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Demographic responses of plateau pikas to vegetation cover and land use in the Tibet Autonomous Region, China

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The role of so-called pest species in alternatively causing, or responding to, changing rangeland conditions remains contentious. Most scientists have concluded that high densities of plateau pikas (Ochotona curzoniae) on the Qinghai-Tibet Plateau, China, are a response to sparsely vegetation conditions, but demographic studies to support this hypothesis are lacking. During February–July 2009 we captured, weighed, and released plateau pikas monthly on 16 plots arrayed along a continuum of vegetation cover and pika density, both of which reflected differing land use for livestock management. We estimated apparent survival of adults using the Cormack–Jolly–Seber approach and recruitment of juveniles using the Pradel approach (in program MARK), modeling both as functions of habitat conditions, including vegetation cover. The probability of an adult pika captured in February being alive and present where initially captured in late July was ~0.04; male and female survival rates were similar. Best-supported models of survival included vegetation cover and an index of late winter pika density; survival was negatively related to percent vegetation cover. Pika body condition varied monthly, and was negatively associated with percent vegetation cover during February–May, but positively associated in June. Pikas living where yaks had reduced vegetation cover displayed no lower recruitment, and higher survival, than where vegetation cover was higher. Thus, our results support the hypothesis that high pika density is a response to, rather than a cause of, “rangeland degradation.” Reducing undesired high pika densities will require addressing root causes of undesirable rangeland conditions.

Key words: China, Ochotona curzoniae, plateau pika, Qinghai-Tibet Plateau, rangeland degradation, recruitment, survival

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Small mammals in rangeland ecosystems are often deemed pests by government authorities and pastoralists, particularly when they reach high densities, because their foraging, burrowing, and vegetation clipping are considered to adversely affect livestock husbandry. However, Delibes-Mateos et al. (2011) have argued that species considered pests often play important roles within local ecosystems when at high densities. The tension between these contrasting views plays out on the Qinghai-Tibet Plateau of western China in management of the plateau pika (Ochotona curzoniae).

Some investigators have argued that small mammals in western China degrade rangelands by reducing plant cover and should be considered pests (Liu et al. 1980; Limbach et al. 2000; Wang 2004; Wei et al. 2007). Xia (1984) assumed that plateau pikas were a principal cause for such “degradation” on the Qinghai-Tibet Plateau in part because he suggested that pikas competed with livestock for forage (although Jiang and Xia [1985] and Jiang and Xia [1987] documented that dietary overlap was minor unless pikas were at very high densities; we note that the term “rangeland degradation” is rarely defined rigorously in the literature on plateau pikas [Harris 2010]; we repeat it here when referencing papers that use it). For the past half-century, Chinese management has generally been favorable to controlling or entirely eradicating “rodent pests” (in the Chinese lexicon, pikas, although lagomorphs, are often lumped together as rodents [Zhang et al. 1998]), which have been poisoned to control their populations (Jing et al. 2006; Pech et al. 2007; Delibes-Mateos et al. 2011). Some 208,000 km² was poisoned to reduce or eliminate plateau pika populations in Qinghai Province alone during 1960–1990 (Fan et al. 1999).
Conversely, the plateau pika has been categorized as a keystone species (Power et al. 1996) because of its function in creating disturbance and fostering biodiversity (Smith and Foggin 1999; Wangdwei et al. 2008). Mounds of excavated soil created when pikas dig burrows have higher macronutrient content than surrounding areas (Hogan 2010; Liu et al. 2010b), and create habitat for many endemic plant species (Bagchi et al. 2006; see Wesche et al. [2007] for documentation of similar effects with Ochotona pallasi in the Mongolian Gobi). Plateau pikas serve as important prey items for both birds of prey and mammalian predators (Li et al. 2004; Xu et al. 2006; Badingqiuying 2008; Harris 2008). The Tibetan fox (Vulpes ferrilata) evidently occurs only where plateau pikas are present, and is probably an obligate predator of these small mammals (Clark et al. 2008; Liu et al. 2010a). Many native birds (Lai and Smith 2003; Arthur et al. 2008; Lu et al. 2009; Zeng and Lu 2009), amphibians, and reptiles use pika burrows for shelter (Hogan 2010).

Although inverse correlations between plateau pika abundance and vegetation cover or height, or both, have been commonly documented (Shi 1983; Fan et al. 1999; Holzner and Kriebchaum 2001; Zhang et al. 2003), it remains unclear whether high pika density was a causative factor in these vegetation conditions, or conversely, if these pastures provided superior habitat conditions for pikas, presumably operating through higher survival, higher recruitment, or both. Under the latter hypothesis, we would expect to find a negative correlation between indexes of vegetation density and pika population vital rates. Under the former hypothesis, such a negative correlation would be unlikely because greater forage biomass would seem to provide opportunities for gain of body mass and resulting increases in vital rates. Thus, we sought to test these competing hypotheses empirically by comparing pika vital rates during late winter through spring (the seasons of presumed high mortality—Wang and Smith 1988; Smith et al. 1990:28) within a number of pika coteries upon which differing livestock herding activities had led to heterogeneous habitat conditions. Specifically, our objectives were to examine apparent survival and recruitment of plateau pikas from late winter through early summer as functions of vegetation cover, which, in turn, was related in part to differing patterns of pastoral land use. We hypothesized that apparent survival of adults, in addition to varying seasonally and by sex, would vary among trapping areas that differed in vegetation coverage, an index of pika density in late winter (“density,” hereafter), whether topography was open or hilly, and the density of pika burrows. To that end, we examined a suite of models relating apparent adult survival to sex and these 4 covariates. We examined the same suite of variables in an examination of juvenile recruitment. We also examined body mass dynamics as functions of sex, time, and percent vegetation cover.

