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Short Communication

Life history of the plateau pika (*Ochotona curzoniae*) in alpine meadows of the Tibetan Plateau

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ABSTRACT

The life history of a species is a result of natural selection and reflects how the species is adapted to its environment. Knowledge of life history is crucial for further ecological studies and conservation management. This paper presents aspects of the life history of the plateau pika (*Ochotona curzoniae*), a small mammal native to alpine meadows of the Tibetan Plateau. The mean lifespan of juveniles from first litters was longer than the mean lifespan of juveniles from second litters. The population consisted of more juveniles than adults (over-wintered animals) in August and these juveniles came primarily from the first litter of the year. The sex ratio of juveniles was female-biased even though the sex ratio of adults did not differ from 1:1. The mortality rate of juveniles and adults during the warm season (May–August) was greater than the mortality rate of these groups during the cold season (September–April). Mean juvenile growth rate during the warm season was 1.4 g/d and the growth rate of the first litters was remarkably slower than that of the second litters.

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The life histories of animals are the result of natural selection and are determined by multiple factors, such as food type (Kasparian and Millar, 2004), climate (Castellarini et al., 2002), population density (Karels and Boonstra, 2000) and predation (Korpimäki et al., 2002). Examinations of life histories give critical insight into how species adapt to their environment.

The plateau pika (*Ochotona curzoniae*) is small lagomorphs endemic to the alpine meadow of Tibetan Plateau. It is regarded as a keystone species since it provides foods for predators and nests for small birds which live in the burrow of pikas (Lai and Smith, 2003). However, detailed information on the life history of this species is scarce. Pikas are non-hibernators and winters in this region are long (September to April) and cold (average winter temperature is −14 °C). The breeding season lasts from April to August. Over this time, females can produce between two and five litters (litter size range = 2–7) with a 3-week interval between each litter (Shen and Chen, 1984; Wang and Dai, 1991; Qu et al., 2012). Pikas are social mammals that live in family groups consisting of two to five adults and their young (up to eight) that do not disperse in their year of birth (Dobson et al., 1998). In August, population densities may range from 100 to 400 pikas ha⁻¹ (Liu et al., 1982).

Plateau pika evolved with the uplifting of the Tibetan Plateau (Yu et al., 2000). It inhabits areas from 3200 to 5300 m above

sea level; however, in this study we examine plateau pikas at an elevation that is at least about 800 m higher than the elevation in previous research on this species (Smith and Wang, 1991; Wang and Dai, 1991; Dobson et al., 1998; Nie, 2005). The environmental conditions in our site are characterized by a growing season that is at least one month shorter and by ambient temperatures that are at least 5 °C and 3 °C colder in winter and summer, respectively. Mountain-dwelling small mammals exhibit different patterns of life history characteristics in habitats at different elevations (Dobson and Murie, 1987). Using mark-recapture we followed the fate of individual plateau pikas over four years. Specifically, we (1) determined the age distribution, lifespan and sex ratio, (2) quantified the mortality rate in the cold and warm seasons and (3) estimated the growth rates of juveniles during the warm season.

The study was conducted from May to August, 2005–2008 in the northeastern region of Tibetan Plateau, 17 km east of Dawu (34°24′N, 100°21′E, elevation 3946 m) in Qinghai Province, China. The climate of the study site is cold and dry. Annual mean temperature is <0 °C and daily temperature varies from −15 °C to 0 °C in January and 0 °C to 16 °C in July. No season is frost-free and in the winter the soil may be frozen to a depth of >2 m. More than 70% of yearly precipitation (330–500 mm) occurs between June and August. Heavy snowfalls during winter are rare. The dominant plants in our alpine meadow study site are *Kobresia humilis*, *Stipa* spp., *Kobresia pygmaea*, *Elymus unmans*, *Ajania tenuifolia*, *Leontopodium nanum*, *Aconitum szechenyianum*, *Gentiana straminea* and *Morina chinensis.* The growing season begins in May and it lasts for

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110–130 d (Wang et al., 2004a). The region is grazed year round by domestic herbivores (yak, sheep and horses). Common predators of plateau pikas in the region include weasel (*Mustela altaica*), steppe polecats (*Mustela eversmannii*), ravens (*Corvus corax*) and upland buzzards (*Buteo hemilasius*). Several other small mammal species have been observed at this study site including lacustrine voles (*Microtus limnophilus*), pine mice (*Pitymys irene*), Himalayan marmots (*Marmota himalayana*) and woolly hares (*Lepus oiostolus*).

