Social Class and Group Size as Predictors of Behavior in Male *Equus kiang*

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Abstract - Ethograms provide a systematic approach to identify and quantify the repertoire of behaviors of an organism. This information may assist animal welfare in zoos, increase awareness of conservation needs, and help curb high-risk behaviors during human-wildlife conflict. Our primary objective was to utilize an equid ethogram to produce activity budgets for *Equus kiang* males, a social ungulate that is among the least-studied mammals worldwide, and unknown to the ethological literature. We recently reported the existence of three social classes of this species; Territorial males, Bachelor males and 'Transient' males. Therefore, our secondary objective was to compare activity budgets in each of these three groups. We found that kiang spent >70% of their time performing six behaviors: vigilance (34%), locomotion (24.2%), resting (14.2%), mixed foraging (12.5%), browsing (5.1%), and antagonism (1.1%). Over 2% of the total behavioral investment was spent on olfactory investigations (genital sniffing, sniffing proximity and flehmen). Eleven of the eighteen behaviors differed by class. Habitat selection differed strongly by each group, with Territorial males favoring mesic sites with greater vegetation abundance. Vigilance also differed according to habitat selection, but not group size. Animals in the xeric, least vegetation-rich area were far less vigilant than animals at more attractive sites. We found that the full repertoire of behaviors, and relative investments in each, differ according to social class. These findings are a reminder that researchers should make every effort to disambiguate social class among ungulates– and other taxa where behaviors are class-dependent.

Ethograms offer a systematic means to identify the repertoire of behaviors of a particular species or taxon, and the variations of behavior within a species by age and sex. They are especially important to the empirical description of a particular organism (usually a species) because they provide a definition and catalog of all behaviors exhibited, and from which the relative time and energy invested into each behavior can be calculated. The terminologies and discrete events that comprise each behavior are particularly important to neuroethology and comparative psychology because they provide a mechanism to characterize and assess the causative (e.g., hormones, genes, nerve impulses) and ontogenetic mechanisms that underlie species-specific behaviors (Bateson & Laland, 2013; Tinbergen, 1963). Knowledge of this information – the typical or 'wild-type behavior' – may then be used to assist animal husbandry for a wide variety of taxa in zoos and sanctuaries (de Waal, 1988; Horback, Miller, Andrews, Kuczaj, & Anderson, 2012; Watters, Margulis, & Atsalis, 2009). Ethograms have been identified as a tool for conservation needs for taxa as diverse as canids (Boitani, Asa, & Moehrenschlager, 2004) and primates (Nekaris & Jayewardene, 2003), and may assist wildlife-management through the curbing of problematic human-wildlife conflict (Poiani, Coulson, Salamon, Holland, & Nave, 2002; Sayre & Clark, 2001). Perhaps most importantly, they can be used as a template to document the impacts of anthropogenic activities on a species by examining human-influenced changes in behaviors (Jordan & Burghardt, 1986).

Whereas ethograms have been constructed for organisms as diverse as wasps (Mandujano, Flores-Prado, & Chiappa, 2016) and primates (Stevenson & Poole, 1976), some taxa remain surprisingly bereft of behavioral data. Among these organisms, little to no data is available to quantify activity budgets or evaluate how well these species conform to pre-existing published ethograms. In particular, little is known about some herbivores in remote areas such as the western Himalayas (Sharma, Clevers, Graaf, & Chapagain, 2004), yet these animals may be particularly vulnerable to the impacts of climate change (Luo et al., 2015), and may subsequently encroach on areas of remote pastoralism. Ironically, this human wildlife conflict involves a species that is virtually unknown to the ethological literature (Bhatnagar, Wangchuck, Prins, Van Wieren, & Mishra, 2006).

Model Species

Tibetan wild asses, *Equus kiang*, are social, free ranging ungulates that range across the hard-to-access, cold, windswept deserts of the Tibetan Plateau. Due to their inaccessibility, they have been recognized as one of the least-studied mammals in the world (Sharma et al., 2004). They are found in harsh, remote, high-altitude areas where human populations have not been well established (Fox & Bårdsen, 2005). Therefore, we have limited knowledge about this species, and no known behavioral assays or activity budgets have been produced other than reports of foraging behavior as it varies with vegetation quality and seasonal abundance (St-Louis & Côté, 2012) and an examination of the frequency of social behaviors in males from three social classes, territorial males, bachelors and 'transients' (Kannan et al., 2016). Sharma et al.(2004) has described kiang habitat selection in Upper Nepal, while resource selection and area-use has been quantitated in the presence and absence of livestock by Hussain, Qureshi, and Rawat (2010). Lastly, although little has been formally documented about their behavior, there is widespread agreement that foraging competition exists between kiang, other wild ungulates and livestock (Bhatnagar et al., 2006). Livestock are the mainstay of nomadic-pastoral economies, whereas other ungulates such as wild sheep and goats form the majority of diets of local predators such as the snow leopard (*Panthera uncia*, Bhatnagar et al., 2006), and have been studied more thoroughly than the kiang. Thus, it is essential to systematically document kiang behaviors. Because so little is known about kiang behavior, this information should help inform the management and conservation for this species. For instance, it is especially important to document how vigilant these animals are, the amount of time and effort spent foraging, how they are influenced by group size, and whether their behavioral repertoire is unique among equids.

Most of what we suspect about the behavior of kiang is based on behaviors of other equids. For instance, male and female ungulates often perform disparate behaviors. These may include obvious gender-specific behaviors such as flehmen inspection, chasing intruders (McDonnell & Haviland, 1995) or differing levels of vigilance (Burger & Gochfeld, 1994; McDonnell & Haviland, 1995). Different classes within genders may also differ dramatically in their respective investment into particular behaviors. While constructing our first activity budgets, we learned that there were three social classes of male (Kannan et al., 2016): social bachelors, solitary territorial males, and 'sneaky' transient males. The latter class represented either an alternative reproductive strategy or a transitional state between bachelors who were not yet ready to challenge a rival. Because the relative investment into each behavior by social class was so different, we elected to provide activity budgets for all three social classes for comparison.