**Materials and Methods**

**Geographic context.**—Livestock husbandry, primarily of yaks (Bos grunniens), sheep (Ovis aries), and goats (Capra hircus—Goldstein et al. 1990; Miller 1999), is the principal land-use type on the Qinghai-Tibet Plateau (Miller 1995; Miehe et al. 2009). Pastoralists of the Qinghai-Tibet Plateau have traditionally used pastures in a seasonal fashion, migrating among known pastures with different seasonal function and vegetation types and phenologies for at least 8,800 years (Miehe et al. 2009). However, the traditional grazing pattern has been altered in nomadic areas (Wu and Richard 1999; Fox et al. 2004). Land tenure, which historically had been flexible and varied from single household to cooperative among many families, has become quasi-privatized under an extension of the household responsibility system implemented earlier in agricultural areas. Although land has been leased by the government to pastoralists for a few decades, only in the most recent decade has an emphasis been put on boundary demarcation via fencing (Wu and Richard 1999).

Traditionally, grassland subject to yak grazing can be divided into bedding areas (used during evening) and pasture areas (used for feeding during daylight hours). Bedding areas of yaks in winter are usually adjacent to pastoralists’ houses, and vegetation there is reduced greatly. In addition to vegetation coverage, vegetation composition coverage and the number of small-mammal burrows differ between pasture and bedding areas (Wangdwei and Tsomo 2009).

**Study site.**—Our study area (29°46′–29°46′N, 92°16′–92°20′E) was located in the Nyhian (Nian in Chinese) Valley, Rotug (Riduo in Chinese) Township, Medrogonkar (Mozhu Gongga in Chinese) County, Lhasa Prefecture, Tibet Autonomous Region, China. Pastoralists mainly depended on yaks, sheep, and goats for food, cloth, and shelter, but also collected medicinal caterpillar fungus (yartsa in Tibetan and dongchong xiaocao in Chinese) during early summer to increase personal income (Wangdwei and Tsomo 2009). According to local pastoralists, livestock numbers had been relatively constant at about 1,000 head during the years 1998–2009. Elevations in the study area range from 4,423 to 5,015 m.

Mean annual temperature during 1980–2010 at the nearest meteorological station (Medrogonkar, 29°50′N, 91°42′E, ~4,000 m elevation, about 60 km distant) was 4.2°C and annual precipitation averaged 582 mm, 99% of which occurred during May–September (Chudor, Institute of Tibetan Plateau Atmospheric and Environmental Sciences, pers. comm., February 2012). April 2009, during our study, was the 4th driest April and 2nd warmest April during the 1980–2010 time period.

Most of the study area consisted of alpine meadow dominated by sedges of the genus Kobresia. This vegetation formation is characterized by a 10- to 30-cm-thick turf layer, intermixed with various grasses and forbs (less commonly dwarf shrubs and cushion plants). Particularly on slopes, this turf layer is often incised from the hooves of livestock, solifluction, or other erosive forces, creating terracelike structures that ease pika burrowing. Within these Kobresia meadows, we further categorized 4 main vegetation types based on dominant species as Kobresia pygmaea–Carex spp.,
Table 1.—The 6 trapping areas in which pikas (*Ochotona curzoniae*) were marked during February–July 2009, arrayed along a 22-km gradient from elevations of 4,443 to 4,834 m in Medrogonkar County, Tibet Autonomous Region, China. Within each, we selected four 30 × 30-m plots for trapping. Shown are means with standard deviations in parentheses. Vegetation types are: KC = *Kobresia pygmaea*—Carex spp.; KF = K. *pygmaea*–forb; KS = K. *pygmaea*–shrub species; K = K. *pygmaea*–K. *fragilis* (pure *Kobresia*).