The study site is located in an alpine basin surrounded by mountains. A 4.0-ha (200 m × 200 m) area was used for this study, which was divided into 10 m × 10 m grid cells. Each grid cell was further divided in to 1 m², which was used as a location parameter. We determined the location of all capture events and behavioral observations with respect to the stakes to an accuracy of 1 m. Our mark-capture study was conducted in the middle 1.0 ha of the study area in 2005 and 2006 and the middle 2.56 ha of the study area in 2007 and 2008.

Plateau pikas were live-captured using string nooses anchored near the active burrow entrances with chop sticks. We trapped for pikas every day when it did not rain between late-April to late-August in each year of this study. Researchers monitored the active nooses from a distance of ~30 m and the pikas were removed from nooses immediately after capture. Captured animals were anesthetized using gaseous Metofane and were permanently marked with metal ear tags with unique numbers and collared with plastic disks to facilitate field identifications. The fur on the heads of males and the backs of females was also marked with black hair dye to allow us to determine the sex of individuals at a distance. Live-captured juveniles that weighed less than 30 g were only marked with hair dye. Following each capture, we recorded the mass, capture location, gender and reproductive condition of each animal. Animals recovered from anesthetic within 10 min and were released at the location of capture.
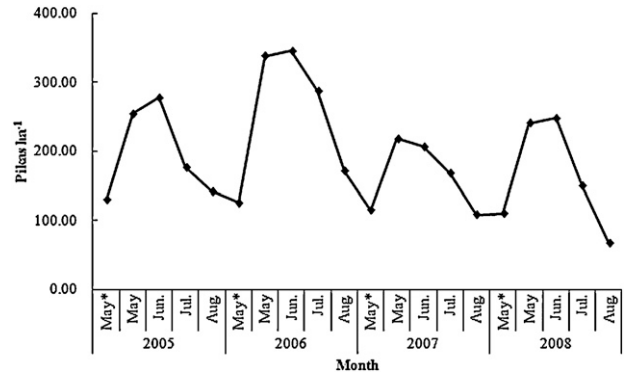

Fig. 1. Population density of plateau pika from May to August, 2005–2008, near Dawu county, People's Republic of China. May* indicates the population density of pika in early-May when no juveniles were observed.

Absolute density was obtained by MNA method (minimum number of individuals known to be alive) (Buckland, 1980). Individuals were grouped into juveniles (the mass of juvenile pikas at first capture was <60 g) and adults (over-wintered animals; the mass of all adult pikas at first capture in their second year was >110 g). Juveniles were further divided into two discrete groups: juveniles that first emerged in May late April–early May (L1 = first litter juveniles) and juveniles that were first observed in June late May–early June (L2 = second litter juveniles). We also knew whether juveniles came from L1 or L2 because we were able to follow essentially all reproductive events of all females on our study areas. The proportions of adults as well as L1 and L2 juveniles were square root transformed for all analyses. Post hoc least squared difference tests were used to compare the proportions of these groups in May and August.
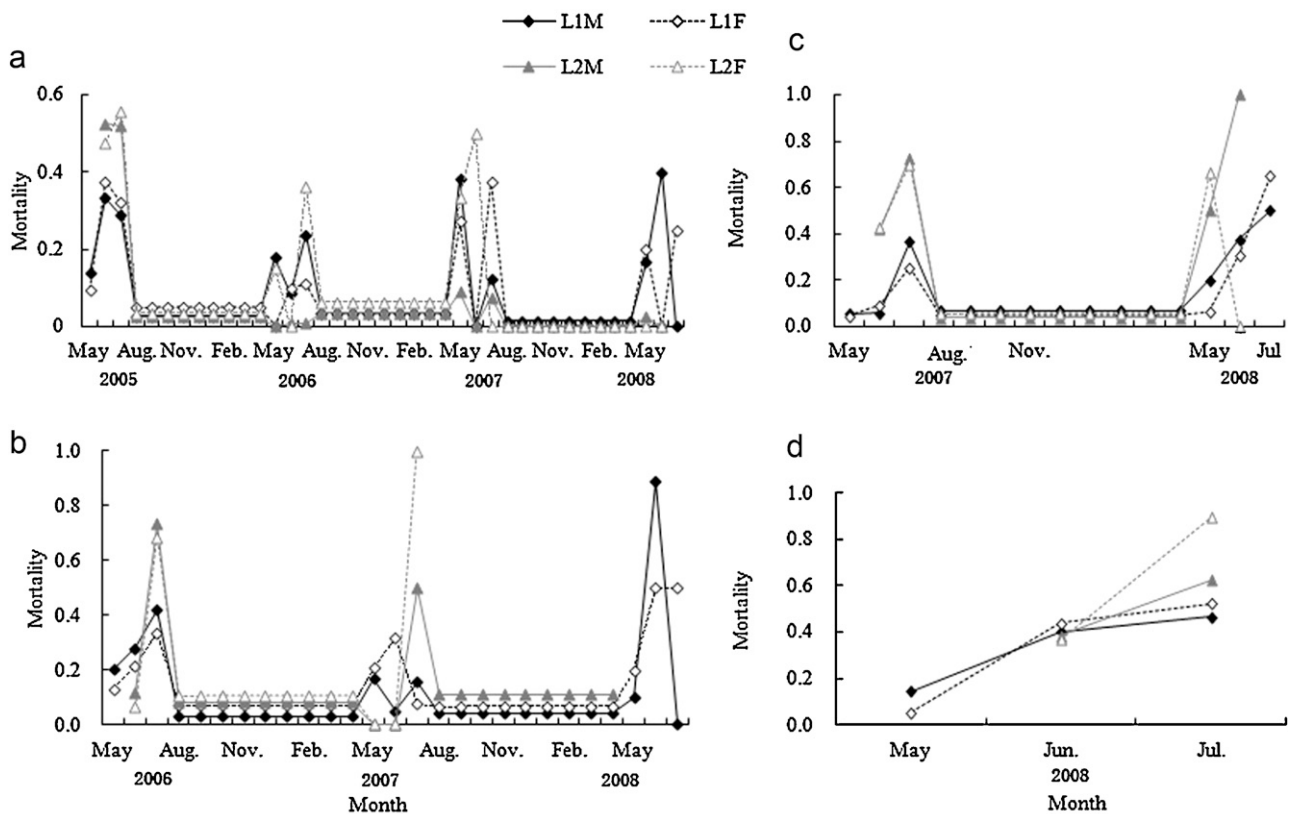