Objectives

Our objectives were firstly, to produce the first activity budgets for *Equus kiang* based on 18 prominent behaviors from a well-known ethogram of equid male behaviors (McDonnell & Haviland, 1995) and three additional feeding behaviors (Parsons, Lamont, Davies, & Kovacs, 2006). Our secondary aim was to determine whether, using an ethogram, we could predict differences in the behavior of this species based on social class, and lastly to consider the impacts of group size for influencing other behaviors, most prominently vigilance.

Methods

Subjects

We collected 335, 20-min, continuous focal observations (Altmann, 1974). Males were selected as our focal sex because they were easy to identify based on external genitalia, scarring, and frayed, shortened, and occasionally missing tail-tufts. Males were selected at random. Eleven males were pre-identified as controls to provide an indication of how often we were repeating our viewing of the same animal. Animals sometimes aggregated in groups of 12 to 50 individuals. Thus, in order to record the most variation in behavior between groups, we were careful to leave the area after any two individuals were sampled from the same aggregation.

Study Site

All observations took place within the 30 km² Tso Kar basin (33.21° N; 78.2° E, 4,511 m) of the Changthang Wildlife Sanctuary of the Tibetan plateau in Ladakh, India. The high Changthang Plateau is a wind-swept cold desert with barren hills. The soil is sandy or consists of sandy loam; borax deposits and dried marshy areas are a common feature along the lakeshores. The strong and unpredictable winds make the area inhospitable; with aridity being the most distinguishable characteristic (Chandan, Chatterjee, & Gautam, 2007). Summer temperatures range from 0 °C to 30 °C and winter temperatures range between −40 °C to −10 °C (Chandan et al., 2007).

There are two primary habitat types of varying interests to wildlife, alpine steppe and marsh meadow, dominate the Tsokar basin. The vegetation on the marsh meadows is much greener than that of the alpine steppes in summer, and thus, marsh meadows are vital for *Equus kiang* (Bhatnagar et al., 2006). These areas are closer to two lakes (one brackish, one fresh-water) found in the center of the basin, and are dominated by riparian vegetation, including bog sedges, *Kobresia pygmea, K. royleana, K.schoenoides,* sedges including *Carex sagaensis, C. melanantha* and cinquefoil *Potentilla anserina* (Uniyal, Awasthi, & Rawat, 2005). The alpine steppes are farther from the lakes and are characterized by short bushes such as *Caregana versicolor*, and thornless *Eurotia ceratoides* and grasses such as *Stipa* spp. (Uniyal et al., 2005). The Tso Kar Basin was divided into quadrants based on vegetation and proximity to the two lakes (Table 1).

Table 1

Contrasting Four Sites Where Behaviors Were Observed among Three Social Classes of Equus kiang.

Area	Coordinates	Vegetation	Mean group size
Pambuk	33.15° N; 78.3° E, 4399 m	~ 60% is Alpine steppe, with stands of *Stipa* interspersed with thorny bush *Caregana*. Remaining 40% consists of riparian sedge meadows, especially on the shores of Stasaphuk Tso. Vegetation is about 0.3 – 0.6 m high.	14.9 ± 3.2[b]
Tasaphuk	33.14° N; 78.1° E, 4475 m	~ 90% consists of riparian sedge meadows with *Kobresia* and *Carex*. These sedges can be up to knee high in some places. Remaining 10% are *Stipa* stands near the hills at edges of the marsh meadows. *Stipa* are around 7 – 14 cm high.	35.8 ± 7.6[a]
Panganau	33.22° N; 78.7° E, 4423 m	~ 60% is Alpine steppe, consisting of stands of thorny bushes *Caregana* and _Eurotia_, with stands of *Stipa* interspersed (but less abundant than in Pambuk). ~ 25% consists of short, cushion-like mesic vegetation that line the shores of salt-water lake Tso Kar (unlike the knee-high sedge meadows of freshwater lake Startsapuk Tso). Remaining 15% consists of riparian sedge meadows, with *Kobresia* and *Carex*.	21.6 ± 2.4[b]
Thukje	33.21° N; 78.1° E, 4599 m	~ 80 % consists of stands of thorny *Carex* interspersed with *Stipa*, which shelters thorny bushes like *Eurotia*. Remaining 20% consists of cushion-like mesic vegetation that lines the shores of Tso Kar.	11.4 ± 3.8[b]

Note. Mean group size was significantly different across areas ($F(3,325)$ = 4.43 $p < 0.005$). Superscript denotes difference according to Tukey's post-hoc.

Procedure

Observations were made in the high altitude Trans-Himalayas in Ladakh, India between July and Sept. 2014. We conducted observations from dawn to dusk using binoculars with a Cannon 70D SLR Camera and a Sigma 150–500mm telephoto lens that recorded HD video with 21.2 Mp resolution at a distance of 400 – 500 m (Kannan et al., 2016). This observer distance was selected because it is twice the distance (200 m) required to avoid observer presence influencing the behavior of focal animals. One observer recorded behaviors. Data collection did not involve restricted habitat or interference with other species, and was in compliance with all international guidelines for ethical conduct in the care and use of nonhuman animals in research. We used Permit CCFWL/2014/290-G1 by the Jammu and Kashmir Wildlife Protection Department to undertake research in the protected region.

Behaviors, States and Events

Behaviors can be measured as instantaneous events by frequency (number of occurrences) or as states (time spent performing behavior, Altmann, 1974), or contextualizing events within states, when several events are clustered within a state (Tardin, Pinto, Alves, & Simão, 2014). Because there are no known ethograms, activity budgets, or behavioral assays for this species, and because we had high definition videos that could be repeatedly rescored, we elected to record states by four measures: the number of times each behavior was recorded (discrete events), total duration of all discrete events, the mean duration of each behavior, and the percentage of the behavior across the focal period. We selected 18 prominent behaviors from the equid literature (McDonnell & Haviland, 1995; see Table 2 for descriptions; Figure 1 for illustrations) along with three foraging behaviors (Parsons et al., 2006). Animals spend much of their time procuring resources, and how they go about selecting foods is seminal to understanding the species. Among equids, such as horses, feeding behavior should occupy half of the time budget (McDonnell & Haviland, 1995). Both patch-use and habitat-type selected relate to how a species is shaped by evolution (Kotler, Morris, & Brown, 2016), and is of relevance to conservation, wildlife management and potential for human-wildlife conflict. Therefore, we sub-divided foraging into browsing, which involves mobility and active searching for food, grazing which involves limited mobility and a continual depletion of available forage, and mixed grazing (punctuated by both types foraging), and noted the habitat-type of each selected patch.

