Journal of Applied Ecology 2007
44, 615–624

Population dynamics and responses to management of plateau pikas *Ochotona curzoniae*

ROGER P. PECH,* JIEBU,† ANTHONY D. ARTHUR,* ZHANG YANMING‡ and LIN HUI§

**CSIRO Sustainable Ecosystems, GPO Box 284, Canberra, ACT 2601, Australia; †Tibet Academy of Agriculture and Animal Sciences, Lhasa, Tibet, 850023, People's Republic of China; ‡North-west Plateau Institute of Biology, Chinese Academy of Sciences, Xining, Qinghai, 810001, People's Republic of China; and §Tibet Bureau of Agriculture and Animal Husbandry, Lhasa, Tibet, 850000, People's Republic of China*

Summary

1. Plateau pikas *Ochotona curzoniae* are considered a pest species on the Tibetan Plateau because they compete with livestock for forage and their burrowing could contribute to soil erosion. The effectiveness of pest control programmes in Tibet has not been measured, and it is not known whether changes in livestock management have exacerbated problems with plateau pikas or compromised their control. This study measured the impact of control programmes and livestock management for forage conservation on populations of plateau pikas in alpine meadow in Naqu District, central Tibet, during 2004 and 2005.

2. Current techniques for controlling plateau pikas in spring cause large reductions in abundance, but high density-dependent rates of increase result in no differences between treated and untreated populations by the following autumn. Rates of increase from spring to autumn are not influenced by standing plant biomass or concurrent grazing by yaks *Bos grunniens* and Tibetan sheep *Ovis aries*.

3. In autumn there was significantly lower biomass outside fenced areas with year-round livestock grazing compared with inside fenced areas with equivalent or higher numbers of plateau pikas but predominantly winter grazing by livestock. Inside fenced areas, control of plateau pikas in spring produced no detectable effect on standing plant biomass at the end of the following summer compared with uncontrolled populations of plateau pikas.

4. Regardless of their initial density, populations of plateau pikas declined rapidly over winter outside fenced areas where there was very low standing plant biomass in autumn. However, inside fenced areas with higher plant biomass in autumn, low-density populations of plateau pikas declined more slowly than high-density populations.

5. *Synthesis and applications*. Current control programmes have limited effect because populations of plateau pikas can recover in one breeding season. There was no apparent increase in forage production in areas where plateau pikas were controlled. However, plateau pikas appear to benefit from changes in grazing management, with low-density populations declining less over winter inside fenced areas than elsewhere. It was not evident that control programmes are warranted or that they will improve the livelihoods of Tibetan herders.

Key-words: alpine meadow, grazing system, pest control, plateau pika, rate of increase, Tibetan sheep, yak

Journal of Applied Ecology (2007) **44**, 615–624
doi: 10.1111/j.1365-2664.2007.01287.x

Correspondence: Roger Pech, Landcare Research, PO Box 40, Lincoln 7640, New Zealand (fax +64 3321 998; e-mail PechR@landcareresearch.co.nz). Zhang Yanming, North-west Plateau Institute of Biology, Chinese Academy of Sciences, Xining, Qinghai, 810001, People's Republic of China (e-mail zhangym@nwipb.ac.cn).

Introduction

Plateau pikas *Ochotona curzoniae* Hodgson 1858 are small lagomorphs (females 120–170 g; males 150–210 g) endemic to parts of the Tibetan Plateau in the People's Republic of China, India and Nepal (Zhang *et al.* 1998; Smith & Foggin 1999; Bagchi, Namgail & Ritchie 2006). They are social animals that tend to be spatially clumped (Smith & Wang 1991; Zong *et al.* 1991) and can reach very high population densities of > 350 ha^{-1} (Wang *et al.* 1997). They are typically diurnal and interact with their environment through foraging and digging activities, recycling nutrients, serving as prey for a suite of top predators and constructing burrows that are used as shelter and nest sites by other species (Lai & Smith 2002; Zhang 2002; Zhang *et al.* 2005).

Plateau pikas are considered a keystone species because of their pivotal role in the community dynamics of high-altitude grasslands (Smith & Foggin 1999). However, they are also regarded as a pest species because they appear to compete with livestock for scarce food resources and because their foraging and burrowing activity can lead to grassland degradation (Liu, Zhang & Xin 1980; Xia 1984; Fan *et al.* 1999). Poisoning programmes have been used to control plateau pikas on the Tibetan Plateau since 1958. Zinc phosphide was used to control various species of small mammals, including plateau pikas, plateau zokors *Myospalax fontanierii* Milne-Edwards 1867, plateau voles *Pitymys irene* Thomas 1911 and Himalayan marmots *Marmota himalayana* Hodgson 1841. By the early 1960s, poisoning campaigns occurred in 20 counties in Qinghai Province alone and more than 208 000 km^2 of grassland had been treated by 1965. Zinc phosphide was replaced with NH_4^+–fluoroacetate but both agents caused secondary poisoning and raised concerns about loss of biodiversity. In the mid-1980s, anticoagulants, such as diphacinone-Na, and botulin toxin C were gradually introduced for controlling populations of small mammals on the Tibetan Plateau. Even though the use of poisons can achieve high, immediate reductions in the number of plateau pikas, populations at lower altitudes on the plateau usually recover rapidly after control (Liang 1981) and these programmes have not solved the linked problems of overgrazing and grassland degradation.

