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Reintroduction of takhi, *Equus ferus przewalskii*, to Hustai National Park, Mongolia: time budget and synchrony of activity pre- and post-release

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Abstract

A harem of takhi (*Equus ferus przewalskii*) was observed during introduction to the Hustain Nuruu Steppe Reserve of Mongolia. The goals were to examine whether the harem exhibited significant behavioural synchrony, whether release had an effect on time budget, and what the implications might be regarding acclimatisation to the wild. Behaviours were scan sampled every 10 min between the hours of 06:00 and 22:00, twice before release, twice immediately after release, and twice 2 years after reintroduction. Time budgets were constructed from these data. Considerable behavioural synchrony was evidenced both before and after release. Crepuscular grazing and midday resting were typical, regardless of the date relative to release. Upon release, the amount of time spent moving doubled for all age classes. It is suggested that this increase resulted from exploration. The amount of time spent grazing and standing remained unchanged; the increased amount of time spent moving came at the expense of resting. Two years later, the horses still spent more time moving than when captive. Somewhat less time was spent grazing, although the difference was not significant. More time was spent resting in 1996 than immediately after release. These time budgets provide evidence of successful acclimatisation to the wild. Trekking between favoured sites could account for the persistent increase in time spent moving, with concomitantly less time needed to meet nutritional needs by grazing and more time available for resting. Housing captive takhi in large enclosures is evidently insufficient to permit the amount of movement exhibited by this wild harem. The time budget of the 1- and 2-year olds was more similar to that of adults than foals, indicating approaching adulthood. That 1- and 2-year olds were nursed, without loss of body condition by the dam, provided additional evidence that the takhi achieved excellent nutritional status in the wild.

Keywords: Equids; Przewalski's horses; Takhi; Behaviour patterns; Time budgets; Behavioural synchrony; Reintroduction

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1. Introduction

Lack of knowledge about endangered species hinders conservation efforts (Stanley Price, 1989; Jackson, 1994). Many reintroductions are not documented (Stanley Price, 1991; Beck et al., 1994) or the information is not quantified (Ounsted, 1991). Monitoring reintroduced animals permits evaluation of their response to the new environment (Stanley Price, 1989; Miller and Vargas, 1994). Reintroduced animals face environmental changes when brought to the reintroduction site; they must acclimate and also cope with additional changes upon release if the reintroduction is to succeed. Time budget studies can provide information on whether organisms are coping with changes (Duncan, 1985; Boyd, 1988a).

Many reintroductions fail because stress on the animals disrupts social bonds, increasing the chance of scattering upon release and making individuals more vulnerable to predators (Stanley Price, 1989). Social facilitation in group-living ungulates produces behavioural synchrony, which enhances group cohesiveness (Sambraus, 1973; Clayton, 1978; Benham, 1982). Measures of synchrony might be used to evaluate whether immigrants brought together at the site of reintroduction have bonded into a stable social unit that will stay intact upon release. As group cohesiveness is an integral part of many antipredator strategies (Jarman, 1974; Bertram, 1978), synchrony may be critical for the successful reintroduction of captive-born prey species into habitat containing predators.

Takhi (*Equus ferus przewalskii*, also known as Przewalski's, Mongolian or Asian Wild Horses) are an endangered species and the only extant wild horse. They are the closest living relative of domestic and feral horses (*Equus caballus*) and hybridisation is possible. They are considered to be a distinct species because they possess an additional pair of chromosomes in comparison with domestic horses (Benirschke et al., 1965).

In 1880 when Colonel Nikolai Przewalski announced his discovery of takhi, they were restricted to the border of China and Mongolia (Bouman and Bouman, 1994). Various expeditions around the turn of the century brought juvenile takhi into captivity. The last wild-caught horse was captured in 1947. By the 1960s the wild population was extinct, due to hunting, competition with domestic livestock, and a series of severe winters (Van Dierendonck and Wallis de Vries, 1996). Successful propagation by zoos and private breeding programs resulted in a captive population of over 1000 animals by 1991 (Ryder, 1994). This numerical strength made reintroduction possible.