Fig. 2. Monthly mortality of male and female L1 and L2 juvenile plateau pikas in (a) 2005, (b) 2006, (c) 2007, and (d) 2008.
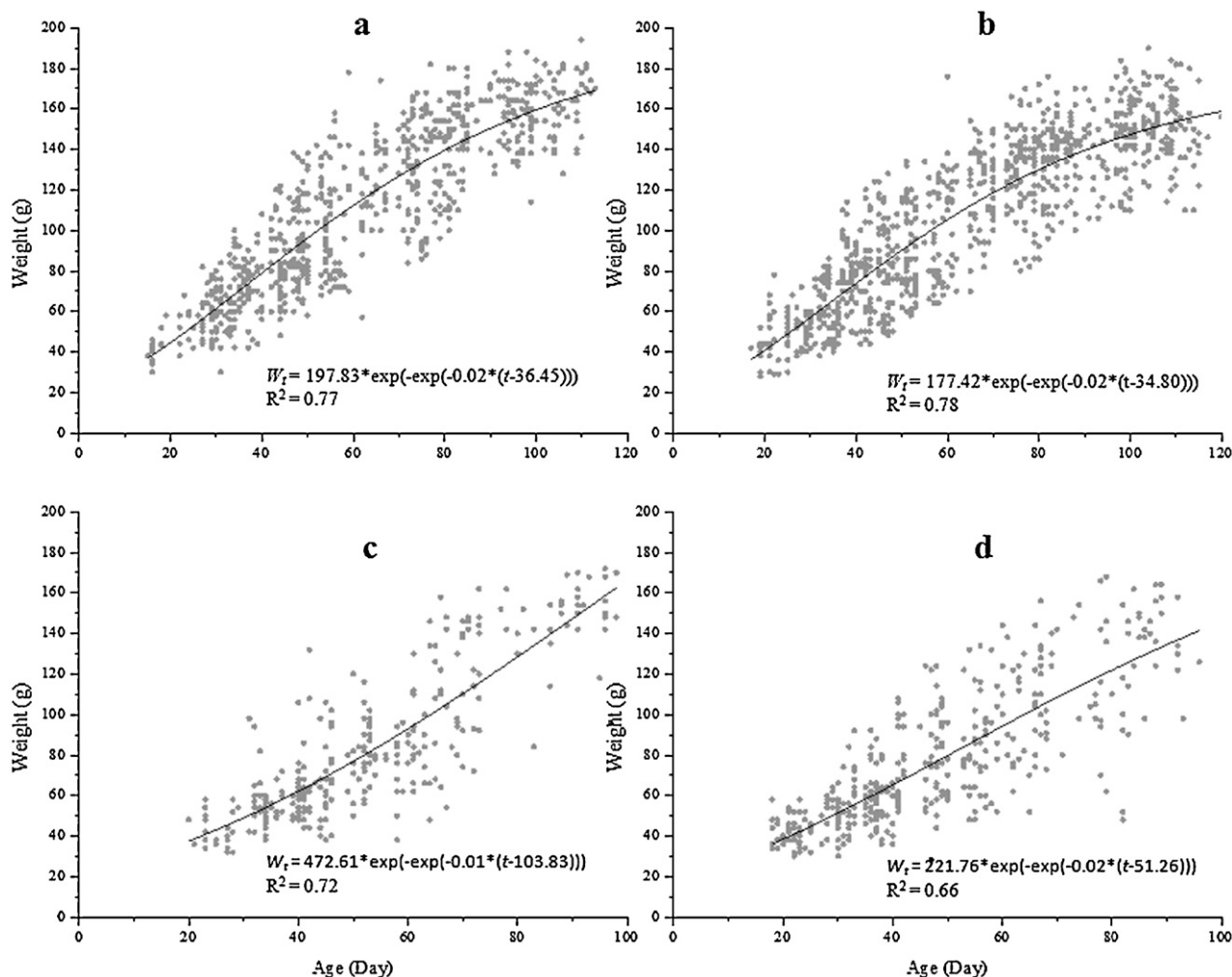
Fig. 3. The growth rate of juvenile plateau pikas with respect to days since emergence, where M_t is the mass of the individual at time t. The line of best fit represents the Gompertz model estimate of the masses of (a) L1 males, (b) L1 females, (c) L2 males, and (d) L2 females over the course of their first summer of life. P values were <0.05 in four models.