Grassland degradation has been a problem across much of western China for more than 25 years (Zhang *et al.* 1998; Zhang, Zhong & Fan 1999; Zhou *et al.* 2005). During this period livestock numbers, including yaks *Bos grunniens* and Tibetan sheep *Ovis aries*, have increased rapidly (Jing *et al.* 1991; Zhang *et al.* 2003; Dong *et al.* 2004), generating conflict with the conservation of native herbivores (Lai & Smith 2002; Mishra *et al.* 2004) but coinciding with outbreaks of some species of small mammals that appear to have benefited by a shift to heavily grazed, short pasture (Liu *et al.* 1991; Zhong *et al.* 1991; Fan *et al.* 1999; Zhang *et al.* 2003). In an interesting contrast, the abundance of field voles *Microtus agrestis* has declined in British upland grasslands, possibly because of increased competition for food when sheep numbers doubled between 1950 and 1990 (Evans *et al.* 2006).

In addition to poisoning campaigns against small mammals, attempts have been made to prevent further degradation by improving grassland management in western China through the use of fencing to reserve areas of forage for winter grazing. With the current government policy of devolving responsibility for grassland to local farmers, the traditional nomadic herders in Tibet have adopted a more sedentary lifestyle centred on small villages. In Qinghai Province, private responsibility for land has been in place since 1990. For example, in the region around Qinghai Lake, the most developed region for livestock husbandry on the Tibetan Plateau, 20–30% of the total area of usable grassland was fenced by 2004. Changes in land management have been slower in the Tibet Autonomous Region (TAR), even though the policy of private responsibility for land was introduced at the same time. In TAR, responsibility for grasslands was given initially to local town government rather than families. Villages acquired these privileges in 1997 and it was not until 2004 that this was extended to individual farmers. The current estimate is that 9500 km^2 of grassland has been fenced in TAR, which is approximately 2·2% of the grasslands used for livestock production (Wu 2005).

In Naqu County in central Tibet (altitude *c.* 4500 m), the local people are dependent on the production of yaks and sheep for their livelihoods. Although some areas have been fenced to conserve forage for winter, villagers usually have to purchase supplementary food for their animals. They consider the shortage of forage is partly because of the increased numbers of livestock but that it is exacerbated by competition from plateau pikas, which appear to have increased in abundance compared with a generation ago (Baima Cuo, unpublished data). The Grasslands Station of the Naqu Bureau of Animal Husbandry provides materials and advice for pest control programmes but the villagers provide the labour to carry out the control. In recent years, areas around some villages have been treated to reduce the abundance of plateau pikas but many areas have had no recent control.

Although it is widely considered that overgrazing is the primary cause of grassland degradation, it is also generally agreed that solutions will need to integrate improved livestock management and pest control. Better understanding of how populations of plateau pikas respond to control programmes and to changed patterns of livestock grazing might lead to management strategies that prevent grassland degradation and potentially include concepts of ecologically based pest management that have been promoted elsewhere (Zhong *et al.* 1991; Singleton *et al.* 1999; Hinds, Pech & Singleton 2004). In this study in Naqu County in central Tibet, we addressed the following two questions. (i) How rapidly do populations of plateau pikas recover from current

Table 1. Locations (degrees, minutes, seconds) of study sites and date of programmes to control plateau pikas

Site number	Location Latitude	Longitude	Village	Time of control
3	N 31 21 07·7	E 92 01 38·0	Sang long	None
4	N 31 19 26·6	E 92 02 35·5	Na ka quk	April 2005
5	N 31 16 32·0	E 92 05 38·5	Ke ma	None
6	N 31 16 16·0	E 92 10 08·7	Gen ma	2002, April 2005
8	N 31 27 53·6	E 92 07 38·2	Qi long Nang ba	April 2004
9	N 31 26 26·6	E 92 16 37·4	Duo Su	April 2004

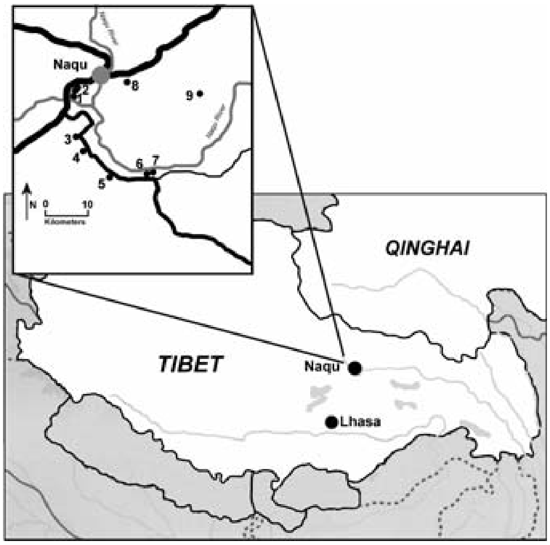

Fig. 1. Locations of study sites in Naqu District, Tibet (insert, sites 3–6, 8 and 9 are listed in Table 1; sites 1, 2 and 7 were not relevant to this paper).

control programmes? (ii) How does the conservation of forage in fenced areas affect plateau pika populations and their recovery from control?