Resting is typically the second largest expenditure of time (25 – 35%) for equids (Ransom & Cade, 2009), followed by locomotion to and from resources. This is particularly important in arid environments where resources are spread widely. Vigilance is often inversely associated with other behaviors, such as rest, foraging or social behaviors (Stankowich & Blumstein, 2005). This costly behavior may be affected by the presence of a perceived threat, and increased displacement or flight may expend important energy reserves (Cassirer, Freddy, & Ables, 1992; Rumble, Benkobi, & Gamo, 2005; Ydenberg & Dill, 1986). It should be noted that *Equus kiang* appears to be especially sensitive to human presence (Fox & Bårdsen, 2005; Hussain et al., 2010), and flee if one tries to approach them closer than 200 m.

As technology improves (Parsons et al., 2017), olfaction is increasingly recognized as important for influencing the social behavior and welfare of equids (Krueger & Flauger, 2011). Therefore, we were interested in sub-dividing this group of behaviors into sexual, territorial, and general inspection behaviors: flehmen, sniffing proximity, and genital sniffing. Stallions defecate into fecal middens (sometimes called stud piles, Ransom & Cade, 2009). The scent plumes generated from these piles facilitate a breadth of communication, including territoriality, social rank, and diet (Krueger & Flauger, 2011). Thus, we noted the use of defecating and urinating onto middens (marking by dung, or marking by urine) as well as sniffing proximity. Finally, we looked at appeasement behaviors such as allogrooming (including face-licking and mutual grooming, and retreats), antagonism, dueling, chasing males, herding females, retreating from males (being chased), and also maintenance behaviors such as dust bathing to remove ectoparasites.

Table 2

Descriptions of Common Male Equid Behaviors Observed in the Present Study.

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Vigilance	Rigid stance with neck elevated and ears held stiffly upright (Figure 1A), often indicates hyper alert state.
Locomotion	Acts of tetrapodal movement that may include walking (Figure 1B), trotting or running, when otherwise not chasing, foraging or engaging in ancillary behaviors. An aggregate score.
Rest	Sitting, standing or lying down without performing in absence of other behaviors.
Sniffing proximity	The act of sniffing scent plumes from the air. May include sniffing of feces (Figure 1C), forage matter, or the general vicinity.
Mixed foraging	A punctuated type of foraging or food seeking that includes bouts of stop and start across multiple food patches. One of the important criteria for estimating the impact of herbivory on plant species.
Browsing	A type of selective foraging that includes short bouts (< 1 min) and highly specified food selection at multiple plant stands. A nutrient-enrichment strategy.
Grazing	A type of foraging that includes continuous eating motion within the same food patch. A non-selective, but energy efficient, means of foraging, that may not be diverse in nutrient acquisition.
Chasing males	One male chasing one or more males from the vicinity (Figure 1D).
Herding	Focal stallion chases a mare or herd of mare at a trot with head lowered in direction of mares (Figure 1E), ears pinned back, lips curled, and usually accompanied by braying and whinnying vocalizations.
Appeasement	An aggregate behavior that may include mutual grooming (e.g., focal animal standing beside another individual, usually head-to-shoulder or head-to-tail, grooming each other's neck, rump and tail by gentle nipping, nuzzling or rubbing. Can occur between two stallions and also between a stallion and mare, usually prior to mating in the latter), retreats, circling, and snapping (Figure 1F – I).
Antagonism	Focal animal approaches another stallion walking with head lowered, ears pinned back, and neck outstretched in direction of stallion threat is being directed at, usually precedes chasing and dueling. Threat postures that may include biting threats (Figure 1J, K).
Marking	Defecation or urinating on or near dung piles (Figure 1L) in a classic sequence: sniff dung, step forward, defecate, pivot or back up and sniff dung again. Stallions of other species have been documented competing to be the last to defecate on a dung pile (McCort, 1984).
Flehmen	Head elevated and neck extended, upper lip curled back exposing incisors and gums (Figure 1M), eyes rolled back, ears rotated to the side, head may roll from side to side, usually occurs in association with olfactory investigation of dung.
Reproductive	May include courtship and nipping between a stallion and mare, as well as copulating (Figure 1N).
Dust bath	Focal male drops from standing to sternal recumbency, then rotating one or more times from sternal to dorsal recumbency, tucking legs against the body (Figure 1O). This is usually preceded by pawing or nosing the ground and followed by body shaking. May be an anti-parasite strategy to remove arthropod vectors or other ectoparasites.
Duel	Involves, biting, kicking, and boxing (Figure 1 P – R) and sparring with front legs between focal stallion and another stallion.
Genital sniffing	Olfactory investigation of a con-specific, ostensibly for reproductive health or challenge potential. Usually commences with heads aligned (Figure 1S) and proceeds to genital inspection.
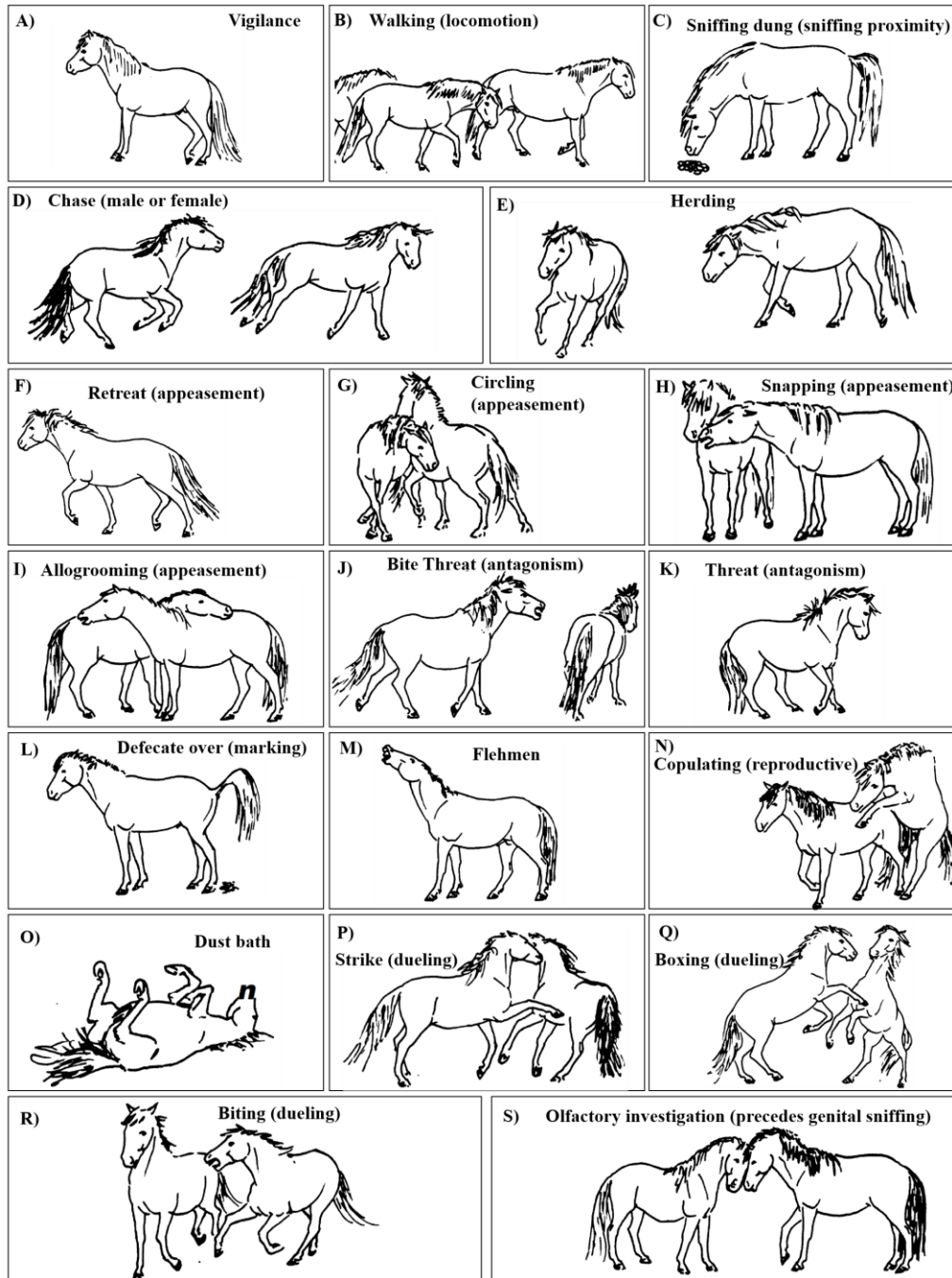
Figure 1. Exemplar behaviors of the Family Equidae performed by *Equus kiang* in Changthang Wildlife Sanctuary near Ladakh, India. Reproduced and modified with permission from McDonnell and Haviland (1995).