Little is known about the behaviour of takhi in the wild prior to their extinction (Bouman and Bouman, 1994), although time budgets of captive takhi have been well studied (Bubenik, 1961; Boyd, 1988a,b; Boyd et al., 1988; Hogan et al., 1988; Van Dierendonck et al., 1996). The reintroduction project in Hustain Nuruu, Mongolia, presented the first opportunity to study the behaviour of newly released takhi as they acclimated to life in the wild. In order to examine the degree of behavioural synchrony and changes in the time budget resulting from reintroduction, one of the harems was observed just prior to release and again immediately subsequent to release in 1994. Follow-up observations were made 2 years later at the same time of year.

2. Methods

2.1. Study animals and study site

The Foundation Reserves Przewalski Horse (The Netherlands) and the Mongolian Association for Conservation of Nature and Environment entered into a co-operative project to restore takhi to Mongolia (Bouman et al., 1994; Bouman, 1998). The Hustain Nuruu Steppe Reserve was established 100 km southwest of Ulaanbaatar. The 57,000 ha Reserve consists of mountain and upland steppe and is home to a diversity of wildlife (Van Dierendonck and Wallis de Vries, 1996; King, this volume). Restoration and preservation of the Reserve's biodiversity is the main aim of the project (Bouman, 1998). The area attained national park status in 1997 (Tserendeleg, 1999).

In 1992, 16 captive-born takhi were flown to Mongolia and placed in 45 ha enclosures within the Reserve for acclimatisation. Streams run through each enclosure and sufficient forage is present so that no supplemental provisioning is necessary. An initial behavioural study was undertaken by Van Dierendonck et al. (1996) from July 1992 to October 1993 while the takhi were still within fences. In the summer of 1994 the first two harems were released and new shipments of takhi replaced them in the enclosures. A harem from the second shipment was released in 1995, a fourth harem was released in 1996 upon arrival in Mongolia, and the other acclimated harem from the second shipment was also released in 1996. Mares from the last released harem joined another harem, so by July 1996 there were four free-roaming harems, and a bachelor group formed from deposed stallions and Mongolian-born juveniles who had dispersed from their natal bands.

The harem of the stallion Khaan was selected for this study because it was the most habituated to humans and could be followed on foot at distances of 30–50 m, both before and after release, without any apparent effects on behaviour. Theirs was a ''soft'' release; the gates to the enclosure were opened on 29 June 1994, and the takhi allowed to leave at will, which took place the evening of 2 July 1994. Table 1 lists harem members in 1994 and 1996. In 1994, five adults, one yearling, and three foals were present. In 1996 the harem consisted of six adults, two 2-year olds, a yearling, and three foals. The yearling and 2-year olds are combined to form a subadult age class for 1996 data presentation.

2.2. Data collection

The same methodology of data collection was used throughout and was similar to that used by Van Dierendonck et al. (1996) for observations of this harem while in captivity. Scan samples of the entire harem were taken every 10 min between the hours of 06:00 and 22:00. As observations were made in summer (June and July), this time period covered the hours between dawn and full darkness. Typically the observations were conducted in 2 h blocks. All hours between 06:00 and 22:00 were equally represented. Two rounds of observations (32 h, 192 scans) were made in the period from 4 to 2 weeks prior to release. Two rounds of observations were made from 2 to 4 weeks after release, and during the month of July 1996 two rounds of follow-up observations were conducted.

The scan samples obtained prior to release were made by five biologists using the same methodology. Although, no formal interobserver accuracy tests were conducted, all five