Methods

STUDY SITE

The Tibetan Plateau occupies 2·5 million km^2 in the west of the People's Republic of China, approximately 25% of the country's area (270–400 N, 750–1050 E; average altitude > 4000 m). An estimated 70% is high-altitude grassland and pastoralism is the primary land use (Ekvall 1968; Miller 1995; Miller & Craig 1997). The climate is strongly seasonal, with an annual mean temperature < 0 °C (Xia 1988). There is no frost-free season and extensive areas of permafrost occur in mountains and grasslands (Smith *et al*. 1986). Principal soil types are alpine meadow soil, alpine scrubby meadow soil and bog soil (Zhang, Zhang & Liu 2003). The major plant communities are alpine meadow, alpine shrub, alpine prairie and alpine steppe meadow, and the dominant forms are *Carex* spp., *Kobresia* spp., *Stipa* spp., *Achantherum splendens* and *Potentilla fruticosa* (Xia 1988). The study was conducted near Naqu (altitude 4500–4600 m), approximately 330 km north of Lhasa, the capital of TAR, from April 2004 to September 2005 (Fig. 1). At Naqu the mean annual temperature is −1·9 °C (ranging from 22·6 °C in July to −41·2 °C in January), and the mean annual precipitation is 430 mm, 70% of which occurs between June and August.

Personnel from the local grassland station provided assistance in selecting study sites with known histories of pika control and where villagers were prepared to modify pest control programmes to fit the experimental design. Study sites were selected in April 2004 near six different villages in Naqu District for a nested experimental design: first whether or not plateau pikas were controlled at a site, and then within each site whether pasture was grazed year-round or fenced to restrict access by livestock in summer. Apart from some additional sites not relevant to this paper, they were spaced a minimum of 3·4 km apart (the maximum distance to next closest site was 14·4 km; Fig. 1). Sites were selected in short alpine meadow, which is the most extensive plant community in the district, and avoided areas of taller marsh vegetation, where plateau pikas were not considered to be a problem. At five villages, plateau pikas had never been controlled, while at one village plateau pikas had been controlled in the area containing the sites in 2002 (Table 1). At each of the properties we selected paired areas: one area inside a paddock fenced to conserve forage for winter grazing, and one area outside the fence where there was year-round grazing by livestock. Pikas were controlled on sites 8 and 9 in 2004 and on sites 4 and 6 in 2005 (Table 1). All sites consisted of gently undulating terrain with low, sparse alpine meadow grazed by yaks and Tibetan sheep. Stocking rates appeared to be similar for all sites but could not be quantified; although villagers keep detailed records of livestock numbers, the areas used for summer and winter grazing have not been measured and appear to be not well defined. Observations of plateau pikas and their predators (for example upland buzzards *Buteo hemilasius* Temminck & Schlegel 1844 and Tibetan foxes *Vulpes ferrilata* Hodgson 1842) during road-based surveys indicated the study sites were representative of the general area around Naqu (C. Davey, T. Arthur, S. Henry & R. Pech, unpublished data).

COUNTS OF PLATEAU PIKAS

At each site, plateau pikas were counted during four sessions, two in spring (24–28 April 2004, 17–25 April

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2005) and two in autumn (10–15 September 2004, 13–21 September 2005). Walked transects were used to measure the abundance of plateau pikas at a spatial scale representative of fenced areas. They were conducted simultaneously on both sides of the fence at each site between 09:00 and 11:30, which is the period when almost all plateau pikas are present on the surface (Zeng, Wang & Han 1981; Zong & Xia 1987; Zhang *et al*. 2005). An observer counted all plateau pikas in a 20-m wide belt transect, with counts recorded for each of 10 contiguous 100-m sections along a route that sampled a core area of approximately 7–10 ha starting 50 m inside the fence (i.e. counts covered in total 2 ha within the core area). A similar transect sampled a core area starting 50 m outside the fence. We assumed that all pikas within the strip were observed, to derive a density estimate (count per unit area). For each session, the plateau pikas in each area were counted on four mornings, once by each of four observers, to account for observer bias.

COUNTS OF PLATEAU PIKA BURROWS

Belt transects were use to count burrow entrances as an alternative index of the abundance of plateau pikas and a resource affecting their rate of increase. Also the counts provided a measure of site differences and changes in the density of burrows following pika control programmes. At each site in April and September 2005, all burrow entrances were counted in 10 contiguous 4×100-m strips set out along a route to sample the core areas inside and outside the fence. In September, active entrances (characterized by clear openings and fresh soil) and inactive entrances (characterized by openings with undisturbed material such as plant litter or spider webs) were counted separately. It was not possible to distinguish active and inactive entrances unambiguously in April.