<table>
<thead>
<tr>
<th>Plot (30 × 30 m)</th>
<th>Land-use category</th>
<th>Vegetation cover %</th>
<th>Vegetation type</th>
<th>No. burrows</th>
<th>Minimum no. pikas</th>
<th>Elevation (m)</th>
<th>Open/sheltered</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Current bedding area</td>
<td>41 (5)</td>
<td>KC</td>
<td>248</td>
<td>26</td>
<td>4,712</td>
<td>Open</td>
</tr>
<tr>
<td>2</td>
<td>Current bedding area</td>
<td>70 (31)</td>
<td>KC</td>
<td>192</td>
<td>42</td>
<td>4,666</td>
<td>Open</td>
</tr>
<tr>
<td>3</td>
<td>Current bedding area</td>
<td>69 (45)</td>
<td>KC</td>
<td>148</td>
<td>43</td>
<td>4,432</td>
<td>Open</td>
</tr>
<tr>
<td>4</td>
<td>Old winter house</td>
<td>33 (12)</td>
<td>KF</td>
<td>146</td>
<td>8</td>
<td>4,800</td>
<td>Sheltered</td>
</tr>
<tr>
<td>5</td>
<td>Pasture</td>
<td>87 (36)</td>
<td>KS</td>
<td>99</td>
<td>8</td>
<td>4,673</td>
<td>Sheltered</td>
</tr>
<tr>
<td>6</td>
<td>Pasture</td>
<td>61 (13)</td>
<td>KF</td>
<td>208</td>
<td>10</td>
<td>4,808</td>
<td>Sheltered</td>
</tr>
<tr>
<td>7</td>
<td>Pasture</td>
<td>82 (19)</td>
<td>K</td>
<td>168</td>
<td>28</td>
<td>4,432</td>
<td>Open</td>
</tr>
<tr>
<td>8</td>
<td>Pasture</td>
<td>76 (17)</td>
<td>KF</td>
<td>202</td>
<td>18</td>
<td>4,719</td>
<td>Sheltered</td>
</tr>
<tr>
<td>9</td>
<td>Old bedding area with fence</td>
<td>28 (3)</td>
<td>KF</td>
<td>349</td>
<td>60</td>
<td>4,800</td>
<td>Open</td>
</tr>
<tr>
<td>10</td>
<td>Old bedding area</td>
<td>54 (41)</td>
<td>KC</td>
<td>228</td>
<td>23</td>
<td>4,446</td>
<td>Open</td>
</tr>
<tr>
<td>11</td>
<td>Old bedding area</td>
<td>46 (35)</td>
<td>KF</td>
<td>206</td>
<td>33</td>
<td>4,781</td>
<td>Sheltered</td>
</tr>
<tr>
<td>12</td>
<td>Old bedding area</td>
<td>65 (11)</td>
<td>KC</td>
<td>179</td>
<td>21</td>
<td>4,680</td>
<td>Sheltered</td>
</tr>
<tr>
<td>13</td>
<td>Fenced area</td>
<td>78 (23)</td>
<td>KF</td>
<td>161</td>
<td>11</td>
<td>4,423</td>
<td>Open</td>
</tr>
<tr>
<td>14</td>
<td>Fenced area</td>
<td>79 (8)</td>
<td>KF</td>
<td>49</td>
<td>15</td>
<td>4,423</td>
<td>Open</td>
</tr>
<tr>
<td>15</td>
<td>Fenced area</td>
<td>71 (24)</td>
<td>KF</td>
<td>210</td>
<td>16</td>
<td>4,423</td>
<td>Open</td>
</tr>
<tr>
<td>16</td>
<td>Fenced area</td>
<td>86 (8)</td>
<td>K</td>
<td>200</td>
<td>16</td>
<td>4,423</td>
<td>Open</td>
</tr>
</tbody>
</table>


The study area included both pasture areas, typically used primarily for yak foraging, and associated bedding areas, adjacent to pastoralist tent sites, used during nighttime by female and young yaks. The latter also included fenced areas (varying in size from approximately 2 to 15 ha) where yaks and wild ungulates were excluded during the growing season to preserve forage for extreme winter conditions. Bedding areas were used by pastoralists and their yaks from the end of April (upon return from wintering areas) until the beginning of September (at which time they departed again for winter areas). Pastoralists used stone fences to corral yaks during the cold period near winter houses. We assigned land-use types to 6 categories: current yak bedding areas, old bedding areas with fence, yak pasture areas, old bedding areas, fenced areas (for excluding grazing by large herbivores), and old winter house areas that had been abandoned by pastoralists.

The study area contained approximately 300 blue sheep (*Pseudois nayaur*) and 20 Tibetan gazelles (*Procapra picticaudata*); neither were commonly observed on areas where we trapped and observed plateau pikas. We observed a few woolly hares (*Lepus oiostolus*) and Stoliczka’s mountain voles (*Alticola stoliczkanus*), the latter only in alpine meadows of the fenced area. Himalayan marmots (*Marmota himalayana*) overlapped in habitats used to some degree with plateau pikas.

Pika captures.—To estimate survival and recruitment, we used mark–recapture methods. We subjectively selected 16 trapping areas (measuring 30 × 30 m) that represented pika populations in the 6 land-use types (Table 1). Current (in-use) and past bedding areas had similar vegetation characteristics; we therefore combined them into the single category “bedding areas.” Pasture areas were located at least 200 m (and most were > 1 km) from bedding areas. We surveyed pastures for locations to establish pika trapping grids that would represent pasture plots. If we detected no pikas on a particular pasture, we set up a line transect, walking until we located a pika coterie. Fenced areas were located in flat areas dominated by *Kobresia* sedge (plots 13–16; Table 1). These fenced areas had been subjected to pika poisoning activity 1–2 years before our sampling.

We conducted pilot observations in all yak bedding areas (i.e., tent sites) before establishing trapping sites. If we found > 1 old yak bedding area, we randomly selected 1 by selecting from slips of paper with identification for each. The total area covered by all 16 trapping sites was 1.44 ha, and sites were distributed along a 22-km-long belt, with elevations ranging from 4,423 to 5,015 m.