Data Analysis

One summer season allowed sufficient time for us to establish whether behaviors were representative for their social class. Two observers analyzed all videos using BORIS (Behavioral Observation Recording Information Systems; V. 2.0, Torino, Italy) to characterize the incidence and time spent (seconds) on each behavior. Bouts were considered to have commenced when the video began playing. The behavior encoding ensued until the 20-min video completed. There were no formal observer reliability tests, however, to provide confidence in the data-entry, we streamlined the ethogram (Watters et al., 2009) by focusing on clear, non-ambiguous behaviors (Table 2). Secondly, two observers blindly

scored an early subset of 35 videos during a training period. Following agreement of the two observers on the incidence and proportion of each behavior type during training, the second observer repeated the scoring on all remaining videos. We scored all videos where social interactions were taking place, and where we could follow a focal male (e.g., he did not become hidden behind other males).

Eighteen behaviors were recorded. We also computed an aggregate group size as the total number of other males, females, and foals in the vicinity (within 300 m). The latter allowed us to assess whether group size influenced vigilance, which can in turn, influence other behaviors inversely (Roberts, 1996). We quantified a specific behavior as the proportion of time (in seconds) spent on that behavior out of the 20-min (1,200 s) observation period. We then calculated the overall behavior as the proportion of time spent performing all behaviors within that category. For example, percent grazing is the total number of seconds spent grazing divided by 1,200 s. Likewise, percent overall foraging is the total number of seconds spent grazing or browsing divided by 1,200 s.

Univariate Analysis of Variance (ANOVA) was used to assess whether each behavior or the variable 'group size' differed among the three social classes. For instance, each behavior was an outcome variable and social class was the predictor. ANOVA was also used to test whether group size was different at either site, among four habitat-types. Tukey's post hoc test was performed to determine how the behaviors differed according to group. Pearson's Chi-squared test was used to determine potential habitat preference for any of the social classes. General Linear Model (GLM) was used to determine the influence of predictors, social-class, group size and site on vigilance. All descriptive statistics and inferential analyses were performed using Minitab V 17 (State College, PA). Statistical significance was set at $p \leq 0.05$.

Results

Three hundred thirty-five focal observations were recorded in 20-min blocks and analyzed for 18 behaviors for all classes. None of the 11 pre-identified males were ever observed more than once during the same day. The ten most common behaviors were categorized into "prominent behaviors," whereas the remaining eight behaviors were referred to as "accessory" behaviors. Among the prominent behaviors for all social classes combined (Figure 2A), animals spent the most time being vigilant ($34.0 \pm 1.81\%$), followed by locomotion ($24.2 \pm 0.7\%$) and mixed foraging ($12.5 \pm 1.3\%$). Animals spent less time browsing ($5.1 \pm 0.7\%$) and grazing ($1.87 \pm 0.5\%$). Sniffing proximity was performed ($1.8 \pm 0.3\%$) of the time while antagonistic behaviors composed ($1.05 \pm 0.2\%$). All other behaviors were produced less than 1% of the time (Figure 2A, B).

