Foraging behaviour at multiple temporal scales in a wild alpine equid

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Abstract Forage abundance, forage quality, and social factors are key elements of the foraging ecology of wild herbivores. For non-ruminant equids, forage-limited environments are likely to impose severe constraints on their foraging behaviour. We used a multi-scale approach to study foraging behaviour in kiang (Equus kiang), a wild equid inhabiting the high-altitude rangelands of the Tibetan Plateau. Using behavioural observations and vegetation sampling, we first assessed how patterns of plant abundance and quality affected (i) the instantaneous forage intake rate (fine scale) and (ii) the proportion of time spent foraging (coarse scale) across seasons. We also tested whether foraging behaviour differed among group types, between sex in adults, and between females of different reproductive status. At a fine scale, intake rate increased linearly with bite size and increased following a type II curvilinear function with biomass on feeding sites. Forage intake rate also increased linearly with plant quality. Male and female kiangs had similar intake rates. Likewise, gravid and lactating females had similar intake rates as barren and non-lactating females. At a coarse scale, kiangs spent longer time feeding in mesic than in xeric habitats, and spent more time feeding in early summer and fall than in late summer. Groups of adults with foals spent less time feeding than male groups and groups of adults without foals. Our findings suggest that kiangs use flexible foraging behaviours in relation to seasonal variations of vegetation quality and abundance, a likely outcome of the extreme seasonal conditions encountered on the Tibetan Plateau.

Keywords Foraging · Scale · Equids · Arid environment · Equus kiang

Introduction

Studying the factors driving foraging behaviour in grazing herbivores is not trivial, as it may provide valuable insights about mechanisms determining resource selection, and thus further our understanding of plant-herbivore relationships (Spalinger and Hobbs 1992; Bailey et al. 1996; Wilmshurst et al. 2000). In grassland ecosystems, phenological stages of plant maturation are known to influence the abundance and nutritional quality of vegetation patches, which in turn affect the foraging behaviour of grazing herbivores (McNaughton 1985; Fryxell 1991; Spalinger and Hobbs 1992; Wilmshurst et al. 2000). The effect of plant abundance and quality on forage intake depends extensively upon the digestive efficiency of herbivores (reviewed in Van Soest 1996), which mainly depends on their body size and digestive anatomy (Jarman 1974; Janis 1976; Demment and Van Soest 1985). In addition to food resources, social and demographic-related factors such as group size (Jarman 1974; Giraldeau and Caraco 2000), age-sex classes (Côté et al. 1997; Ruckstuhl 1998; Pérez-Barbería et al. 2008), and reproductive status of females (Hamel and Côté 2008) are known to influence foraging behaviour in ungulates.
In grazing herbivores, bite size is generally positively related to plant biomass on food patches (Illius 2006). As bite size increases so does the time needed to handle bites (i.e., cropping and chewing; Spalinger and Hobbs 1992). Biting rate is thus typically negatively related to bite size, which often leads to a type-II functional response (Spalinger and Hobbs 1992; Hobbs et al. 2003). Moreover, because plant digestibility generally declines with plant abundance in grasslands, plants on high-biomass swards allow a fast dry matter intake but take longer to digest than plants on low-biomass sward (Van Soest 1994; Laca et al. 2001). Grazing ruminants constrained by their digestive capacity thus face trade-offs between short- and long-term nutrient intake (Wilmshurst et al. 2000; Fortin et al. 2002). Alternatively, non-ruminant equids are little constrained by forage retention time in the digestive tract and can possibly feed for long periods on tall swards, potentially maximizing nutrient intake at both long and short temporal scales (Janis 1976; Duncan et al. 1990; Fortin et al. 2002). Burchell’s zebra (*Equus burchelli*), an equid adapted to temperate environments, typically feed for longer periods and have higher forage intake rate than sympatric ruminants (Okello et al. 2002; Twine 2002). On the other hand, arid environments with limited forage like deserts or mountains may impose severe constraints on the foraging behaviour of wild equids, restricting their capacity to achieve a high dry matter intake (Rubenstein 1989). Previous studies suggested that equids adapted for arid environments make trade-offs between the nutritional quality of plants and their abundance when selecting food resources (Rubenstein 1989; Kaczensky et al. 2008; St-Louis 2010), which may impose trade-offs among temporal scales of foraging behaviour as well. How the scarcity and fluctuating quality of the vegetation in forage-limited ecosystems affect foraging behaviour and functional response in wild equids, however, has rarely been addressed.