To mark and recapture pikas, we placed 45 Sherman live traps (5.2 × 6.5 × 16.7 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) in an array of 9 rows × 5 columns at roughly 6- to 7-m intervals at each of the 16 trapping sites during forty-eight 2-h-long trapping sessions (allocated to 4 contiguous sessions within 2 days in each of 6 months, February–July 2009). We considered contiguous sessions to be nonindependent, and thus elected not to employ a robust design in analysis, and instead aggregated captures during the 8 same-day sessions into a single occasion. Traps were baited with cookies, carrots, and roasted barley. Trapped animals were weighed and sexed, and total body length was recorded. We assigned pikas to 1 of 3 categories (adult females, adult males, and juveniles); adults were defined as animals born during the previous spring–summer or earlier; juveniles (sampled only in May, June, and July 2009) were identified based on smaller body size. We tagged individual animals using Rabbit Ear Tags (part 1841, ~1-cm diameter; National Band and Tag Company, Newport, Kentucky) for adults and small, laboratory animal tags (Monel 1005-1, ~0.7 cm long) for juveniles. We measured body mass of all adult pikas captured on each session using Pesola spring scales (Pesola AG, Baar, Switzerland). We defined a body condition index as the ratio of body mass to total length.
Quantification of environmental covariates.—To document vegetation condition, we quantified species-specific plant cover at randomly placed plots. In July 2009, we divided each of the 16 trapping sites into 9 plots measuring 10 × 10 m, selecting 4 at random for vegetation measurement. We then sampled a randomly chosen 1-m$^2$ subplot within each of these plots (i.e., 64 vegetation plots) on which we overlaid a 4-m rope to identify the subplot boundary. All species within subplots were identified, and the percentage cover of each species was visually estimated.

Because pika burrows act as a shelter from the ambient environment, we also counted all active pika burrows within all trapping plots during February (i.e., the 1st trapping period). We did not quantify smaller burrows created by voles, which we found could easily be differentiated from pika burrows by their smaller size (we captured and observed voles at only 1 plot). We defined as “open” areas that had negligible slope for > 50 m distance in all directions from trapping areas and as “sheltered” areas with slope > 5° for < 20-m distance from the nearest hills (Table 1). Based on presence of pastoralists as they migrated between winter and summer pastures, we defined winter as February, March, and April; spring as May; and summer as June and July.

Analyses of apparent survival and recruitment.—We used the Cormack–Jolly–Seber mark–recapture approach, as implemented in program MARK (Cormack 1964; Jolly 1965; Seber 1965; Cooch and White 2008), to model apparent survival probabilities of adult plateau pikas in relation to our selected suite of explanatory factors (Table 1). Although our interest was in true survival, we lacked the ability to distinguish it from emigration and thus refer to apparent survival throughout, although note that plateau pikas are largely philopatric and most dispersal is small scale (Dobson et al. 1998). We used MARK’s implementation of generalized linear models to examine effects on apparent monthly survival ($\phi$) and capture rate ($p$) as functions of sex, season, percent vegetation cover, number of burrows, open (versus sheltered), and relative pika late-winter density (as indexed by number of unique pikas captured at each site during the accumulated February and March capture occasions [Table 1]). We also examined all models containing 2 covariates and their corresponding interaction models, but did not examine more complex (3 or 4 covariate) models.

We also examined candidate models that included the factor vegetation type as an explanatory variable. We judged these factorial models to be unsatisfactory because we had only a single sample ($n = 4$) of the $K$. pygmaea–shrub species type, and only 2 samples of the pure Kobresia type. These models were always ranked well below those with other variables, so we did not consider them further and do not report them here.

We also used Pradel models (Williams et al. 2002:511—implemented in MARK as “survival and recruitment only”) to model juvenile recruitment ($f$) as functions of the same set of covariates used in the Cormack–Jolly–Seber analysis. We made no attempt to model recruitment of adults because the duration of sampling permitted only immigration, and apparent immigration of adults was always $< 1$.

To examine possible overdispersion in our data, we estimated the variance inflation factor $c$ using the median procedure in MARK. Our global model was based the group × time model accounting for adult males and females; total parameters were 22. Because our model included covariates (and MARK can only estimate $c$ for a model excluding covariates), we constructed a separate model with this structure but excluding covariates. In implementing the median $c$ procedure, we specified a minimum 1 and maximum 4, with 10 replicates at each of 40 intermediate points. Goodness-of-fit tests performed by program RELEASE suggested no significant overdispersion (females: $\chi^2_{20} = 11.881$, $P = 0.293$; males: $\chi^2_{20} = 7.251$, $P = 0.510$; juveniles $\chi^2_{20} = 2.075$, $P = 0.385$). However, to be conservative and minimize the possibility of overfitting, we used the value returned by the median procedure in program MARK throughout, which was 1.092. We then used quasi-Akaike’s information criteria adjusted for small sample size (QAIC$_c$) to rank models (Burnham and Anderson 2002). Competing models with ΔQAIC$_c$ values < 2 were considered to enjoy similar support (Burnham and Anderson 2002).

Analyses of body condition.—To examine if body condition exhibited similar patterns to those identified in survival models, we modeled adult body condition as a function of sex, month, and vegetation cover (and 2-way interactions—Pinheiro et al. 2012). Animal was introduced as a random factor to account for repeated sampling of animals. A likelihood-ratio test comparing the fit of an ordinary linear model without the random factor (and hence assuming independence among observations) to a linear mixed model with the random factor (and hence, accounting for dependence among observations obtained from a single animal) provided convincing evidence that the linear mixed model fit improved on the fit of the ordinary linear model ($l_r = 27.36$, $P < 0.0001$ using $d.f. = 1$ [Pinheiro and Bates 2000]). The significance of the fixed factors and vegetation cover also were assessed using likelihood-ratio tests. We were concerned that the dearth of repeated measurements might affect the linear mixed parameter estimators because 52% of the body mass measurements were obtained from animals weighed only once. Models fit using only animals weighed more than once, and more than twice, led to the same inferences as when all animals were used. Consequently, the results presented below were obtained using all animals.