Comparisons at the social class level by univariate ANOVA with each behavior as the response and social class as the predictor (Figure 2A, B) revealed 11 of the 18 behaviors were performed differently across the three groups. These behaviors included: resting ($F(2, 334) = 3.0$, $p < 0.05$; $r^2 = 0.012$), browsing ($F(2, 334) = 3.1$, $p < 0.05$; $r^2 = 0.012$), herding ($F(2, 334) = 3.4$, $p < 0.05$; $r^2 = 0.012$), appeasement ($F(2, 334) = 7.3$, $p < 0.05$; $r^2 = 0.014$). Similarly, the following behaviors were performed by two or less of the three social groups (chasing males, marking, flehmen, reproductive, dust bathing, dueling and genital sniffing). Group size ($\bar{x} = 16.6 \pm 1.4$) did not differ across the three classes ($F(2, 334) = 1.7$, $p < 0.1$), but did differ across the four sites, with Tasaphuk having larger average group size than the other three areas. The Chi-square test of independence showed that habitat selection was different among the four sites ($\chi^2 (3) = 63.8$, $p < 0.001$). Territorial males favored the vegetation (nutrient) enriched sites of Pambuk and Panganau (Table 1), areas close to the two lakes, and were never seen at Thukje. Bachelors were the only animals found at Thukje, and were found in lower numbers in Pambuk and Tasaphuk. Mean group size differed between the three sites, with larger average group size at Tasaphuk.
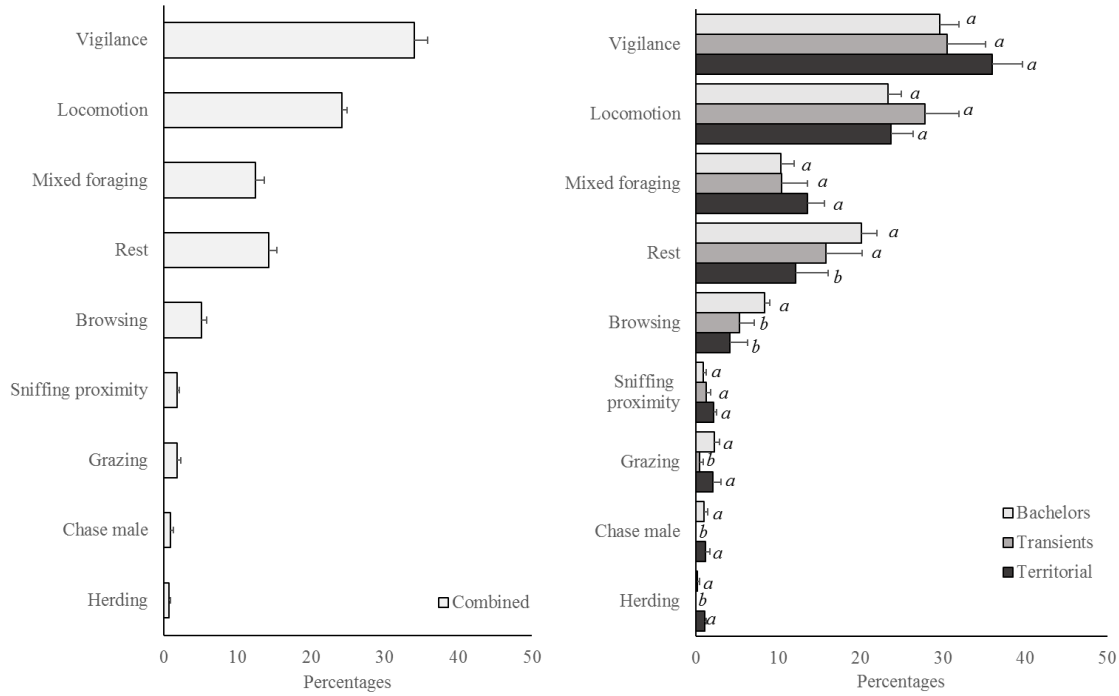
Figure 2A. Comparison of nine prominent behaviors performed by all groups combined (left) and social classes (Bachelors, Transients, Territorial Males; right) of *Equus kiang* from 3 July – 28 September, 2014 in Changthang Wildlife Sanctuary near Ladakh, India. Subscript refers to Tukey's post-hoc test, or when a behavior was rarely or never performed by one of the social classes.
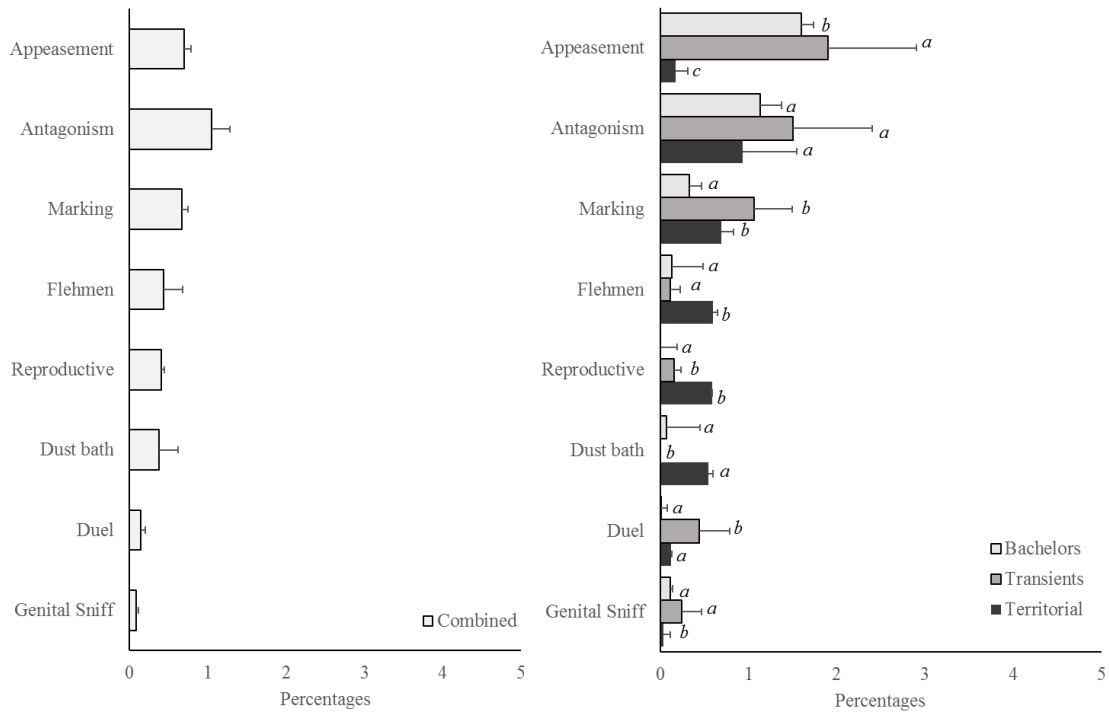

Figure 2B. Comparison of eight accessory behaviors performed by all groups combined (left) and social classes (Bachelors, Transients, Territorial Males; right) of *Equus kiang* from 3 July – 28 September, 2014 in Changthang Wildlife Sanctuary near Ladakh, India. Subscript refers to Tukey's post-hoc test, or when a behavior was rarely or never performed by one of the social classes.