Table 1
Composition of Khaan's Harem in 1994 and 1996

Name	Gender	Sire	Dam	Date of birth	Year present
1764 Lely. 16 Khaan	Stallion	915 Koln 10 Apoll	770 Marwell 33 Lola	8.VII.88	1994/1996
1912 Askania 187 Belka	Mare	821 Askania 45 Parad	602 Askania 20 Geran	30.VI.89	1994/1996
1961 Askania 192 Riska	Mare	896 Askania 55 Pusik	1119 Askania 80 Gernika	14.IV.90	1994/1996
1970 Askania 203 Vetochka	Mare	1159 Askania 84 Perun	524 Askania 12 Viola	12.V.90	1994/1996
1978 Askania 212 Svetlaia	Mare	1159 Askania 84 Perun	766 Askania 41 Veska	12.VII.90	1994/1996
2082 Ooij 6 Shuurga	Mare	1278 Nikolaev 3 Vagur	1314 Lelystad 2 Nyam	26.III.90	1996
2619 Hustain 1 Manlai	Colt	1764 Lely. 16 Khaan	1912 Askania 187 Belka	21.VI.93	1994
2683 Hustain 3 Jan	Colt	1764 Lely. 16 Khaan	1961 Askania 192 Riska	21.V.94	1994
2686 Hustain 4 Amar	Colt	1764 Lely. 16 Khaan	1970 Askania 203 Vetochka	23.V.94	1994/1996
2692 Hustain 6 Ireedui	Filly	1857 Askania 181 Patron	1890 Lely. 18 Hjalgana	28.V.94	1996
2703 Hustain 9 Tuul	Filly	1764 Lely. 16 Khaan	1912 Askania 187 Belka	7.VI.94	1994
2799 Hustain 12 Oesoech (Ycyx)	Filly	1764 Lely. 16 Khaan	1970 Askania 203 Vetochka	14.V.95	1996
2899 Hustain 20 Delgareth	Filly	1764 Lely. 16 Khaan	1912 Askania 187 Belka	25.IV.96	1996
2912 Hustain 21 Chotzj	Filly	1764 Lely. 16 Khaan	1961 Askania 192 Riska	9.V.96	1996
2915 Hustain 24 Az Dzargal	Colt	1764 Lely. 16 Khaan	1970 Askania 203 Vetochka	10.V.96	1996

1993 and 1994 foals were born in the acclimatisation enclosures prior to release. The 1996 foals were wild born.

had trained with one another and frequently went out in pairs while observing. One of these biologists (Boyd) subsequently collected all post-release samples.

During the scans the behaviour of each harem member was recorded onto data sheets. The ethogram was that of Boyd and Houpt (1994). The behavioural categories are condensed for presentation here into grazing, moving (walk, trot, or run), standing (no grazing, locomotion, or resting posture exhibited), resting (including standing rest and recumbent rest) and all other behaviours. For juveniles, the additional category of suckling behaviour was distinguished.

If an individual horse was out of sight during the scan, that observation was discarded and the total number of scans reduced accordingly when the data for that individual were analysed. No individual was out of sight during more than 5% of the observations. The average percentage of scans in which an individual was out of sight was 1.4% in 1994 prior to release, 2.3% in 1994 post-release, and 0.8% in 1996.

Post-release in 1994, and in 1996, ambient temperature was recorded every hour using a small thermometer. Body condition of each horse was scored monthly. In 1994 the method of Van Dierendonck et al. (1996) was used. By 1996 body condition was scored as described by Bos (1999), based on the widely-used system of Carroll and Huntington (1988).

2.3. Statistical analyses

Proportions were arcsine transformed prior to statistical testing. As the same individuals were observed before and after release and again in 1996, the samples were considered to be related. Time budgets from 1994 pre-release, post-release, and 1996 were compared using Friedman two-way analysis of variance (ANOVA) and pairwise comparisons of the three time periods were made using Wilcoxon matched pairs signed-ranks tests (Siegal and Castellan, 1988). Although, the same individuals were observed pre- and post-release in 1994, the composition of the harem changed somewhat from 1994 to 1996. The data used in the test statistics came from the five adults present throughout, the 1994 yearling and the 1996 yearling, and the three foals present each year. Obviously the 1996 foals are different individuals from the 1994 cohort, but they were born to the same dams and sire. Data from the mare who joined the harem after 1994 and from the 2-year olds were not used, to make the samples from each period comparable. Additionally, the differences between 1994 pre- and post-release amounts of time harem members spent in each behaviour were compared using Spearman rank correlation coefficients (Siegal and Castellan, 1988).

Time budgets of captive juvenile and adult takhi are known to be different (Boyd, 1988b), and the behaviour of captive harems is influenced by time of day (Boyd et al., 1988), so these factors were examined separately. Mann–Whitney *U*-tests were used to compare the amount of time spent by foals to the amount of time spent by adults for each behaviour in 1994. In 1996, when multiple subadults were present, Kruskall–Wallis one-way ANOVA was used to compare time spent by foals versus subadults versus adults in each behaviour. With the exception of the single yearling present in 1994, data from all harem members were used in these statistical tests. Data were tabulated by 2 h intervals between the hours of 06:00 and 22:00. Friedman two-way ANOVA was used to test for time-of-day effects on each behaviour and Wilcoxon matched pairs signed-rank tests were used for multiple comparisons if significant differences were found (Siegal and Castellan, 1988).