Results

We captured 387 individual pikas from February through July 2009 (Table 2). Most were captured only once or twice. Categorized by season, of 181 pikas 1st captured in winter, 79 were never recaptured, 70 were recaptured once, 28 were recaptured twice, and 3 were recaptured ≥ 2 times. Of 35 pikas 1st captured during spring, 19 were never recaptured, 11 were recaptured once, and 4 were recaptured twice. Of 171 pikas 1st...
captured in summer, 144 were never recaptured and 27 were recaptured once. Of the 150 juveniles, 53 were caught only in the final (July) capture occasion.

In Cormack–Jolly–Seber survival analyses, time-constant (“dot”) models for both apparent survival and capture probability were consistently ranked below their corresponding seasonal analogues. Thus, our subsequent efforts considered only models in which both apparent survival and capture probability were free to vary by season (winter, spring, or summer). Similarly, we found that models allowing for sex-specific apparent survival of adults were consistently ranked below their corresponding model with sexes combined (because apparent survival of females and males was similar). Thus, we report both separate sex and combined sex seasonal survival rates, but to maintain our focus on environmental determinants, show only the combined sex models in Table 3.

Monthly adult apparent survival was high in winter (model-averaged combined sex $\hat{\phi} = 0.910, SE = 0.066$), lower in spring (model-averaged combined sex $\hat{\phi} = 0.690, SE = 0.160$), and very low in summer (model-averaged combined sex $\hat{\phi} = 0.278, SE = 0.085$). An adult captured in February 2009 would thus have had a mean probability of approximately 4% of being alive and on the original capture site in July 2009. Seasonal apparent monthly survival rates of females tended to be slightly higher than those of males in winter (0.921 versus 0.908, using the top-ranked model but with sexes estimated separately) and spring (0.738 versus 0.685), but not in summer (0.267 versus 0.279); as noted above, model selection suggested inadequate justification for considering sex-specific rates different from one another.

The top-ranked Cormack–Jolly–Seber model explaining variation in apparent adult survival included percent vegetation cover and the relative late-winter density index; the 2nd-ranked model included the interaction between these 2 covariates (Table 3). The model with relative late-winter pika density and burrow number (Table 3, model 3) also was well supported ($\Delta$QAIC$_c = -1.91$). Among models with only a single explanatory variable, that with percent vegetation cover (Table 3, model 5) was ranked highest, approximately 0.35 QAIC$_c$ units better than that with relative late-winter pika density only (model 7); the model with topography only (model 17) had little support ($\Delta$QAIC$_c = 9.91$). The null model, including only seasonal effects but no environmental covariates (model 15), also had little support ($\Delta$QAIC$_c = 8.95$). A likelihood-ratio test similarly indicated that model 3 (with the single explanatory variable vegetation cover) was a better fit to the data than the null model ($\chi^2_1 = 6.307, P = 0.012$).

Apparent adult survival was higher on capture plots with low vegetation cover than on plots with high vegetation cover (Table 4). Although negative coefficients relating apparent survival to vegetation cover were low, standard errors also were low, suggesting these effects were real. Apparent adult survival was slightly more weakly related to our index of late-winter pika density. Surprisingly, this relationship was consistently positive, suggesting some degree of inverse density-dependence, at least at the observed densities. In a closely related dynamic, apparent adult survival was positively related to the number of burrows counted in February (Table 3).

### Table 2.—Pikas (*Ochotona curzoniae*) captured during February–July 2009 in Medrogonkar County, Tibet Autonomous Region, China, by age and season when 1st captured.

<table>
<thead>
<tr>
<th>Season</th>
<th>Adults</th>
<th>Juveniles</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>181</td>
<td>0</td>
<td>181</td>
</tr>
<tr>
<td>Spring</td>
<td>23</td>
<td>12</td>
<td>35</td>
</tr>
<tr>
<td>Summer</td>
<td>33</td>
<td>138</td>
<td>171</td>
</tr>
<tr>
<td>Total</td>
<td>237</td>
<td>150</td>
<td>387</td>
</tr>
</tbody>
</table>