Equids have also evolved complex social systems, where species in mesic environments form stable harem groups whereas species in arid environments form only temporary associations (Klingel 1977; Rubenstein 1986; Sundaresan et al. 2007). Males living in these “fission–fusion” society are typically territorial and associate only temporary with female groups. Neuhaus and Ruckstuhl (2002) observed that male and female zebras living in stable harem groups had similar activity budget and foraging behaviour (but see Rubenstein 1986, 1994). In arid environments, however, the scarcity of the food resource may exacerbate differences in energetic requirements between males and females, especially lactating ones, thereby causing differences in their activity budgets and foraging behaviour (Rubenstein 1989, 1994).

In this study, we investigated factors influencing foraging behaviour in an arid-adapted equid, the kiang (*Equus kiang*). The kiang inhabits the high altitude steppes of the Tibetan Plateau, a highly seasonal environment with harsh climatic conditions and scarce vegetation (Schaller 1998). Predation risks are perceived low for kiangs (St-Louis and Côté 2009). There are indications that kiangs live in a fission–fusion social system (Denzau and Denzau 1999; St-Louis and Côté 2009) and that they select resources in relation to both forage abundance and quality (St-Louis 2010). It is not known, however, how resource selection patterns are related to foraging behaviour, which may provide important cues about the constraints faced by this wild equid adapted to extreme environmental conditions.

Our main objectives were twofold: (1) to assess the effects of vegetation abundance and quality on foraging behaviour in kiangs, and (2) to determine if foraging behaviour differs among groups of different composition in terms of age-sex classes, between males and females, and between reproductive (gravid or lactating) and non-reproductive females. We first evaluated how vegetation varied in terms of abundance and quality across habitat types and throughout the summer and the fall, and then assessed how vegetation and social factors influence the foraging behaviour of kiangs at two temporal scales: (i) the instantaneous intake rate of focal individuals (fine scale) and (ii) the percentage of time spent feeding by kiang groups during activity budgets (coarse scale). Doing so, we also considered the potential effect of the time of the day, since foraging behaviour may also be influenced by daily patterns of temperature or daily movements (Berger 1986, Duncan 1992). We hypothesized that (a) bite size should increase with biomass on feeding site; (b) intake rate should increase with bite size in a curvilinear fashion following a type II functional response, given that biting rate should increase with bite size; (c) intake rate should relate positively to vegetation biomass on food patch following a type II functional response, given that biting rate should also decline with biomass; (d) intake rate should be higher on green vegetation than on dry vegetation, since green leaves are easier to handle and chew; (e) kiangs should spend more time feeding in morning and evening than during the middle of the day, thereby avoiding being active during the warmest period of the day; (f) the proportion of time spent foraging should be negatively related to plant quality; (i) females and males should have comparable intake rates and time spent feeding because of their similar body size; (j) similarly, gravid/lactating females and barren/non-lactating females should have similar intake rates, but (k) females in groups with
foals should spend more time foraging than females in groups without foals.

Methods

Study area

We conducted this study in fall 2003 (29-Aug to 21-Nov), summer 2004 (17-Jun to 25-Aug) and summer 2005 (26-Jun to 20-Aug) in a 390-km² area located in the Tso Kar basin, Eastern Ladakh, India (32°15’N, 78°00’E). This area is part of the extensive Tibetan Plateau, and represents the westernmost and driest part of the kiang’s distribution range, with mean annual precipitation <100 mm (Schaller 1998; St-Louis and Côté 2009). The elevation within the Tso Kar basin ranges from 4,550 to 6,000 m, and the climate is that of high altitude/cold desert ecosystems, with annual temperatures ranging from −40°C to 30°C. The vegetation is typical of alpine and desert steppes (Schaller 1998), mainly composed of grasses (Poaceae), sedges (Cyperaceae), and short dicotyledonous forbs and shrubs (Mani 1978; Rawat and Adhikari 2005). Most common plant genera are Stipa, Carex, Leymus, Eurotia, Artemisia, Oxytropis, Elymus, Kobresia, Alyssum, Caragana, and Potentilla (Rawat and Adhikari 2005). We identified three main habitat types at Tso Kar: (a) meadows, a mesic habitat located below 4,600 m with vegetation cover ≥20%; (b) plains, a xeric habitat located <4,600 m characterized by vegetation cover <20%, slope ≤5°; and (c) hills, a xeric habitat located at ≥4,600 m with vegetation cover <20% and slope >5° (St-Louis 2010; ESM 1). Tibetan wolves (Canis lupus chanco) occasionally prey on kiangs, but they occur in small numbers in the Tso Kar basin (Pfister 2004). An estimated 250 kiangs inhabit the area on a yearly basis (Fox et al. 1991).