The κ coefficient of agreement (Siegal and Castellan, 1988; Rook and Penning, 1991) was used to quantify the degree of synchrony among adult harem members. This statistic varies between 0 and 1, with higher values indicating greater synchrony. Juvenile data were excluded, because in captivity their time budgets are different from those of adults (Boyd, 1988b). An overall κ coefficient was calculated, and then calculated separately for each of the five behavioural categories for 1994 pre-release, 1994 post-release, and 1996.

The proportion of scans in which 100% of the adult takhi were engaged in the same activity was also quantified. By 1996 one of the mares had foaled in three successive years and all of her offspring were still present. We quantified the proportion of time in which 100% of this matriline was in synchrony during our 1996 observations. Finally, scans in which all but one of the adults were in synchrony were examined to see if any individuals were consistent outliers across all years.

3. Results

3.1. Effects of release on time budget

Table 2 gives the time budget for Khaan's harem, before and after release in 1994, and in 1996. For adults, the most labile behaviours appear to be the amount of time spent moving and resting. In 1996 there was a decline in the amount of time spent grazing. The yearling present in 1994 was not suckling, but two of the three subadults suckled in 1996. For subadults also, the most labile elements were the amount of time spent moving and resting, and again there was a decline in the amount of time spent grazing in 1996. The biggest differences in foal time budgets were also seen in the categories of moving and resting. The amount of time foals spent grazing increased post-release and in 1996.

There was no significant difference in the amount of time harem members spent grazing or standing before and after release ($\chi^2 > 4.7$, d.f. $= 2$, $P = 0.1$, $n = 9$). Amounts of time

Table 2
Total time budgets (percent time spent, mean ± S.E.)

	1994 pre-release	1994 post-release	1996
Adults	$n = 5$	$n = 5$	$n = 6$
Graze	53.7 ± 2.4	54.7 ± 0.8	44.3 ± 1.9
Move	8.4 ± 0.6	16.8 ± 0.8	13.4 ± 1.2
Stand	12.0 ± 0.6	7.8 ± 0.7	8.6 ± 0.6
Rest	23.8 ± 1.9	19.9 ± 0.6	32.6 ± 1.2
Other	2.1 ± 0.2	0.8 ± 0.2	1.2 ± 0.3
Subadult(s)	$n = 1$	$n = 1$	$n = 3$
Graze	50.0	51.5	38.2 ± 3.9
Move	9.8	20.5	14.7 ± 1.9
Stand	6.3	8.0	10.7 ± 1.7
Rest	30.9	19.5	33.1 ± 2.2
Suckle	0	0	0.5 ± 0.0
Other	3.0	0.5	3.3 ± 1.5
Foals	$n = 3$	$n = 3$	$n = 3$
Graze	11.1 ± 1.6	24.7 ± 0.6	26.5 ± 2.7
Move	11.8 ± 0.9	24.4 ± 1.2	16.3 ± 1.2
Stand	17.3 ± 0.7	16.7 ± 1.8	16.8 ± 2.9
Rest	53.5 ± 1.5	29.6 ± 0.2	33.6 ± 2.2
Suckle	2.8 ± 0.5	3.0 ± 0.7	1.9 ± 0.4
Other	3.5 ± 0.5	1.5 ± 0.5	4.9 ± 1.1

spent moving and resting were significantly different ($\chi^2 = 16.2$ and 8.2, respectively, d.f. $= 2$, $P = 0.003$ and 0.016, respectively, $n = 9$). Pairwise comparisons indicated that all three periods differed significantly in the amount of time spent moving (all $z > -2.4$, all $P < 0.016$). Amount of time spent resting was significantly greater prior to release and in 1996 than immediately after release (both $z = -2.6$, $P = 0.01$).