### Table 3.—Top-ranked models from the Cormack–Jolly–Seber analysis of apparent adult pika (*Ochotona curzoniae*) survival rate ($\hat{\phi}$), February–July 2009, Medrogonkar County, Tibet Autonomous Region, China. All models in table used a seasonal effect only for the probability of capture (3 seasons). Covariates are as follows: f = female; m = male; Density = accumulated individual adult pikas captured during February and March; PetVegCover = percent of ground covered by vegetation in July 2009; Burrows = total number of pika burrows counted in February 2009; Sheltered = 0 if sheltered topography, 1 if topographic relief present.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\Delta$QAIC$_c$</th>
<th>$w_p$</th>
<th>K</th>
<th>QDeviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Phi$ (season,)*PetVegCover+Density)</td>
<td>0.000</td>
<td>0.412</td>
<td>8</td>
<td>642.60</td>
</tr>
<tr>
<td>$\Phi$ (season,)*PetVegCover+*Density)</td>
<td>1.691</td>
<td>0.177</td>
<td>9</td>
<td>642.21</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Burrows+Density)</td>
<td>1.911</td>
<td>0.158</td>
<td>8</td>
<td>644.51</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Burrows+*Density)</td>
<td>3.803</td>
<td>0.061</td>
<td>9</td>
<td>644.32</td>
</tr>
<tr>
<td>$\Phi$ (season,)*PetVegCover)</td>
<td>4.700</td>
<td>0.039</td>
<td>7</td>
<td>649.37</td>
</tr>
<tr>
<td>$\Phi$ (f<em>season, m</em>season,)*PetVegCover+Density)</td>
<td>5.036</td>
<td>0.033</td>
<td>11</td>
<td>641.37</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Density)</td>
<td>5.056</td>
<td>0.033</td>
<td>7</td>
<td>649.72</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Sheltered+PetVegCover)</td>
<td>6.357</td>
<td>0.017</td>
<td>8</td>
<td>648.95</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Burrows+PetVegCover)</td>
<td>6.759</td>
<td>0.014</td>
<td>8</td>
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</tr>
<tr>
<td>$\Phi$ (season,)*Burrows)</td>
<td>7.110</td>
<td>0.012</td>
<td>7</td>
<td>651.78</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Sheltered+Density)</td>
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<td>0.012</td>
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<td>649.72</td>
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<tr>
<td>$\Phi$ (season,)*Burrows+PetVegCover)</td>
<td>8.222</td>
<td>0.007</td>
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<td>648.74</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Burrows+*PetVegCover)</td>
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<td>0.006</td>
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<td>648.89</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Sheltered+Burrows)</td>
<td>8.681</td>
<td>0.005</td>
<td>8</td>
<td>651.28</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Sheltered)</td>
<td>8.947</td>
<td>0.005</td>
<td>6</td>
<td>655.67</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Sheltered)*Density)</td>
<td>9.181</td>
<td>0.004</td>
<td>9</td>
<td>649.70</td>
</tr>
<tr>
<td>$\Phi$ (season,)*Sheltered)</td>
<td>9.909</td>
<td>0.003</td>
<td>7</td>
<td>654.57</td>
</tr>
<tr>
<td>$\Phi$ (season,)<em>Sheltered</em>Burrows)</td>
<td>10.755</td>
<td>0.002</td>
<td>9</td>
<td>651.27</td>
</tr>
</tbody>
</table>
percent of ground covered by vegetation in July 2009; Burrows
May and 0.11 (SE of per capita juvenile recruitment were 7.29 (predicted juvenile recruitment well. Model-averaged estimates positive (Fig. 1), when body condition was significantly
/ / / (burrows: slope coefficients were exceeded by their standard errors small number of animals measured in this month (Table 6).
/ / / / support (Table 5). In all 3 cases, however, the magnitudes of February. Estimates for July were not reliable because of the
/ / /
(Season) no covariates 0.000 0.286 12 1,678.618
Season+Density*Burrows 0.0207 (0.0086)
Season+PctVegCover 0.0738 (0.0319)
Season+Density 0.0198 (0.0087) 0.2040 (0.3200)

4). Apparent survival tended to be higher in open than in
sheltered areas, although this effect was quite weak.

In contrast to our models of survival, the top Pradel model
predicting juvenile recruitment was the season-only model (i.e.,
no explanatory covariates), although models with number of
burrows (ΔQAICc = 1.043), late-winter pika density (ΔQAICc =
1.632), and vegetation cover (ΔQAICc = 2.046) also received
support (Table 5). In all 3 cases, however, the magnitudes of
slope coefficients were exceeded by their standard errors
(burrows: ß = 0.0042, SE = 0.0044; density: ß = 0.0505, SE = −
0.0779; vegetation cover: ß = −0.0032, SE = 0.0148),
suggesting that none of these environmental covariates
predicted juvenile recruitment well. Model-averaged estimates
of per capita juvenile recruitment were 7.29 (SE = 2.20) during
May and 0.11 (SE = 0.16) during June (at which point
mortality of juveniles had already begun to exceed recruit-
ment).

Mean body mass of adults (including recaptures) over all
capture sessions was 144.6 g (SE = 0.82 g, n = 688), and mean
total length was 12.6 cm (SE = 0.03 cm, n = 638). We found
that body condition (mass/length) was only marginally
associated with sex (a likelihood-ratio test for the significanc
of sex produced lr = 2.79, d.f. = 1, approximate P = 0.095). For
completeness, we retained sex in our models. Body condition
was strongly associated with month and also a function of

<table>
<thead>
<tr>
<th>Model name</th>
<th>Percent vegetation cover</th>
<th>Late-winter density index</th>
<th>No. burrows</th>
<th>Sheltered or open</th>
<th>Percent vegetation cover*</th>
<th>Late-winter density index*</th>
<th>no. burrows</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season+Density+PctVegCover</td>
<td>−0.0219 (0.0085)</td>
<td>0.0785 (0.0312)</td>
<td></td>
<td></td>
<td>−0.0018 (0.0030)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season+Density*PctVegCover</td>
<td>−0.0073 (0.0252)</td>
<td>0.1957 (0.1950)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season+Density+Burrows</td>
<td>0.0829 (0.0321)</td>
<td>0.0049 (0.0023)</td>
<td></td>
<td></td>
<td>0.0017 (0.0078)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season+Density*Burrows</td>
<td>0.0242 (0.1406)</td>
<td></td>
<td></td>
<td>0.0003 (0.0008)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season+PctVegCover</td>
<td>−0.0207 (0.0086)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season+Density</td>
<td></td>
<td>0.0738 (0.0319)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season+Sheltered+PctVegCover</td>
<td>−0.0198 (0.0087)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

TABLE 4.—Slope coefficients (logit scale) relating explanatory variables of selected Cormack–Jolly–Seber models to apparent survival of adult plateau pikas (Ochotona curzoniae), February–July 2009, Medrogonkar County, Tibet Autonomous Region. Shown are top 3 quasi-Akaike’s information criteria adjusted for small sample size (QAICc) models as well as models with only a single explanatory variable. Standard errors are given in parentheses. Model covariates are as defined in Table 3 caption.