The GLM revealed that neither social class ($F(2, 327) = 2.22, p > 0.1$) nor group size ($F(2, 327) = 1.31, p > 0.05$) had a significant influence on vigilance. However, the GLM revealed that vigilance between sites was significantly different ($F(2, 327) = 3.31, p < 0.05$); the effect size for the model showed $r^2 = 0.07$. A further examination (ANOVA) of the site revealed that animals from the site known as Thukje (Table 1, Figure 3) had significantly less vigilance ($F(2, 327) = 4.07, p < 0.05; r^2 = 0.03$) than did animals at the other three sites.
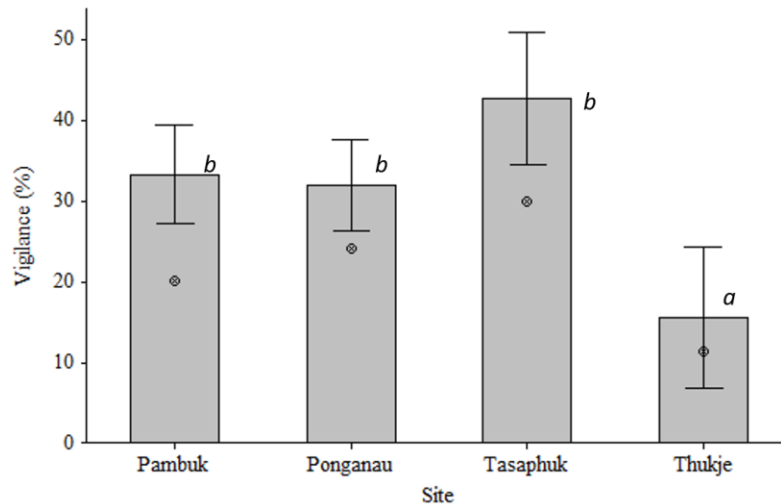

Figure 3. Vigilance performed by all groups combined, at the four sites where *Equus kiang* was observed in Changthang Wildlife Sanctuary near Ladakh, India. Circles within bars indicate medians. Superscript indicates significance by Tukey's post-hoc test, $\alpha = 0.05$.

Discussion

While systematically assessing an ethogram for *Equus kiang*, we learned that kiang spend more than 70% of their time budgets on vigilance (34%), locomotion (24.2%), resting (14.2%), mixed foraging (12.5%), browsing (5.1%), sniffing proximity (1.8%), and antagonism (1.1%). All other behaviors were performed less than 1% of the time. We also learned that the full repertoire of behaviors, and relative investments in each, differ strongly by social class. Eleven of the eighteen behaviors differed by class (Figure 2A, B). Among the most prominent behaviors, Territorial males rested less and browsed less than Bachelors or Transients. These deficits may have been opportunity costs for the time necessary to defend their territories against the often-intruding Transient males (Kannan et al., 2016). Additionally, Territorial males may have rested less because they were defending more productive, greener patches that attract female visitations. Unsurprisingly, Territorial males chased males and herded females more often than the other social classes. Among the accessory behaviors (Figure 2B), Transient males engaged in appeasement related behaviors most often. This finding was expected as Territorial males often harass and chase, but rarely appease, an intruder. Meanwhile, Bachelor males live in mixed-age groups and younger stallions will often appease older males. Conversely, this might explain why Bachelors rarely engaged in marking behavior. As expected, the Territorial males were observed performing reproductive behaviors.

We were surprised that over 2% of the complete behavioral investment was spent sniffing proximity, olfactory investigation of conspecifics (genital sniffing), and flehmen. Olfactory behaviors are increasingly being recognized for their importance in influencing animal behaviors (Parsons et al., 2017), especially among equids (Krueger & Flauger, 2011). However, we found male kiangs to spend more time in olfactory behaviors than even antagonism and appeasement, behaviors typically associated with equids. The causative mechanism is likely due to territoriality, mate receptivity and recognition, predator

awareness and availability and quality of forage (Parsons et al., 2017). There was only one clear difference in foraging patterns across social classes, Transient males did not engage in grazing. Grazing is the most energy efficient of the foraging types (Parsons et al., 2006), however it requires the animal to select, and potentially, defend a preferred food path. As a more mobile group, often intruding, followed by retreats, Transients were unlikely to be observed for very long selecting food from the same patch in a Territorial male's area.

Among the other social class comparisons, foraging was dominated by mixed foraging, which is less energy efficient than grazing, but more likely to provide diverse nutrients in the diet. Habitat selection indicated Territorial males favored the sites that offered the most abundant and diverse forage opportunities (Table 1). Unsurprisingly, the least vigilant males were at the site where Bachelors attended (Thukje) than the other three sites where Territorial males were found. Vigilance was more likely to occur near the lake shores and higher quality vegetation, where up to 200 females could occasionally be seen within a male's territory. Neither group differed according to mean group size or vigilance with conspecifics (males, females or foals) within 300 m, and thus, group size did not explain differences in behaviors between classes.

 Overall, male Tibetan wild asses spent an average of 34% of their time being vigilant, which is higher than African ungulates such as impalas (*Aepyceros* melampus; 10 – 22%) and wildebeests (*Onnochaetes taurinus*; 2.1 – 5%, Hunter & Skinner, 1998), and at rates slightly higher than roe deer (*Capreolus capreolus*), even during hunting season (Benhaiem et al., 2008). Too little is known about the behaviors of this species to make general comparisons to other species. Our observations, however, were conducted during the reproductive season, and thus, competition from other males may have inflated their vigilance.