Correlation of the differences in amount of time spent in each behaviour before and after release in 1994 showed that the decline in amount of time spent resting after release was significantly negatively correlated with the amount of time spent standing, moving, and grazing ($r_s = -0.73$, -0.83, -0.88, respectively; $P = 0.026$, 0.006, and 0.002, respectively).

3.2. Comparison of adult and juvenile time budgets

The amounts of time spent grazing, moving, standing, and resting by the three foals versus the five adults in 1994 were significantly different, both pre- and post-release (MWU, all $P < 0.03$). In 1996 there were significant differences among the three age classes for grazing ($\chi^2 = 7.6$, d.f. $= 2$, $P = 0.02$) and standing ($\chi^2 = 6.6$, d.f. $= 2$, $P = 0.04$) behaviours. Multiple comparisons between the 1996 age classes showed that adults ($z = -2.3$, $P = 0.02$) and subadults ($z = -2.0$, $P < 0.05$) spent significantly more time grazing than did foals. Multiple comparisons of the amount of time spent standing showed a significant difference between adults and foals ($z = -2.3$, $P = 0.02$); adults spent less time standing than did foals.

3.3. Time-of-day effects

The distribution of behaviours across the day was similar prior to and after release. There is a peak of grazing in the early morning and evening (Fig. 1a) when temperatures are cooler, and a peak of resting in midday (Fig. 1d) when the temperature is highest (Fig. 1e). Moving and standing behaviour patterns are fairly evenly distributed across the day (Fig. 1b and c). As patterns appeared similar regardless of date, we chose the 1996 data to analyse further, as the sample size of horses was largest.

All four behavioural categories showed significant time-of-day effects in 1996, which were especially pronounced for grazing and resting, as would be predicted from Fig. 1a and d (grazing: $\chi^2 = 65.7$, d.f. $= 7$, $P = 0.00$; resting: $\chi^2 = 65.8$, d.f. $= 7$, $P = 0.00$; moving: $\chi^2 = 18.4$, d.f. $= 7$, $P = 0.01$; standing: $\chi^2 = 23.5$, d.f. $= 7$, $P = 0.001$). Table 3 presents the average amount of time spent in each behaviour by time of day and indicates which blocks of time are similar.

3.4. Behavioural synchrony

Table 4 gives the proportion of observations during which 100% of the adult takhi were engaged in the same activity. In 1994 the adults were in complete synchrony about half the time. The probability of complete synchrony was highest for grazing and resting behaviours. By 1996 the adults were in full synchrony <30% of the time. The 1996 matriline was in full synchrony 35.4% of the time.