TABLE 5.—Top-ranked models from the Pradel analysis of juvenile pika (Ochotona curzoniae) recruitment (f), February–July 2009, Medrogonkar County, Tibet Autonomous Region, China. All models in table used a seasonal effect only for the probability of capture (p) of adults (3 seasons) and juveniles (2 seasons). Apparent survival (f̄) for both adults and juveniles (not shown) was modeled throughout using the top model covariates from the Cormack–Jolly–Seber survival modeling (Table 2). Covariates are as follows: ad = adult; Juv = Juvenile; f = adult female; m = adult male. Site specific covariates: Density = accumulated individual adult pikas captured during February and March; PctVegCover = percent of ground covered by vegetation in July 2009; Burrows = total number of burrows.

<table>
<thead>
<tr>
<th>Model</th>
<th>ΔQAICc</th>
<th>QDeviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>f (adult), Juv(Season) no covariates</td>
<td>0.000</td>
<td>1,678.618</td>
</tr>
<tr>
<td>f (adult), Juv(Season) + Burrows</td>
<td>1.043</td>
<td>1,677.567</td>
</tr>
<tr>
<td>f (adult), Juv(Season) + Density</td>
<td>1.632</td>
<td>1,678.155</td>
</tr>
<tr>
<td>f (adult), Juv(Season) + PctVegCover</td>
<td>2.046</td>
<td>1,678.569</td>
</tr>
<tr>
<td>f (adult), Juv(Season) + Burrows + PctVegCover</td>
<td>2.421</td>
<td>1,676.842</td>
</tr>
<tr>
<td>f (adult), Juv(Season) + Burrows + Density</td>
<td>2.455</td>
<td>1,676.797</td>
</tr>
<tr>
<td>f (adult), Juv(Season) + Density + PctVegCover</td>
<td>3.621</td>
<td>1,678.043</td>
</tr>
<tr>
<td>f (adult), Juv(Season) + Burrows + Density</td>
<td>3.871</td>
<td>1,676.183</td>
</tr>
<tr>
<td>f (adult), Juv(Season) + Burrows + PctVegCover + Density</td>
<td>3.978</td>
<td>1,676.290</td>
</tr>
<tr>
<td>f (adult), Juv(Season) + Density + PctVegCover</td>
<td>5.405</td>
<td>1,677.718</td>
</tr>
</tbody>
</table>

DISCUSSION

Although we lacked data for the full annual cycle, our results
confirm those of others (Wang and Smith 1988; Wang and Dai
1989; Pech et al. 2007) in showing low survival of free-ranging
plateau pikas. Adult survival at our study site during the 6-
month period February–July 2009 was about 4%. The winter of
1985–1986 was particularly harsh in much of Qinghai
(Schaller et al. 1991), and Wang and Smith (1988) speculated
that this applied to their study site as well, although they did
Table 6.—Parameter estimates and standard errors obtained from linear mixed model fit of pika (*Ochotona curzoniae*) body condition on month, vegetation cover, and sex, Medrogonkar County, Tibet Autonomous Region, China. Vegetation cover has been centered to have mean = 0, so that parameter estimates associated with month are interpretable as the estimated difference in expected body condition between a particular month and the reference month of February given that the animal is a female and mean percent cover = 62.41%. Variance components were estimated to be $\hat{\sigma}_{\text{animal}}^2 = 10.30$, and $\hat{\sigma}_{\text{residual}}^2 = 12.05$, and the intraclass correlation coefficient was $\frac{\hat{\sigma}_{\text{animal}}^2}{\hat{\sigma}_{\text{animal}}^2 + \hat{\sigma}_{\text{residual}}^2} = 0.422$.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Parameter estimate</th>
<th>SE</th>
<th>Wald statistic</th>
<th>Approximate P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>5.188</td>
<td>6.616</td>
<td>0.784</td>
<td>0.433</td>
</tr>
<tr>
<td>Sex (male)</td>
<td>-3.279</td>
<td>1.994</td>
<td>-1.644</td>
<td>0.101</td>
</tr>
<tr>
<td>March</td>
<td>0.041</td>
<td>9.199</td>
<td>0.005</td>
<td>0.996</td>
</tr>
<tr>
<td>April</td>
<td>0.075</td>
<td>8.070</td>
<td>0.009</td>
<td>0.992</td>
</tr>
<tr>
<td>May</td>
<td>17.140</td>
<td>8.732</td>
<td>1.963</td>
<td>0.051</td>
</tr>
<tr>
<td>June</td>
<td>-15.300</td>
<td>8.268</td>
<td>-1.850</td>
<td>0.066</td>
</tr>
<tr>
<td>July</td>
<td>-11.270</td>
<td>20.157</td>
<td>0.559</td>
<td>0.576</td>
</tr>
<tr>
<td>Percent vegetation cover (veg)</td>
<td>-0.184</td>
<td>0.100</td>
<td>-1.837</td>
<td>0.068</td>
</tr>
<tr>
<td>March × veg</td>
<td>-0.078</td>
<td>0.136</td>
<td>0.574</td>
<td>0.566</td>
</tr>
<tr>
<td>April × veg</td>
<td>0.068</td>
<td>0.123</td>
<td>0.555</td>
<td>0.579</td>
</tr>
<tr>
<td>May × veg</td>
<td>0.004</td>
<td>0.135</td>
<td>0.034</td>
<td>0.972</td>
</tr>
<tr>
<td>June × veg</td>
<td>0.533</td>
<td>0.130</td>
<td>4.090</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>July × veg</td>
<td>0.300</td>
<td>0.299</td>
<td>1.003</td>
<td>0.317</td>
</tr>
</tbody>
</table>