Observations

Focal sampling

Focal sampling (Altmann 1974) was performed on foraging individuals to monitor fine-scale foraging behaviour. Focal individuals were chosen randomly among adults in groups located <500 m from the observers, and we ensured that data were balanced across all habitat types for both sexes. Kiangs were not marked, but we could reliably identify individuals within groups during an observation session with the help of natural marks and their position within the groups, allowing us not to observe the same individuals twice during a single day. We noted the sex of individuals and the reproductive status of females. In summer, gravid females are easily recognizable from barren ones because they have a rounder and larger belly. Foals were seen suckling as late as the end of August. From mid-July until late-August, a female kiang accompanied by a foal was therefore noted as lactating. For each focal animal, we recorded during 5-min periods the number of bites and steps taken while feeding on a hand-held tape recorder. A step was defined as a forward movement of any of the front legs. Interruptions in cropping sequences were noted when kiangs raised their head above shoulder level, either for vigilance, walking, or miscellaneous behaviour (e.g., grooming). The measurement of biting rates during continuous cropping sequences (expressed in number of bites−min⁻¹) led to the calculation of the forage intake rate (see details below), which in our study corresponds to the fine temporal scale.

Scan sampling

To monitor the proportion of time spent feeding by kiangs during daylight, we conducted repeated scan sampling of kiang groups (Altmann 1974), performed every 15 min using 15–45× spotting scopes. Kiang observations spanned the entire daylight period (0600–2000 h). Each observation period lasted between 2 and 8 h. Kiang groups were divided in 3 categories: (1) single male, (2) adults without foals, and (3) adults with foals. Because it was often not possible to discriminate males, females and yearlings during scans, the second type encompassed bachelor groups, groups of females and yearlings, and mixed groups with typically 1 male and several females and yearlings. Kiang behaviour was divided into five categories: (1) feeding, (2) standing, (3) lying, (4) walking, and (5) other (i.e. social interaction, running). Scan observations yielded the proportion of time a group spent feeding, which corresponds to the coarse temporal scale. We followed 173 groups between 1 and 8 h, for a total of 557 h of observation.

Habitat and feeding site surveys

The habitat type was noted visually for every group followed during scan sampling. For focal individuals, we surveyed feeding sites within habitat types to assess whether foraging behaviour was influenced by vegetation attributes. Two observers were necessary to locate a feeding site following a focal observation. One observer moved to the site where the focal kiang had been seen feeding and marked the centre of the site, guided through radio contact by the other observer with a spotting scope. The presence of grazing marks was required to confirm the location of the feeding site. Feeding site attributes were estimated by laying six 1-m² plots, randomly placed within a 10-m radius circle centered on the feeding location (Schaefer and Messier 1995). In every plot, plant cover and
percentage of green material were estimated visually using 10% classes in four vegetation groups: grasses (mainly family Poaceae), sedges (family Cyperaceae), forbs (all herbaceous dicots), and shrubs (woody stemmed species). Mean plant height was calculated by measuring five randomly selected plants of each group to the nearest cm using a ruler. To convert plant cover and height into biomass, we clipped individual plants 1 cm above the ground in one randomly chosen plot (out of 6) on each feeding site. Plant samples were dried in the field in paper bags, and then oven dried for 48 h at 60°C, and weighed using a 0.1 g precision scale. We used linear regressions to calculate regression coefficients for plant cover and height, and then estimated biomass for each plant category in all plots (see Hamel and Côté 2007 for details). The feeding site sampling design also allowed us to estimate the mean percentage of green vegetation in three habitat types for each field season. For that purpose, we used only the data collected on random feeding sites. Percentage of plant cover and height were converted into biomass using a multiple regression analysis (ESM 2).