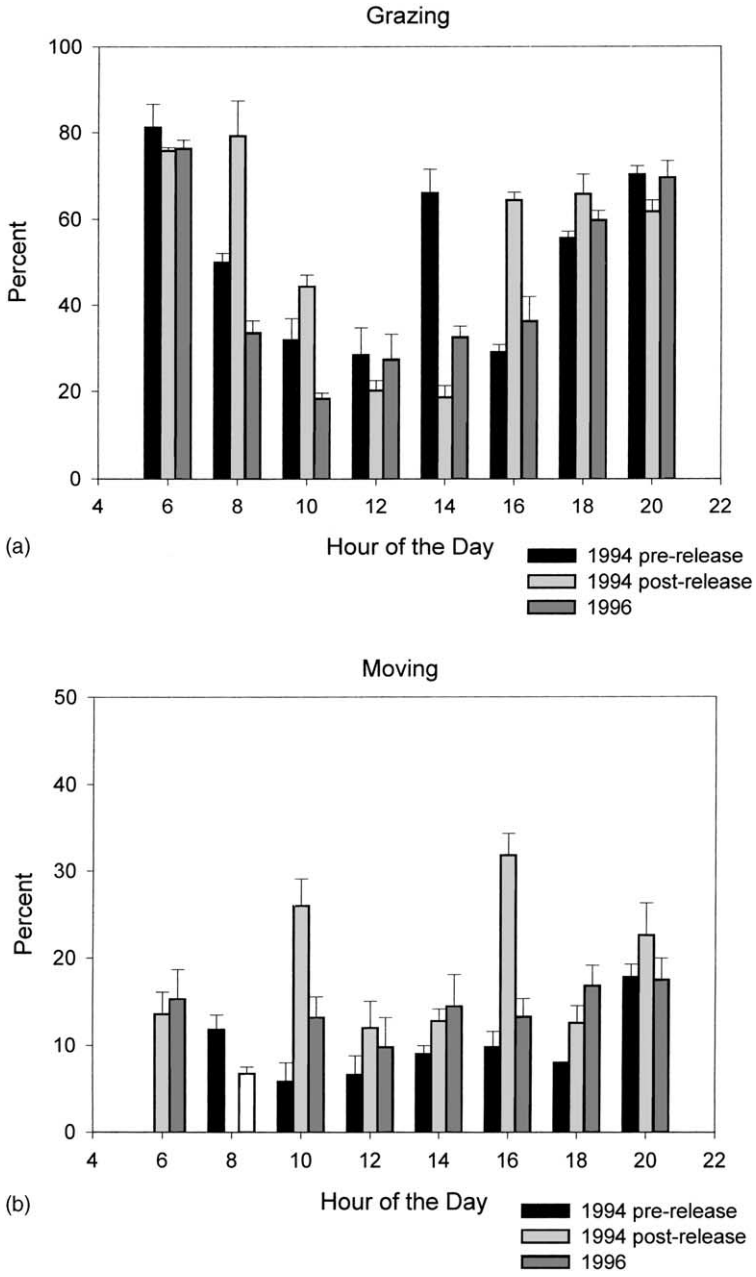
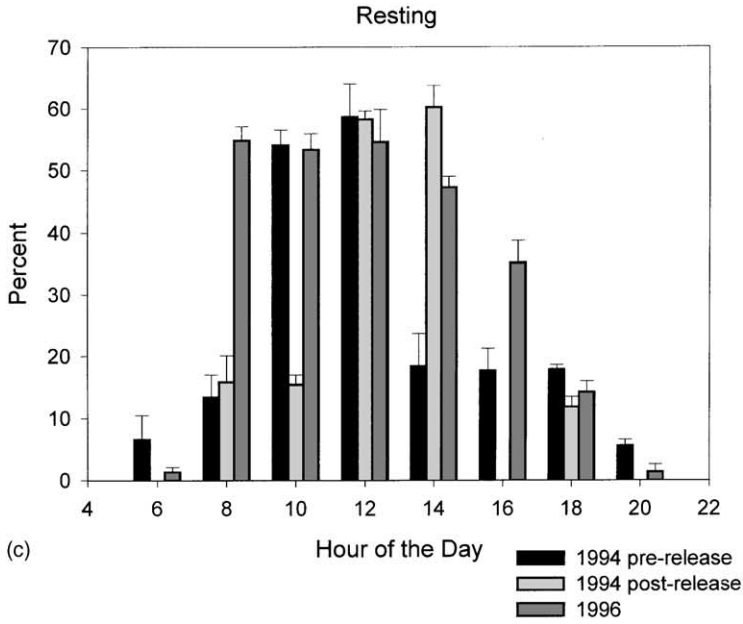
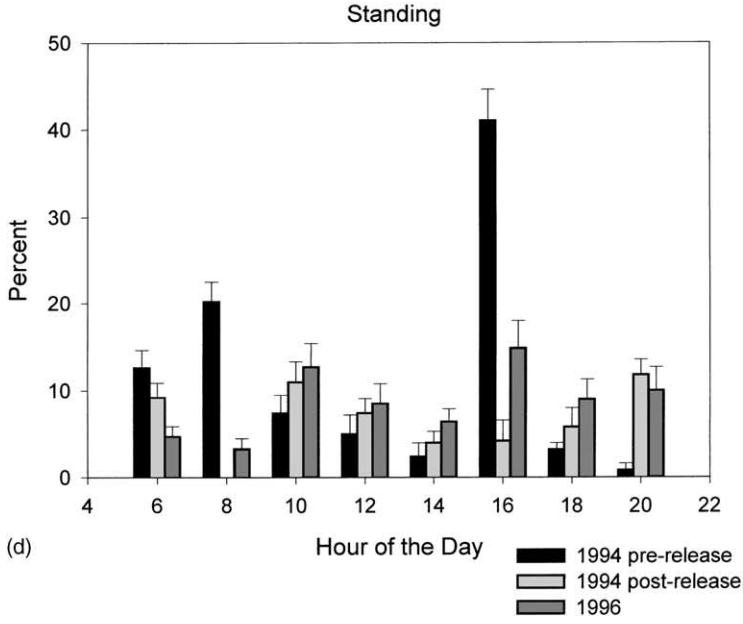