ASSESSMENT OF VEGETATION

The step-point technique (Evans & Love 1957) was used to measure the percentage cover of grass, plant litter and bare soil at each site in April, June and September in 2004, and in April and September 2005. At least 400 step-point readings were recorded within the core areas on each side of the fence at each site. Each point was two steps apart, i.e. with a spacing of 1–1·5 m. Initially we used three categories: 'grass' included dry grass stems still attached to the root mass; 'litter' included all detached plant material lying on the surface; and 'bare soil' included stones, small rocks and cryptogam or lichen crusts on the surface. In September 2005, the 'bare soil' category was subdivided into 'loose bare soil', which was usually associated with eroded areas, and 'solid bare soil', usually consisting of a hard turf layer with a high proportion of grass roots and other organic material. After each set of 10 step points, the average height of grass within 1 m of the observer was estimated. A training period was conducted at the start of each session to ensure consistent use of these categories and measurement protocols by observers.

Step-point cover and height measurements were converted to estimates of above-ground biomass as follows. In September 2005, 41 quadrats (25×25 cm) were chosen randomly within a range of height and cover classes at a subsample of the sites. Dominant plant species were recorded for each quadrat. Vegetation was clipped, stored in paper bags, oven dried and weighed. The relationship between biomass (dry weight) and vegetation height and cover was assessed using a linear model. The resultant formula was then used to calculate biomass based on step-point measurements carried out at all sessions and for all sites.

The effect of fencing and session on vegetation cover and height was analysed with a linear mixed-effects model, with site and observer as random effects. Proportions were arcsine transformed prior to analysis. Height measurements were log transformed prior to analysis.

CONTROL OF PLATEAU PIKAS IN 2004 AND 2005

Under the direction of staff from the Naqu Grassland Station, villagers conducted programmes to reduce the abundance of plateau pikas at four of the six sites (Table 1). Control occurred several days after counts of plateau pikas on sites 8 and 9 in April 2004. On this occasion there was no opportunity or resources for post-control counts. Control programmes were conducted at sites 4 and 6 in April 2005, with counts of plateau pikas on each of 2 days immediately before control and a further series of counts on the 5th, 6th and 7th days of the post-control period. Control was carried out using botulin C on wheat bait placed down pika burrows. The control programme was carried out inside and outside fenced areas over *c*. 35 ha each side of the fence, so that there were extensive, controlled buffer zones around the core sampling areas of < 10 ha.

ANALYSIS OF PIKA POPULATION COUNTS

Counts of plateau pikas (N_t at time t) were standardized for observer differences using a mixed-effects model with observer as a random effect. Log transformation of the data was required prior to analysis. The standardized counts were then used to calculate the rate of increase for each area over summer (April to September) and winter (September to April) as $\ln(N_{t+1}/N_t)$, which was converted to a weekly rate. Factors tested as possible explanatory variables of rate of increase included population density, vegetation biomass, fencing and pika control. Year was also included as an explanatory covariate.

EFFECTS OF FENCING AND CONTROL ON THE NUMBER OF PLATEAU PIKA BURROWS

The effect of poisoning plateau pikas on the density of burrows in September 2005 compared with April 2005

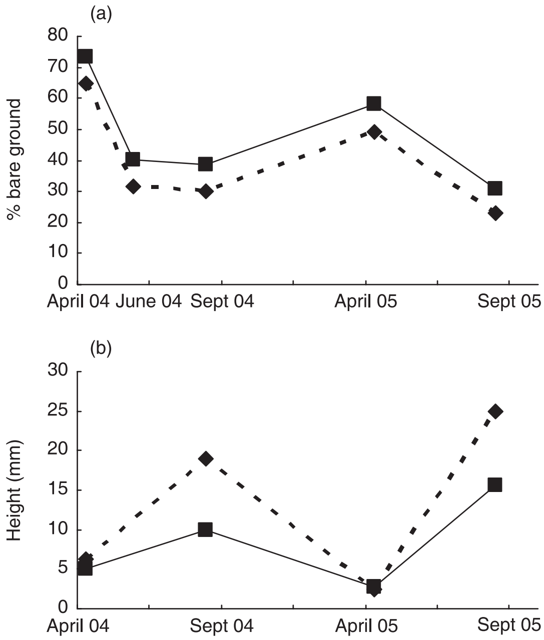

Fig. 2. (a) The percentage of ground that was bare inside (dotted line) and outside (solid line) fenced areas. (b) The height of vegetation inside (dotted line) and outside (solid line) fenced areas. Areas inside fences are grazed by livestock mostly during winter.

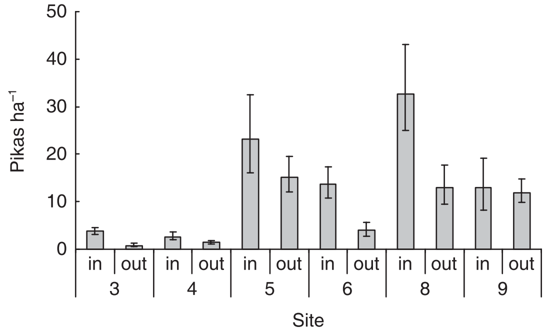

Fig. 3. Population density of plateau pikas (± SE) at the start of the study in April 2004.

was assessed with a mixed-effects model with site as a random effect. The effect of control and fencing on the arcsine-transformed percentage of active burrows was assessed with a linear mixed-effects model.

