Yin et al. (2009)	Smith and Wang (1991); Wang and Dai (1991)	Dobson et al. (1998); Li et al. (1998)	Ding et al. (2000); Zhang and Liu (1996)	Luosang (2002)

[a] Female pikas reproduce in the year of their birth

mortality of parents and their young. There were three main reasons for the actual litter size to be lower than the maximal litter size. Firstly, maternal mortality might be influenced by litter size. Previous studies have suggested that maternal survival declined with excess reproductive investment by reducing the body condition of mothers (Charnov and Krebs 1974; Millar 1973). Second, offspring survival might decline in relation to litter size because generally, pups from larger litters wean at lower body mass than those from smaller litters (e.g., Millar 1977; Johnson et al. 2001). Hence, an intermediate litter size might maximize juvenile recruitment and survival (Morris 1986). This is supported by observations from experiments where litter size has been manipulated in the field, which indicated that the maternal body mass and growth rate of juvenile were significantly higher in reduced litters compared with control litters (Koskela 1998; Mappes et al. 1995). Since plateau pikas are social and territorial mammals (Qu et al. 2007), the larger individuals are generally more competitive and benefit from the ability to defend their territories. Third, the observed variance in the litter size across the population may reflect age-related variation in reproductive strategies. Older individuals may invest more in reproduction because their own future reproductive value is lower (McElligott et al. 2002).

In the Qinghai–Tibetan plateau, the plant growth season restricts the pika breeding season to between 3 and 6 months (Dobson et al. 1998; Li et al. 1998; Smith and Wang 1991; Wang and Dai 1991; Wang et al. 2004b). An increased duration of plant growth can extend the pika breeding season (Table 1). The masses of the reproductive organs, as well as the presence of scrotal testes or pregnancy, confirmed that the breeding season of plateau pikas at Guoluo lasted from mid-April to late June or early July. Our results also suggested that two litters were produced during this breeding season. In another site 5 km away for mark-recapture study, we recorded two cohorts of young pikas in the same year (Qu et al. 2008). Comparing our study with previous findings from other regions, the reproduction of pikas showed a large geographic variation across the Qinghai–Tibetan plateau, with different populations producing from one to five litters per year in different areas (Fig. 1 and Table 1). In Heimahe region, the breeding season also varied in duration across years (early April to early July 1986, from late March to early August 1987, and from mid-April to late July 1988), and adults produced variable numbers of litters in each year (Wang and Dai 1991). At Haibei, the breeding season lasted from early April to early August, and two to four litters per season were produced (Nie 2005; Wang et al. 2004b; Yin et al. 2009). In Guinan and Ganzi, two or three litters were produced even though the altitude in Ganzi was about 700 m higher than in Guinan (Ding et al. 2000; Dobson et al. 1998; Li et al. 1998; Zhang and Liu 1996). In Guoluo and Naqu, the pika breeding season lasted about 3 months, and only one to two litters were produced (Shen and Chen 1984; Luosang 2002; present study). In conclusion, plateau pikas seem to adjust the length and start of the breeding season to match the availability of resources to support reproductive energy demands.

Although the increased spring precipitation resulted in earlier food abundance in Guoluo region, the plant growing season may not be long enough for pika to increase the annual number of litters and litter size. Whether plateau pika in this region can potentially respond to prolonged plant growing season with increased number of litters and litter size will require further investigations.

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