Predator dilution theory (Li & Jiang, 2008; Roberts, 1996) did not appear to be a factor in our results. Whereas some ungulates such as Tibetan gazelles (*Procapra picticaudata*) show decreasing vigilance as group size increases, neither males, females or foals had any influence on vigilance – behavior that could have inversely impacted other foraging and social behaviors. This might be partly because the predator dilution theory can be masked when increasing group size attracts more predators (Ale & Brown, 2007). For instance, larger groups of elk (*C. elaphus,* Hebblewhite & Pletscher, 2002) and caribou (*Rangifer tarandus,* Crisler, 1956) are predated at higher rates by wolves. We infer that habitat-type (preferred areas for browsing and grazing) has a higher influence on vigilance than does predation or anthropogenic actions.

We cannot be certain how our data would have differed had behavioral observations of females and foals been included in our observations. In many instances, females are less vigilant than males (Simpson, Rands, & Nicol, 2012) especially when males are watching for rivals more so than predators. However, females — particularly pregnant or lactating mares – are sometimes more vigilant than males (Houpt, O'Connell, Houpt, & Carbonera, 1986). It was beyond our ability to include females at the distances we observed animals, and this was a limitation of the study.

Overall, the stark differences between classes helped us characterize a species new to the ethological literature, and suggest these findings are a reminder that researchers should make every effort to disambiguate social class among ungulates – and potentially other taxa – when evaluating ethograms.

References

Ale, S. B., & Brown, J. S. (2007). The contingencies of group size and vigilance. *Evolutionary Ecology Research, 9*, 1263.

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*, 227 – 266.

Bateson, P., & Laland, K. N. (2013). Tinbergen's four questions: An appreciation and an update. *Trends in Ecology & Evolution, 28*, 712 – 718.

Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A. M., ...Verheyden, H. (2008). Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Animal Behaviour, 76*, 611 – 618.

Bhatnagar, Y. V., Wangchuck, R., Prins, H. T., Van Wieren, S. E., & Mishra, C. (2006). Perceived conflicts between patoralism and conservation of the kiang *Equus kiang* in the Ladakh Trans-Himalaya, India. *Environmental Management, 38*, 934 – 941.

Boitani, L., Asa, C., & Moehrenschlager, A. (2004). Tools for canid conservation. In D. W. Macdonald & C. Sillero-Zubiri (Eds.), *Biology and conservation of wild canids* (pp. 143 – 159). Oxford, UK: Oxford University Press.

Burger, J., & Gochfeld, M. (1994). Vigilance in African mammals: Differences among mothers, other females, and males. *Behaviour, 131*, 153 – 169.

Cassirer, E. F., Freddy, D. J., & Ables, E. D. (1992). Elk responses to disturbance by cross-country skiers in Yellowstone National Park. *Wildlife Society Bulletin*, *20*, 375 – 381.

Chandan, P., Chatterjee, A., & Gautam, P. (2007, October). *Management planning of Himalayan high altitude wetlands. A case study of Tsomoriri and Tsokar Wetlands in Ladakh, India.* Paper presented at the Proceedings of Taal2007: The 12th World Lake Conference, Jaipur, India.

Crisler, L. (1956). Observations of wolves hunting caribou. *Journal of Mammalogy*, 337 – 346.

de Azevedo, C., Lima, M., Cipreste, C., Young, R., & Rodrigues, M. (2013). Using environmental enrichment to reduce the expression of abnormal behaviours in Greater rhea *Rhea americana* at Belo Horizonte Zoo. *International Zoo Yearbook, 47*, 163 – 170.

de Waal, F. B. (1988). The communicative repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. *Behaviour, 106*, 183 – 251.

Fox, J., & Bårdsen, B. (2005). Density of Tibetan antelope, Tibetan wild ass and Tibetan gazelle in relation to human presence across the Chang Tang Nature Reserve of Tibet, China. *Acta Zoologica Sinica, 51*, 586 – 597.

Ghaskadbi, P., Habib, B., & Qureshi, Q. (2016). A whistle in the woods: an ethogram and activity budget for the dhole in central India. *Journal of Mammalogy*, 97, 1745 – 1752.

Gordon, D. M. (1985). Do we need more ethograms? Zeitschrift für Tierpsychologie, *68*, 340 – 342.

Hebblewhite, M., & Pletscher, D. H. (2002). Effects of elk group size on predation by wolves. *Canadian Journal of Zoology, 80*, 800 – 809.

Horback, K. M., Miller, L. J., Andrews, J., Kuczaj, S. A., & Anderson, M. (2012). The effects of GPS collars on African elephant (*Loxodonta africana*) behavior at the San Diego Zoo Safari Park. *Applied Animal Behaviour Science, 142*, 76 – 81.

Houpt K. A., O'Connell, M. F., Houpt, T. A., & Carbonera, D. A. (1986). Night-time behavior of stabled and pastured peri-parturient ponies. *Applied Animal Behaviour Science, 15*, 103 – 111.

Hunter, L. T. B., & Skinner, J. D. (1998). Vigilance behaviour in African ungulates: The role of predation pressure. *Behaviour, 135*, 195-211.

Hussain, A., Qureshi, Q., & Rawat, G. S. (2010). Tibetan Wild Ass (*Equus kiang*)-livestock interactions in the Changthang Wildlife Sanctuary, Ladakh, India. *Galemys: Boletín informativo de la Sociedad Española para la Conservación y Estudio de los Mamíferos, 22*, 395 – 405.

Jordan, R. H., & Burghardt, G. M. (1986). Employing an ethogram to detect reactivity of black bears (*Ursus americanus*) to the presence of humans. *Ethology, 73*, 89 – 115.

Kannan, P. M., Parsons, M. H., Jamwal, P. S., Chandan, P. S., Parsons, F. E., & Takpa, J. (2016). The discovery of the 'transient'male Tibetan wild ass: alternative 'sneaky' mating tactics in a wild equid? *Behaviour 154,* 1 – 18.