We determined the sex ratio and lifespan of each L1 and L2 juvenile cohort in 2005–2008. Sex ratio was calculated as the number of males divided by the number of females in each litter cohort. Chi-square tests were used to determine whether the sex ratios of the litter cohort were biased towards one sex. Cohort lifespan was calculated from the average estimated age of the juveniles at first capture (based on Nie, 2005) to the average last day that juveniles within the cohort were captured. One-way ANOVA was used to test the differences of lifespan between litters or sexes.

The average growth rate of males and females within the L1 and L2 cohorts from May or June to August were determined using a Gompertz model. The date of birth was estimated according to Nie (2005). Specifically, we used all measures of mass and pooled all four years of data to calculate the average daily growth rate constant K (g/day) for both males and females within the two litter cohorts.

Alpha was set at 5% for all statistical tests. All proportions and means ± SE are reported throughout the text. Kolgomorov–Smirnov tests were used to check for the assumption of normality. The homogeneity of variance assumption was tested using Levine's F test. SPSS version 16.0 (SPSS Inc., Chicago, IL, USA) was used to conduct all statistical analyses.

During the four-year study period, we marked 1599 plateau pikas. Pika densities peaked in May or June, and then declined in July and August. The peak density of pikas in 2006 reached higher densities than in the other three years (Fig. 1).

Of the 1599 pikas captured, 327 were juveniles born and marked in 2005. Among these individuals, 14 were recaptured in 2008. Therefore, the maximum lifespan of plateau pikas was at least 51 months. The mean lifespans of L1 males and females were 8.2 ± 0.4 ($n = 94$) and 7.1 ± 0.4 ($n = 94$) months respectively, whereas the mean lifespans of L2 males and females were 4.9 ± 0.2 ($n = 57$) and 4.1 ± 0.2 ($n = 82$) months respectively. There was no difference in the lifespan of the two litters ($F_{1,52} = 1.341$, $P = 0.301$) or sexes ($F_{1,52} = 0.972$, $P = 0.513$).

The age distribution of our population varied dramatically from May to August (Supplementary material 1). The proportion of L1 juveniles in the entire population differed significantly between the months ($F_{3,28} = 4.4$, $P = 0.012$). Specifically, the proportion of L1 juveniles in May was significantly lower than in other three months ($P = 0.024$, June; $P = 0.009$, July; $P = 0.002$, August; respectively). The proportion of L2 in the entire population was low from June to August (0.09 ± 0.013) and the proportion of L2 juveniles in the population did not differ between these months ($F_{2,21} = 2.454$, $P = 0.110$).

The sex ratio of L1 and L2 juveniles was tested in May and June, respectively (Supplementary material 2). The sex ratio of L1 juveniles was significantly female-biased in 2006 and 2008, whereas the sex ratio did not differ from one to one in 2005 or 2007.