Estimation of bite size

We estimated bite size by first measuring with a ruler the grazing depth of the eight nearest grazed plants from the centre of the feeding site, and calculated the mean grazing depth. Within a 1-m radius circle, we then randomly located three small square quadrats of 6 × 6 cm, corresponding to the approximate width of a kiang’s mouth (Janis and Ehrhardt 1988; St-Louis and Côté 2009), and clipped plants to the average grazing depth. Plant samples were dried in the field in paper bags, and then oven dried for 48 h at 60°C, and weighed using a 0.001 g precision scale.

Analyses

Fine temporal scale

Because sward biomass is known to exert a major influence on bite size in grazing ungulates (Laca et al. 1992), we modelled the relationship between our bite size sample (N = 21) and the biomass on corresponding feeding sites to extrapolate bite size measurements to all feeding sites (N = 52). We calculated the forage intake rate achieved on each feeding site as \( I = S \times BR \), where \( I \) is the intake rate expressed in grams per minute feeding during cropping sequences, \( S \) is the estimated bite size (in grams), and \( BR \) is the biting rate during cropping sequences. We then assessed the influence of group size on intake rate using a general linear model (GLM). Because group size had no statistical influence on this variable (\( F_{1,43} = 2.69, P = 0.20, N = 45 \)), we removed it from subsequent analyses.

Secondly, we assessed the influence of bite size and forage biomass (patch) on forage intake rate (g−min) and biting rates (bite−min) using linear regressions and non-linear Michaelis–Menten functions. We assumed that bites were always visible to kiangs and that the time to reach a new bite was not higher than the time required to crop and swallow a bite, as commonly found for grazing ungulates. Therefore, we used models under the process 3 of Spalin-ger and Hobbs (1992). These models enabled us to assess whether forage intake rate was regulated by foraging mechanisms operating at the bite or at the patch scale. We then analysed the influence of the greenness of plant leaves on intake rate using a GLM.

Coarse temporal scale

The percentage of time kiang groups spent feeding was calculated as the proportion of scans where more than 50% of the individuals were seen feeding to the total number of scans done on a specific group. To take into account potential daily patterns in activity budgets, we first divided our observations in three periods: from 0600 to 1000 (morning), 1000 to 1500 (mid-day), and 1500 to 2000 (evening). Since there was no difference in the time spent feeding between morning and mid-day (\( t_{1,163} = 0.40, P = 0.69, N = 166 \)) we pooled these two classes, and performed our analyses using two daily periods: from 0600 to 1500 (daytime) and from 1500 to 2000 (evening). To take into account the potential influence of group size on foraging behaviour, we analysed the influence of group size on time spent feeding using a GLM, which was not significant (\( F_{1,164} = 1.39, P = 0.24, N = 166 \)). Therefore, we did not include this factor in the analyses. We used a logistic regression to assess the influence of habitat type, date (i.e. number of days since 1 June), period of the day and group type on the proportion of scans where kiangs were feeding. We tested a priori the effect of year on time spent foraging for summers 2004 and 2005. Because there was no difference between the two summer seasons (\( t_{1,163} = -0.88, P = 0.38, N = 166 \)), we pooled the data for these 2 years. Moreover, because the dates of observations in fall 2003 did not overlap with the dates of observations during summers 2004–2005, the factor date was used as a surrogate for the season, and the factor year was removed from the analyses. We then built candidate models as to include combinations of all covariates and interactions between covariates that were biologically relevant to our initial hypotheses. Models were ranked based on the Akaike Information Criterion, corrected for small sample size (\( AIC_c \); Burnham and Anderson 2002). For each candidate model, we calculated the delta \( AIC_c \) (\( \Delta_i \)), the Akaike weight (\( \omega_i \)), and the evidence ratio, expressed as the ratio between the Akaike weight of the best model and the Akaike weight of model i.
This ratio indicates how the first model (i.e., with the lowest AICc value) is likely to be the best model compared to model i. We then calculated the percentage of variance explained by the first model using $R^2 = 1 - SSR/SSTO$, where $SSR = \Sigma((Y_{\text{observed}} - Y_{\text{predicted}})^2)$, and $SSTO = \Sigma((Y_{\text{observed}} - \bar{Y})^2)$ (Xu 2003).