Not document weather conditions. Based on a multiyear study, Wang and Dai (1989) reported that 1-year survival was 15.7% and 2-year survival only 1.5%; they also suggested pika mortality may be highest in summer. In contrast, Smith and Wang (1991) reported very little mortality during summer, but high overwinter mortality. Dobson et al. (1998), however, reported a considerably higher annual survival of 23.5% (adults and juveniles combined) in Guinan, County, Qinghai Province. Spring and early summer 2009 in our study area were characterized by drier and warmer conditions than long-term averages. Local pastoralists reported that drought during April was generally associated with poor forage conditions during the remainder of the growing season; they lost many more yaks to weather than was usual. We found little evidence that survival differed among sexes.

We found substantial support for the hypothesis that apparent survival of adult pikas was inversely related to percent vegetation cover. Particularly during winter, pikas appeared to fare better in areas commonly considered “degraded” because of low vegetation cover; survival rates exceeded those in yak pastures with greater overwinter (perennial) vegetation cover. In contrast, we found that juvenile recruitment (in early summer) was uncorrelated with vegetation cover. Accounting for site-independent temporal variation, winter body condition among adult pikas living in sites with low vegetation cover exceeded that of pikas living in pastures with high vegetation cover. By June, body condition dynamics had reversed, becoming positively associated with percent vegetation cover, whereas survival remained higher on sparsely vegetated areas. Taken together, these findings suggest that high vegetation cover may have interfered with the pikas’ ability to evade predators, thus reducing survival. In winter, additional vegetation evidently provided no advantage to pikas; with fresh growth in spring, pikas gained relatively more body mass where vegetation was more abundant, but vital rates were not enhanced by the addition of vegetation.

These results differ partially from those of Pech et al. (2007), who documented density-dependent growth, but no relationships between either standing vegetation biomass or the availability of burrows and these rates of increase. Unlike our study, Pech et al. (2007) did not measure individual survival, basing their estimates of $\lambda$ on repeated yearly counts. Pech et al. (2007) focused on recovery from artificially low densities caused by control programs; our
study took place during a naturally poor year for survival. Thus, our finding of an apparent inverse density effect in survival may be anomalous, or may simply reflect the confounding of percent vegetation cover with our index of late-winter pika density ($r = -0.41$; Table 1). Alternatively, faced with challenging weather conditions, in which most animals succumb in any case, we speculate that advantages conferred by being able to huddle together underground (Smith and Wang 1991) may overcome any reduction in body condition related to higher pika density. The fact that the body condition of pikas in higher density capture sites exceeded those in lower density areas suggests that density did not limit either forage or body condition. We also speculate that a higher density of pikas allowed for a higher degree of group-level vigilance and warning of predators, although if so, it failed to prevent considerable mortality from occurring regardless of vegetation cover.

We found some weak evidence that sheltered sites were more dangerous for pikas, which is consistent with a predation-mediated hypothesis. Most avian predators are provided an advantage by topography, which allows them elevated perches to observe pika activity, and also allows them to more easily gain flight. Similarly, Bian et al. (1999) speculated that lower pika density in fenced compared with unfenced areas resulted from advantages to avian predators provided by these artificial perch sites. The primary ground predator of plateau pikas, the Tibetan fox, also tends to favor foraging in areas with topographic complexity; earlier studies (Liu et al. 2007) found that Tibetan foxes tended to avoid open areas, presumably to reduce their own exposure to avian predation.

Our findings support Delibes-Mateos et al. (2011) in concluding that the habitat dynamics of plateau pikas are similar to those of North American prairie dogs (Cynomys spp.) in response to livestock grazing. As earlier suggested by Knowles (1986) for prairie dogs, pikas evidently are more successful in sparsely vegetated areas than in fenced compared with unfenced areas resulted from advantages to avian predators provided by these artificial perch sites. Our demographic data provide a mechanistic explanation for these observed differences in densities (albeit with vegetation cover measured instead of vegetation height). Because livestock husbandry has such a long history and is so ubiquitous on the Qinghai-Tibet Plateau, we can only speculate about the vital rates of plateau pikas prior to the domestication of wild yaks (B. grunniens mutus) and introduction of domestic sheep and goats. However, we would hypothesize that, in a similar way that prairie dog dynamics responded to the appearance and departure of large herds of American bison (Bison bison), plateau pikas evolved to take advantage of vegetative conditions occasionally produced by large herds of wild yaks. We therefore conclude that where reducing pika density is a justifiable management goal, restoring vegetation is likely to be a more effective approach than direct, lethal control (Pech et al. 2007).

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**Literature Cited**


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