Results

VEGETATION

There was less bare ground in summer and autumn following the growing season than in spring following winter ($F_{4,48}$ = 76·73, P < 0·0001), and less bare ground inside areas conserved for winter foraging than outside these areas ($F_{1,5}$ = 13·9, P = 0·014; Fig. 2a). On average, vegetation was taller in autumn following the growing season than in spring ($F_{3,58}$ = 521·0, P < 0·0001), and taller inside areas conserved for winter foraging than outside these areas ($F_{1,5}$ = 18·21, P = 0·008; Fig. 2b). However, there were also significant differences in vegetation height between sites (all terms highly significant in a site × session × fence model).

For the clipped quadrats, vegetation height ($F_{1,31}$ = 49·2, P < 0·0001) and cover ($F_{1,31}$ = 67·0, P < 0·0001) explained 78% of the variation in dry biomass, with no significant interaction. The relationship was dry biomass (g m^{-2}) = –26·8 + 1·13 (% cover of vegetation) + 2·29 (height of vegetation in mm). Applying this equation to the step-point measurements indicated that in September 2004 standing plant biomass inside fenced areas ranged across the sites from 66·5 g m^{-2} to 112·5 g m^{-2}, and outside fenced areas it ranged from 43·0 g m^{-2} to 83·4 g m^{-2}. In September 2005 biomass inside fenced areas ranged from 100·1 g m^{-2} to 125·2 g m^{-2}, and outside fenced areas it ranged from 81·3 g m^{-2} to 94·1 g m^{-2}. Assuming the calibration equation could be applied to spring measurements, the corresponding results were 4·2–26·0 g m^{-2} inside fenced areas and 2·8–33·6 g m^{-2} outside fenced areas in April 2004, and 20·7–51·9 g m^{-2} inside fenced areas and 0·0–47·4 g m^{-2} outside fenced areas in April 2005.

PLATEAU PIKAS

Population densities and effect of control

At the commencement of the study in April 2004, before any pest control, there were significant differences in the densities of plateau pika populations at the sites ($F_{5,5}$ = 17·3, P = 0·004) and generally more plateau pikas inside fenced areas than outside fenced areas ($F_{1,5}$ = 13·7, P = 0·014; Fig. 3).

In April 2005, populations of plateau pikas on sites 4 and 6 had declined by 84–97% by the end of the week following control (poison effect $F_{1,7}$ = 133·4, P < 0·0001). In the absence of data, we assumed a similar level of impact, i.e. a 92% reduction in population density, from a similar control programme conducted at sites 8 and 9 in 2004.

Summer increase and recovery post-control

There was a strong density-dependent increase in plateau pika populations between April and September 2004 and between April and September 2005 (i.e. over summer). There were slight differences in the relationship between summers, with higher increases over the summer of 2004 compared with 2005 for a given starting population density. The fitted model was $r = \beta_0 + \beta_1$ ln(population density of plateau pikas in number ha^{-1}) + β_2(summer) [ln(density) $F_{1,21}$ = 178·5, P < 0·0001; summer $F_{1,21}$ = 12·6, P = 0·002; β_0 = 0·155, β_1 = –0·037, β_2 = 0·0 for 2004; β_2 = –0·027 for 2005; Fig. 4]. Neither fencing nor the biomass of vegetation at the end of the growing season, nor the availability of burrows, affected the rate of increase of plateau pikas.

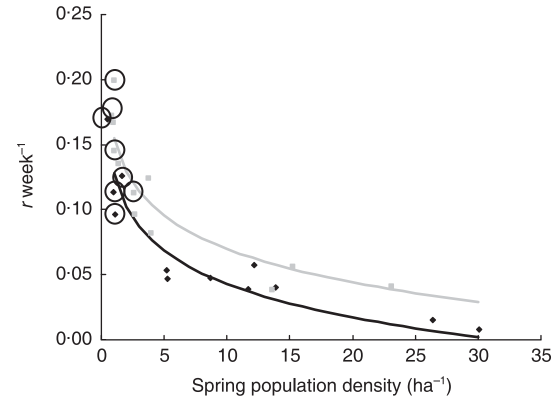

Fig. 4. Rate of increase (r) over summer 2004 (grey dots and line) and summer 2005 (black dots and line) plotted against the preceding spring population density. Populations indicated with open circles were controlled on either side of the fence at two sites in spring 2004 and on either side of the fence at two different sites in spring 2005.