Statistical linear models were implemented using SAS 9.1 (SAS Institute Inc. 2003), while non-linear models of functional response were analysed using SigmaPlot 8.0 (SPSS Inc. 2002). Means are presented ±SE. Significance level was set at 0.05 for all statistical analyses.

**Results**

**Vegetation parameters on feeding sites**

Feeding sites in meadows were greener than those in plains ($t_{2,45} = 2.03, P = 0.048, N = 52$) and hills ($t_{2,45} = 5.36, P < 0.001, N = 52$) during fall, but there was no difference in vegetation greenness on feeding sites among the three habitat types during summer. Meadows had higher forage biomass than plains ($t_{2,47} = 6.33, P < 0.001, N = 52$) and hills ($t_{2,47} = 8.74, P < 0.001, N = 52$) during both seasons. Vegetation greenness and date were negatively related, as leaves turned brown during the fall season, i.e., after mid-September ($R^2 = 0.76, F_{1,50} = 163.55, P < 0.001, N = 52; \text{Fig. 1}$).

**Fine temporal scale**

Bite size increased with biomass in a logarithmic fashion, following the relationship: $\ln[\text{bite size}] = 4.03 + 0.254 \times \ln[\text{biomass}]$ ($R^2 = 0.29, P = 0.012, N = 21$). At the bite scale, intake rate increased linearly with bite size under the range observed, since linear regressions and non-linear Michaelis–Menten functions fitted the data very similarly ($R^2 = 0.48, F_{1,50} = 45.98, P < 0.001, N = 52$; Fig. 2a). There was no relationship between biting rate and bite size, whether fitted by a linear ($R^2 < 0.01, F_{1,50} = 0.01, P = 0.84, N = 52$) or a non-linear function ($R^2 < 0.01, F_{1,50} = 0.20, P = 0.66, N = 52$). At the patch scale, forage intake rate increased asymptotically with forage biomass, showing a type II functional response for both feeding sites with mainly brown and green leaves (vegetation <50% green: $R^2 = 0.75, F_{1,11} = 33.13, P < 0.001, N = 14$; vegetation >50% green: $R^2 = 0.51, F_{1,36} = 37.74, P < 0.001, N = 38$; Fig. 2b). The model showed that forage intake rate started to level at a biomass of around 20 g m$^{-2}$, and that the maximum intake rate was 6.22 g mm$^{-1}$ (Fig. 2b). There was also no relationship between biting rate and biomass on feeding sites (linear regression: $R^2 < 0.01, F_{1,50} = 0.01, P = 0.90, N = 52$; non-linear Michaelis function: $R^2 = 0.02, F_{1,50} = 2.20, P = 0.14, N = 52$). Forage intake rate increased linearly with plant greenness ($R^2 = 0.20, F_{1,50} = 14.01, P < 0.001, N = 52$; Fig. 3). Accordingly, intake rate decreased with date, being larger in summer than during the fall ($R^2 = 0.13, F_{1,50} = 7.58, P = 0.008$). Sex of adult kiangs had no influence on intake rate ($F_{1,49} = 1.17, P = 0.28, N = 52$). Lactating and non-lactating females had similar intake rates ($F_{1,13} = 0.24, P = 0.63, N = 15$).

**Coarse temporal scale**

The proportion of time spent feeding during activity budgets was mainly explained by the interaction of habitat type and group type ($\chi^2 = 17.63, df = 4, P = 0.002, N = 173$), the period of the day ($\chi^2 = 36.63, df = 1, P < 0.001, N = 173$) and the date (exponent 2) after 1 June ($\chi^2 = 49.72, df = 1, P < 0.001, N = 173$). This model had an Akaike weight of 0.93 (see ESM 3 for the complete list of candidate models). Kiangs generally spent 1.2 and 1.3 more time feeding in meadows than in plains and hills (Fig. 4). Groups with foals spent generally less time feeding than the other two group types, especially in hills (Fig. 4). The proportion of time spent feeding by kiangs was about 70% in early summer, declined to approximately 30% in late summer, and further increased to about 50% very late in the summer and during autumn (Fig. 5). Kiangs spent 1.5 more time feeding at the end of the afternoon than during daytime (daytime: 39 ± 2%; evening: 58 ± 3%).