Kotler, B. P., Morris, D. W., & Brown, J. S. (2016). Direct behavioral indicators as a conservation and management tool. In O. Berger-Tal & D. Saltz (Eds.), *Conservation Behavior: Applying Behavioral Ecology to Wildlife Conservation and Management* (Vol. 21, pp. 307-350). New York: Cambridge University Press.

Krueger, K., & Flauger, B. (2011). Olfactory recognition of individual competitors by means of faeces in horse (*Equus caballus*). *Animal Cognition, 14*, 245 – 257.

Li, Z., & Jiang, Z. (2008). Group size effect on vigilance: Evidence from Tibetan gazelle in Upper Buha River, Qinghai-Tibet Plateau. *Behavioural Processes, 78*, 25-28.

Luo Z., Jiang, Z., & Tang, S. (2015). Impacts of climate change on distributions and diversity of ungulates on the Tibetan Plateau. *Ecological Applications, 25*, 24-38.

MacNulty, D. R., Mech, L. D., & Smith, D. W. (2007). A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *Journal of Mammalogy, 88*, 595 – 605.

Mandujano, V., Flores-Prado, L., & Chiappa, E. (2016). Behavioral analysis and ethogram of mating in the wasp, *Sphex latreillei* (Lepeletier) (Hymenoptera: Crabronidae). *Neotropical Entomology, 45*, 369 – 373.

McCort, W. D. (1984). Behavior of feral horses and ponies. *Journal of Animal Science, 58*, 493 – 499.

McDonnell, S., & Haviland, J. (1995). Agonistic ethogram of the equid bachelor band. *Applied Animal Behaviour Science, 43*, 147 – 188.

Nekaris, K., & Jayewardene, J. (2003). Pilot study and conservation status of the slender loris (*Loris tardigradus* and *L. lydekkerianus*) in Sri Lanka. *Primate Conservation, 19*, 83 – 90.

Parsons, M. H., Apfelbach, R., Banks, P. B., Cameron, E. Z., Dickman, C. R., Frank, A. S. K., ...Blumstein, D. T. (in press). Biologically meaningful scents: A framework for understanding predator-prey research across disciplines. *Biological Reviews*.

Parsons, M. H., Lamont, B. B., Davies, S. J., & Kovacs, B. R. (2006). How energy and coavailable foods affect forage selection by the western grey kangaroo. *Animal Behavior, 176*, 45 – 53.

Poiani, A., Coulson, G., Salamon, D., Holland, S., & Nave, C. D. (2002). Fertility control of eastern grey kangaroos: Do levonorgestrel implants affect behavior? *The Journal of Wildlife Management*, *66,* 59 – 66.

Ransom, J. I., & Cade, B. S. (2009). Quantifying equid behavior—A research ethogram for free-roaming feral horses. *Publications of the US Geological Survey*, 26, 1 - 23.

Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour, 51*, 1077 – 1086.

Rumble, M. A., Benkobi, L., & Gamo, R. S. (2005). Elk responses to humans in a densely roaded area. *Intermountain Journal of Sciences, 11*, 10 – 24.

Sayre, R. W., & Clark, L. (2001). Effect of primary and secondary repellents on European starlings: An initial assessment. *The Journal of Wildlife Management*, *65,* 461 – 469.

Schleidt, W. (1985). In defense of standard ethograms. *Zeitschrift für Tierpsychologie, 68*, 343 – 345.

Schleidt, W., Yakalis, G., Donnelly, M., & McGarry, J. (1984). A proposal for a standard ethogram, exemplified by an ethogram of the bluebreasted quail (*Coturnix chinensis*) 1. *Zeitschrift für Tierpsychologie, 64*, 193 – 220.

Sharma, B. D., Clevers, J., Graaf, R. D., & Chapagain, N. R. (2004). Mapping *Equus kiang* (Tibetan Wild Ass) habitat in Surkhang, Upper Mustang, Nepal. *Mountain Research and Development, 24*, 149 – 156.

Sigurjónsdóttir, H., van Dierendock, M., & Thórhallsdóttir, A. (2002). *Friendship among horses—Rank and kinship matter. In* Havemeyer Foundation Workshop on Horse Behavior. Retrieved April 15, 2017, from http://www3.vet.upenn.edu/labs/equinebehavior// hvnwkshp/hv02/hv02auth.htm..

Simpson H. I., Rands, S. A., & Nicol, C. J. (2012). Social structure, vigilance and behaviour of plains zebra (*Equus burchellii*): A 5-year case study of individuals living on a managed wildlife reserve. *Acta Theriologica, 57*, 111 – 120.

St-Louis, A., & Côté, S. D. (2012). Foraging behaviour at multiple temporal scales in a wild alpine equid. *Oecologia, 169*, 167 – 176.

Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society of London B: Biological Sciences, 272*, 2627 – 2634.

Stanton, L. A., Sullivan, M. S., & Fazio, J. M. (2015). A standardized ethogram for the felidae: A tool for behavioral researchers. *Applied Animal Behaviour Science, 173*, 3 – 16.

Stevenson, M. F., & Poole, T. B. (1976). An ethogram of the common marmoset (*Calithrix jacchus jacchus*): General behavioural repertoire. *Animal Behaviour, 24*, 428 – 433.

Stoinski, T. S., & Beck, B. B. (2001). Spontaneous tool use in captive, free-ranging golden lion tamarins (*Leontopithecus rosalia rosalia*). *Primates, 42*, 319 – 326.

Tardin, R. H., Pinto, M. P., Alves, M. A. S., & Simão, S. M. (2014). Behavioral event occurrence differs between behavioral states in *Sotalia guianensis* (Cetarctiodactyla: Delphinidae) dolphins: A multivariate approach. *Zoologia (Curitiba), 31*, 1 – 7.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20*, 410 – 433.

Uniyal, S. K., Awasthi, A., & Rawat, G. S. (2005). Biomass availability and forage quality of *Eurotia ceratoides* Mey in the rangelands of Changthang, eastern Ladakh. *Current Science Bangalore, 89*, 201 – 205.

Watters, J. V., Margulis, S. W., & Atsalis, S. (2009). Behavioral monitoring in zoos and aquariums: A tool for guiding husbandry and directing research. *Zoo Biology, 28*, 35 – 48.

Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior, 16*, 229 – 249.