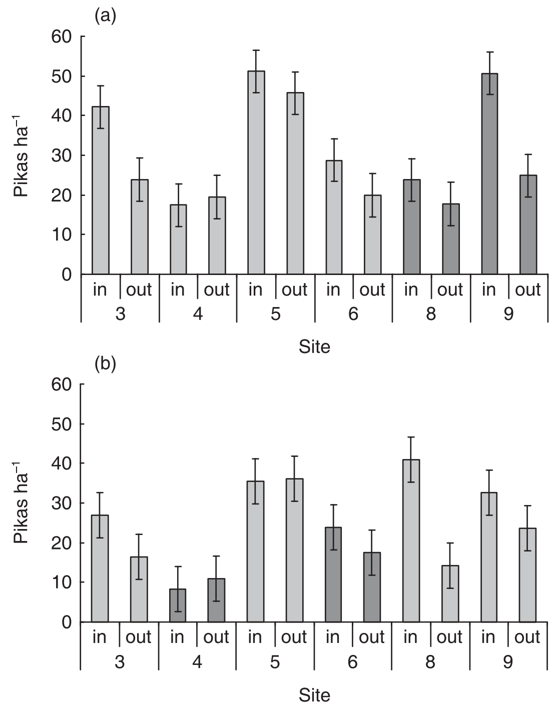

Fig. 5. The density of plateau pika populations (± SE) at the end of the breeding season in (a) autumn 2004 and (b) autumn 2005. The darker shaded columns indicate sites that were controlled in the preceding spring.

The high density-dependent rate of increase on controlled sites resulted in most controlled populations returning to high densities after only one summer in 2004 (Fig. 5). In 2005 populations on controlled sites appeared significantly lower than populations on other sites ($F_{1,10}$ = 5·75, P = 0·037) but this was more to do with the underlying site differences than an effect of control. This is evident by comparing Fig. 5a,b, i.e. there was no evidence that control on sites 4 and 6 in April 2005 resulted in any reduction in peak abundances of plateau pikas on these sites in September 2005

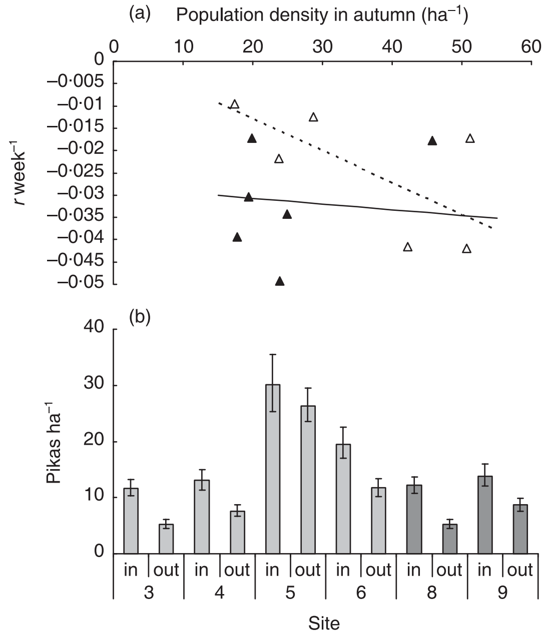

Fig. 6. (a) Rate of increase over winter 2004–2005 (r) plotted against autumn population density in 2004. The solid line indicates outside fenced areas, the dotted line inside fenced areas. (b) Population density of plateau pikas in April 2005 (± SE). The darker shaded columns indicate sites that were controlled in spring 2004.

relative to other sites (model of relative population density with treatment and fence as factors $F_{3,8}$ = 0·319, P = 0·81).

Winter decline: September 2004–April 2005

There was some evidence that plateau pika populations declined more rapidly outside fences, regardless of the starting population in autumn, than inside fences, where the population decline was more density-dependent (fence main effect $F_{1,3}$ = 18·5, P = 0·02; fence by autumn density interaction $F_{1,3}$ = 6·01, P = 0·09; Fig. 6a). This resulted in much higher pika populations in spring 2005 inside fenced areas than outside fenced areas ($F_{1,5}$ = 27·40, P = 0·003; Fig. 6b), consistent with what we observed at the start of the study (see above). There was no evidence of an effect of plant biomass in autumn on the rate of decline of plateau pika populations.

PLATEAU PIKA BURROWS

On average there were 345 more burrows ha^{-1} inside fenced areas than outside ($F_{1,5}$ = 8·31, P = 0·034). There was some evidence that poisoning plateau pikas in April 2005 decreased the number of burrows present on poisoned sites in September 2005 by about 33%, while the number of burrows on untreated sites increased by about 10% over the same period ($F_{1,4}$ = 9·77, P = 0·035). Control of plateau pikas in April 2005 did not affect the proportion of active burrows in September 2005 ($F_{1,4}$ = 3·71, P = 0·126). A much higher proportion

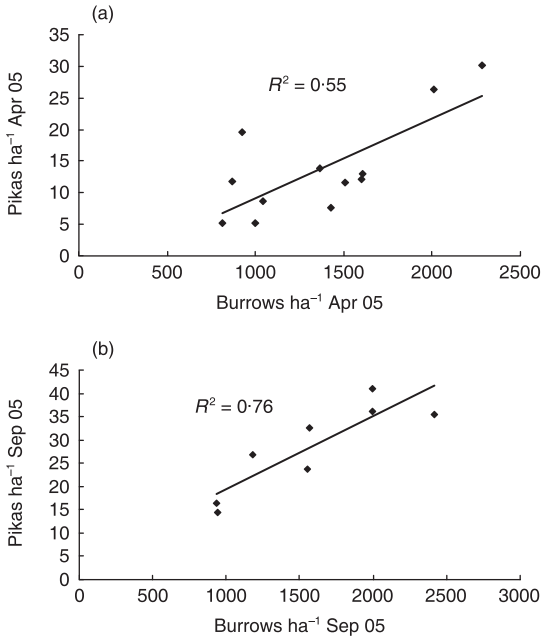

Fig. 7. Relationship between the density of plateau pika populations and the total number of burrow entrances. (a) Spring; plateau pikas (ha^{-1}) = −3·4 + 0·0125 × burrow entrances (ha^{-1}). (b) Autumn; plateau pikas (ha^{-1}) = 3·58 + 0·0157 × burrow entrances (ha^{-1}).