**Discussion**

In this paper, we assessed the influence of vegetation and social factors on the foraging behaviour of a wild equid.
adapted to a highly seasonal environment. To our knowledge, this is the first study to investigate foraging behaviour in an arid-adapted equid at several temporal scales simultaneously. As expected for an equid, kiangs achieved a higher forage intake rate on habitats and patches with high plant biomass, but the important role of vegetation quality on fine-scale foraging processes is a novel finding. Here, we discuss how vegetation and social factors influence foraging behaviour in kiangs at both fine and coarse temporal scales, and conclude with implications for equids living in highly seasonal environments.

Fine scale processes

We first hypothesized that intake rate would increase with bite size following a type II functional response. We rather observed that intake rate increased linearly with increasing bite sizes, without showing any deceleration. Large bites
therefore did not take more time to chew than small bites under the range of bite sizes observed (0.07–0.22 g−bite). This does not preclude, however, that an asymptotic relationship between bite size and intake rate exists in kiangs. It is likely that bites taken by kiangs were too small to detect such an asymptotic relationship. For example, Gross et al. (1993) observed that intake rate increased linearly for several large herbivores (including domestic horses) until bite size reached 1.5 g. The low bulk density or height of the grass available to kiangs may thus have physically restricted bite sizes below this minimum value. At the patch scale, our results support the hypothesis that intake rate increases with biomass in a curvilinear fashion following a type II functional response, as observed in several studies on grazing ungulates (Gross et al. 1993; Hobbs et al. 2003; Illius 2006). Our results show that the maximum intake rate is achieved on feeding sites that contains more than 120 g plant per square-m. Short-term intake rate is thus best achieved on feeding sites and habitat types containing more food. However, this maximum point is far from what could theoretically be achieved by a wild equid. Gross et al. (1993) observed that the maximum intake rate by horses was approximately 30 g−min. A likely explanation is that kiangs crop plants only partially in abundant food patches, possibly to maintain a high biting rate, and therefore leading to an asymptotic relationship between bite size and patch biomass. Previous authors have stressed the importance of correctly describing the gain function, i.e. the relationship between bite size and patch biomass as swards are progressively depleted, in order to understand movements between food patches and across landscapes (Stephens and Krebs 1986; Shipley 2007). Asymptotic gain functions are common for grazers feeding on long grass swards, where bite size decreases consistently as patches are depleted (Laca et al. 1994). The decelerating functional response that we observed in kiangs on feeding sites with both dry and green vegetation seems best explained by the log-shaped function between feeding site biomass and bite size rather than by the time constraint to handle large bites.

Forage palatability is known to increase daily voluntary intake in ruminants (Van Soest 1994), and our results indicate that a similar pattern may exist in equids as well, at least in a forage-limited environment. Hence, the strong relationship we found between intake rate and plant greenness is one of the most important findings of our study. As green leaves are easier to handle than dry leaves (Van Soest 1994; Laca et al. 1992; Shipley 2007), plant quality appears to play a significant role in short-term forage intake rate in kiangs, which has rarely been demonstrated in wild equids. Fleurance et al. (2009) found no influence of increasing fibre content on forage intake rate in horses, except for one pony. If resources are abundant, however, high intake rate is possible on fibrous forage, as shown in horses (Edouard et al. 2008). The strong response of forage intake rate to the nutritional quality of plants in kiangs is possibly a mechanism to maximize their short-term nutrient intake in a highly seasonal and forage-limited environment.

Intake rates did not differ between male and female kiangs, a potential outcome of the slight dimorphism between the two sexes (Berger 1986; St-Louis and Côté 2009). Similarly, gravid and lactating females did not perform higher intake rates than barren and non-lactating females. These results thus support our hypothesis that adult kiangs of similar body sizes should have comparable intake rates. If female of different reproductive status have different energetic requirements, as observed in other ungulates (Therrien et al. 2007; Hamel and Côté 2008), our results suggest that such difference has little implication on fine-scale foraging processes in kiangs.