However, the sex ratio of L2 juveniles was significantly female-biased during all four years of this study. The sex ratio of adults did not differ from 1:1 in any year of this study.

The monthly mortality rates of both juveniles and adults were higher from May to July than during the overwinter period (Fig. 2). The monthly adult mortality rate did not differ between the two sexes. The mortality rate of L1 juveniles was significantly higher than the mortality rate of L2 juveniles during the first two months of life (males: $F_{1,14} = 12.243$, $P = 0.004$; females: $F_{1,14} = 10.952$, $P = 0.005$).

The mean growth rate of L1 and L2 juveniles, pooling both sexes, was 1.4 ± 0.08 g/d. The growth rate of male juveniles was (1.39 ± 0.07 g/d) faster than the growth rate of female L1 juveniles (1.26 ± 0.05 g/d)(Fig. 3a and b). The growth rate of male juveniles from L2 (1.59 ± 0.05 g/d) also exceeded the growth rate of female juveniles from L2 (1.38 ± 0.04 g/day) (Fig. 3c and d). Male juveniles from L1 were significantly larger than female juveniles from L1 in July ($F_{1,507} = 6.822$, $P = 0.009$) and August ($F_{1,300} = 25.418$, $P < 0.001$); however, this mass difference between the males and females from L1 was only a trend in May ($F_{1,251} = 3.148$, $P = 0.077$) and June ($F_{1,656} = 3.413$, $P = 0.065$). L2 males were significantly heavier than L2 females in August ($F_{1,84} = 16.463$, $P < 0.001$).

Since juveniles do not disperse during the summer of their birth (Dobson et al., 1998), population density increases dramatically following the recruitment of juveniles. In each year of our study, the population density of plateau pikas peaked in May or June. These changes in population density can be attributed to the recruitment of juveniles into the population and the death of adults and juveniles over the course of summer. These results differ from the trend reported by Shen and Chen (1984), which reported that the density of pikas peaked in November in the same region. When comparing the density among years, a significantly higher level of abundance was detected in 2006 which could have resulted from the exceptional warm weather in January (Hou and Tang, 2008).

The age distribution of a population reflects its history of reproduction and potential for future growth (Molles, 2002). In August, the population was mainly composed of juvenile pikas, most of which were produced in L1. Since the reproductive potential of 2-year-old adults was much higher than 3-year-old pikas (Nie, 2005), a younger age distribution was beneficial to the reproduction and future growth of the population (Molles, 2002). In this study, the sex ratio of juvenile pikas at emergence tended to be female-biased, especially in L2. These results are consistent with Wang et al. (2004b). However, the work of Shen and Chen (1984) as well as Nie (2005) suggested that the sex ratio of pikas at birth was not biased. One interpretation of this discrepancy is that the sex ratio is not biased at birth, but that pre-emergence mortality is higher in females. The post-emergence sex ratio that we documented in this study is likely to be more important because these are the individuals that will recruit into the population. A possible explanation for the female-biased post-emergence sex ration that we documented in this study is that plateau pikas have a polygynous mating system (Yin et al., 2009); therefore, it is more advantageous for the fitness of females to produce female-biased sex ratio.

Future research is required to determine the sources of mortality following the peak of pika densities in May–June. Rainfall has a negative effect on the survival of juvenile small mammals (Wang and Dai, 1989). Most precipitation (60–70%) on the Tibetan Plateau occurs from June to August in our study area which corresponds to the high mortality of juveniles. Moreover, the higher mortality rate of juveniles from L2 as compared to L1 may be the result of increased competition among siblings compared to the level of competition among juveniles from L1 (Wang et al., 2004b; Hudson and Trillmich, 2007). Interestingly, in our study the mortality rate of plateau pikas in the cold season was quite low compared to the mortality rate in the warm season. These results are consistent with

the results presented in Nie (2005) and they suggest that food limitation in the cold season is not an important factor influencing the mortality rate of pika.

The growth rates of plateau pikas were among the fastest ever documented for lagomorphs (Golian and Whitworth, 1985). The mean growth rate of juvenile plateau pikas (1.4 g/d) also exceeded the growth rate of collared pikas and American pikas, both of which had average growth rates of less than 0.06 g/d (Franken and Hik, 2004). Such a faster growth rate is likely to be an adaptation to shorter growth seasons on Tibetan Plateau. L2 juveniles face a shorter growing period than L1 juveniles before the winter, thus, this may explain why L2 juveniles have faster growth rates than L1 juveniles.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2012.09.005.

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