of burrows were assessed as active inside fenced areas than outside (83% vs. 50%, $F_{1,5}$ = 25·03, P = 0·004). Using data from both inside and outside fences, there were strong relationships between the density of plateau pika populations on our sites and the number of burrow entrances counted in both spring ($F_{1,6}$ = 12·27, P = 0·006) and autumn ($F_{1,10}$ = 19·37, P = 0·005; Fig. 7).

Effect of pikas on biomass of vegetation

Compared with untreated populations, there was no evidence that poisoning plateau pikas in April resulted in a higher biomass of vegetation inside fenced areas in September ($F_{1,9}$ = 0·027, P = 0·87).

Discussion

Control of plateau pikas

The results of this study indicate that, on the Tibetan Plateau, control of plateau pikas in early spring using current techniques greatly reduces their abundance in the short term (by more than 90%) but the populations recover rapidly over the following summer, such that population sizes appear indistinguishable from uncontrolled populations in the following autumn. The results appear to be in contrast with the highly effective control programmes, identified by the presence of collapsed, abandoned pika burrows in areas with a recent history of control, for parts of Qinghai (Lai & Smith 2002) but are similar to the population recovery rate reported by Liang (1981). In our study the outcome was the result of a high density-dependent rate of increase of plateau pika populations over summer.

The lack of marked animals did not allow us to determine unequivocally whether the high summer rate of increase was the result of *in situ* recruitment or recolonization from outside the treated areas. An estimated rate of increase of 0·14 week^{-1} (typical of low-density populations; Fig. 4) is within the reproductive capacity of plateau pikas if summer survival is very high. Recolonization is an unlikely explanation because most dispersal occurs prior to the breeding season (Smith *et al.* 1990) and therefore before the control programmes at the sites in late April 2004 and 2005. Also, plateau pikas usually disperse to an adjacent burrow system (Smith *et al.* 1990; Smith & Wang 1991). This was generally a distance of < 20–30 m at our sites, which is consistent with a home range size of *c.* 0·1 ha (Smith & Wang 1991) and therefore less than the width of the buffer zones around the core sampling areas or the distance of core sampling areas to the fence at each site.

Although plateau pika populations increased 2–50-fold during the period from April to September in 2004, and 2–37-fold in 2005, the autumn values were less than maximum densities recorded at lower altitudes on the Tibetan Plateau, probably reflecting lower productivity and a shorter reproductive season at higher altitudes. For example, the maximum count for a 100-m section was 26 pikas, corresponding to a 'patch' density of 130 ha^{-1} and still less than the population density of 374 pikas ha^{-1} and 4168 burrow entrances ha^{-1} (of which 1167 ha^{-1} were active) recorded by Wang *et al.* (1997) at an altitude of approximately 4100 m in Dari County in Qinghai. Although the rate of increase over summer was density-dependent, the lack of impact of fencing or standing plant biomass suggests that food availability, even in the presence of competing livestock, was not the source of the density dependence. Causes could be intrinsic, which is possible for this highly social species, or extrinsic, for example because of predation by terrestrial and avian predators, which were often observed at the study sites.

Conserving forage

As expected for this environment, the data demonstrate the strong affect of season on vegetation height and cover. Average standing biomass inside fenced areas ranged from 4·2 to 51·9 g m^{-2} in spring (April) and from 66·5 to 125·2 g m^{-2} in autumn (September). Outside fenced areas, it ranged from 0·0 to 47·4 g m^{-2} in spring (April) and from 43·0 to 94·1 g m^{-2} in autumn (September), which overlaps the range of 10–30 g m^{-2} for alpine meadows in China (Zhu 1993) but is low in comparison with grasslands world-wide (Coupland 1993). Grazing by livestock appears to have a stronger influence than plateau pikas on the biomass of standing vegetation in alpine meadows at the end of summer. Control of plateau pikas produced no measurable benefit, indexed by vegetation biomass, at this time of year in fenced areas with little or no grazing by livestock. Conversely, the use of fencing to restrict grazing by livestock produced a small but detectable difference in vegetation height in autumn in the presence of plateau pikas. There was marginal support for a density-dependent over-winter decline of plateau pika populations inside fenced areas compared with generally greater rates of decline outside fences: data from additional winters are needed to verify these relationships. This may suggest that the extra vegetation inside fenced areas benefited pikas over winter, particularly when the autumn population density was relatively low. However, using data from all sites, we could find no relationship between the over-winter decline of plateau pika populations and the amount of vegetation (rather than treating fence as a factor). In April, the alpine meadows had been grazed to a uniformly short plant height, < 1 cm, with no differences either side of fences. This suggests the suite of herbivores removes virtually all usable plant biomass by the end of winter, a conclusion supported by reports from villagers that they need to purchase supplementary food to sustain their animals through winter.