Coarse scale processes

Because instantaneous intake rate is higher in abundant food patches than in patches with scarce plant cover, kiangs should be able to minimize their time spent feeding in habitats with abundant forage (Spalinger and Hobbs 1992; Hobbs et al. 2003). We thus hypothesized that kiangs would need to spend less time feeding in habitats with abundant forage (mesic) than in habitats with sparse forage (xeric). In our study, kiangs spent a higher proportion of their time feeding in mesic habitats with high forage abundance than in xeric habitats with low forage abundance, which contradicts our initial hypothesis. As noted previously, the maximum intake rate achieved by kiangs in our study is much less than the maximum rate achieved in wild equids of comparable size. Since the maximum intake rate occurs on habitats with standing biomass >20 g m−2, kiangs would benefit from eating for extended periods on meadows with abundant forage in order to maximize their daily dry matter intake. Therefore, meadows appear as important feeding habitats for kiangs in the Tso Kar basin.

Our hypothesis that time spent feeding would increase from summer to fall season was partly supported. As leaves become dry in fall, kiangs presumably need to feed for extended periods to compensate for decrease intake rates in order to meet their energetic requirements, as suggested by our results. This suggestion, however, does not explain why time spent feeding was higher early in the summer than later during the season. Increased energetic requirements following harsh winter conditions may prompt kiangs to maximize their forage intake rate at both fine and coarse temporal scales, thereby taking advantage of the vegetation green-up by increasing their instantaneous forage intake rate and daily time spent feeding. In mid-
summer, which coincides with mating and birth seasons, a reduction in feeding time is likely due to an increase in time devoted to activities related to the reproduction period (e.g. chases among males, tending nursery groups, milking foals, increased vigilance of lactating females). Plant digestibility may still be high enough so that kiangs can maintain high short-term nutrient intake while incurring reduced time spent feeding. Similar seasonal patterns were observed in female mountain goats (*Oreamnos americanus*; Hamel and Côté 2008) and Cantabrian chamois (*Rupicapra pyrenaica parva*; Pérez-Barbería and Nores 1996), thereby suggesting a common behavioural pattern among alpine ungulates.

Reproductive female ungulates generally incur higher energetic costs than non-reproductive females, and should thus have higher daily forage intake (Berger 1986; Therrien et al. 2007; Hamel and Côté 2008). The observation that adults in groups with foals spend less time feeding than adults in groups without foals is thus a surprising result, since we expected that lactating females would have to spend more time feeding than non-lactating females (Rubenstein 1994). A possible explanation is that females in groups with foals are more vigilant than females in groups without foals in order to prevent harassment by males and possible infanticide events. As in other equids, infanticide is thought to occur in kiangs (St-Louis and Côté 2009) and harassment of nursery groups has been observed on several occasions in the field. Lactating females in groups tended by a dominant stallion, however, should be able to gain protection from intruding males and thus spend more time feeding in order to meet their increased energetic needs (Rubenstein 1994). Investigating the role of tending stallions on female behaviour in kiangs would be needed to further address this question, which has not been attempted yet.

Implications for equids in highly seasonal environments

Plant phenology and environmental conditions strongly influence the energetic balance and the foraging behaviour of herbivores living in highly seasonal environments (DelGiudice et al. 1990; Albon and Langvatn 1992; Moen et al. 2006; Shrader et al. 2006). In arctic and alpine ecosystems for instance, increasing forage intake following winter is often necessary to regain body condition (Van der Wal et al. 2000; Hamel and Côté 2008), and in tropical grasslands to compensate for a decline in forage quality during the dry season (Shrader et al. 2006). The observation that kiangs closely adjust their foraging behaviour to the seasonal patterns of plant phenology suggests that plant quality is an important driver of their foraging ecology, possibly in response to the extreme nature of their environment. The foraging behaviour of kiangs differs somewhat from patterns typically observed in equids (e.g. Edouard et al. 2008), but is rather similar to ruminant ungulates living in highly seasonal environments such as arctic and alpine ecosystems (e.g. Côté et al. 1997; Van der Wal et al. 2000; Hamel and Côté 2008). In a forage-limited environment, therefore, wild equids selecting food resources on the basis of both forage abundance and nutritional quality potentially increase their nutrient intake at several temporal scales.

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