MANAGEMENT RECOMMENDATIONS

Counts of plateau pikas pre- and post-control in April 2005 indicated a substantial immediate reduction in population density. Although the timing of control in early spring coincided with lowest pasture biomass (and presumably the maximum consumption of bait material), the density-dependent rate of increase over summer prevented any long-term reductions in the abundance of plateau pikas. This is in contrast to conclusions reached for the management of Brandt's vole *Lasiopodomys brandtii* in grassland in Inner Mongolia (Shi *et al*. 2002). However, inside fenced areas, the benefits of lethal control of plateau pikas at the end of summer would also be reduced by the density-dependent rate of increase over winter. We found no evidence that the reductions in plateau pika populations resulted in increased forage production, although our study was not designed specifically to test this. Nevertheless, our results call into question whether any benefit is derived from controlling plateau pikas when autumn population densities are less than *c*. 50 pikas ha^{-1}.

The practice of conserving forage for winter by keeping livestock outside fenced areas appears to benefit plateau pikas, particularly over winter, with higher populations in spring (i.e. after winter) inside fenced areas than outside them. During winter, populations of plateau pikas declined rapidly in areas where there was very low initial plant biomass outside fences, which suggests food was a critical resource in these areas regardless of population density. In contrast, the conditions inside fenced areas appeared to increase survival rates in low-density populations of plateau pikas over winter. The mechanism is not clear because there was no apparent effect of initial plant biomass in autumn. However, the presence of more burrow entrances inside than outside fences could play a role. More burrows might allow better access to forage or they might provide more refuge from predation at a time of the year when prey are relatively scarce and hunting pressure is likely to be intense.

The current control technique leaves burrow systems intact, providing ample shelter for immigrants and animals that survive control programmes. Ripping of burrows, for example as recommended for management of rabbit *Oryctolagus cuniculus* in Australia (Williams *et al*. 1995), would be counter-productive because it would destroy the hard turf layer on the surface, exposing loose material below, almost certainly exacerbating already serious problems with soil erosion and removing potential food for livestock. The rate of natural closure and revegetation of unused burrows has not been measured and is likely to depend on the total grazing pressure from livestock and plateau pikas. In this context, the reduced counts of burrow entrances 5 months after control programmes for plateau pikas on sites 4 and 6 in 2005 were unexpected. Entrances through cracks and small openings in the hard turf layer appear to be relatively durable. However, many burrows are located in erosion patches where lack of constant use could allow them to be covered by loose, friable soil. Field observations of plant re-establishment on ejecta mounds at unused burrows indicate that revegetation could not conceal burrow entrances within one summer, at least in areas with current levels of grazing by livestock.

In our study area at Naqu, plateau pikas are regarded as pests by almost all villagers, some indicating extinction as the preferred outcome of control programmes (Baima Cuo, unpublished data). World-wide, many species of native small mammals have been viewed as agricultural pests, either as consumers of crops or competitors with livestock, and have been the subject of large-scale control campaigns (Stenseth *et al*. 2003). However, small mammals have the potential to provide beneficial ecosystem services through trophic interactions and direct physical impacts (Brown & Heske 1990; Jones, Lawton & Shachak 1994, 1997; Dickman 1999; Reichman & Seabloom 2002). Smith & Foggin (1999) and Zhang, Zhang & Liu (2003) have discussed the positive role of plateau pikas and plateau zokors as keystone species and ecosystem engineers. At present it is not clear whether pikas cause significant problems for livestock production or whether they are merely a symptom of overgrazing in this system. A similar situation applies to Brandt's vole in Inner Mongolia (Zhang *et al*. 2003). The Tibetan Plateau is home to some of the poorest people in Asia (Fan *et al*. 1999) and the local people are dependent on the production of yaks and sheep for their livelihoods. It also has the headwaters of major rivers that service a large part of south-east Asia. Currently more than 20% of the grassland is considered degraded (Fan *et al*. 1999). It is essential that sustainable grazing systems are developed for this region, and it should be possible to achieve this in way that includes the potential ecosystem services provided by plateau pikas. The results obtained under the conditions prevailing during our study provide no support for the continued control of plateau pikas in high-altitude alpine meadows.

Acknowledgements

This project was co-funded by the Australian Centre for International Agricultural Research (ACIAR), AusAID, the Chinese Academy of Sciences and CSIRO. Steve Henry, Chris Davey, Eddie Gifford, Tony Sinclair, Song Xiaoping, Cai Hai Jian, Baima Cuo, Lydia Li and members of the Grassland Station, Naqu Bureau of Agriculture and Animal Husbandry, provided valuable assistance with field work, and two anonymous referees provided helpful criticism of the manuscript. Wang Guanglin, Lydia Li and Baima Cuo assisted with essential translation skills. The project could not have been completed without the friendship and co-operation of people at the villages of Duo Su, Qi long Nang ba, Gen ma, Ke ma, Na ka quk and Sang long.

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Received 4 April 2006; final copy received 17 December 2006
Editor: Simon Thirgood