Fig. 1. Time-of-day effects on adult time budgets. $n = 5$ adults in 1994 and 6 adults in 1996 observed between 06:00 and 22:00. Values shown are mean ± S.E.: (a) percent time spent grazing; (b) percent time spent moving; (c) percent time spent standing; (d) percent time spent resting; (e) average temperature during the scan samples (temperatures were not recorded in 1994 pre-release).



(c)



(d)

Fig. 1. (*Continued*).

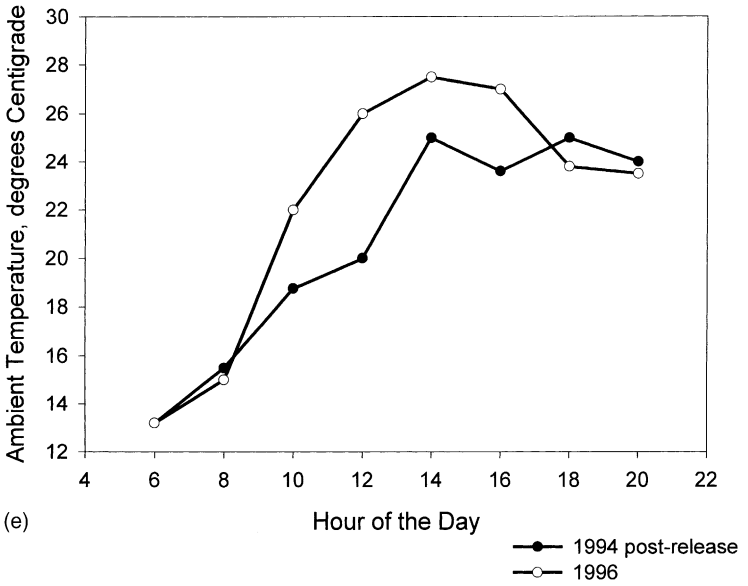


Fig. 1. (*Continued*).

Table 3
1996 Time budgets by time of day (percent time spent, mean ± S.E.)

Time of day	Graze	Move	Stand	Rest
06:00–08:00	64.6 ± 4.2 a	19.1 ± 2.6 ac	9.3 ± 2.7 ab	2.3 ± 0.9 a
08:00–10:00	27.9 ± 2.7 b	11.7 ± 2.2 ac	5.3 ± 1.8 a	47.2 ± 3.3 bc
10:00–12:00	17.8 ± 1.7 c	12.9 ± 1.6 bc	14.1 ± 1.8 bc	50.3 ± 2.4 bc
12:00–14:00	21.8 ± 3.7 bc	7.7 ± 2.0 b	14.3 ± 2.7 c	54.4 ± 3.3 c
14:00–16:00	27.1 ± 2.5 b	14.6 ± 2.0 abc	8.4 ± 1.3 a	48.7 ± 1.7 bc
16:00–18:00	29.8 ± 4.3 b	13.4 ± 1.6 ac	14.2 ± 1.6 bc	42.4 ± 3.3 b
18:00–20:00	50.1 ± 4.1	18.3 ± 1.6 a	14.3 ± 2.2 c	16.6 ± 1.6
20:00–22:00	66.8 ± 3.2 a	18.2 ± 1.9 a	10.3 ± 1.7 abc	1.7 ± 0.8 a

Note: $n = 6$ adults, 3 subadults, 3 foals. Values within the same column which share letters are not significantly different from one another ($P > 0.05$).

Table 4
Proportion of time in which 100% of the adult takhi were engaged in the same activity

	Graze	Move	Stand	Rest	Other	Total
1994 pre-release	0.292	0.021	0.042	0.104	0.005	0.464
1994 post-release	0.349	0.068	0.016	0.109	0.000	0.542
1996	0.151	0.016	0.000	0.104	0.000	0.271

Table 5
Observed (P(A)) and expected (P(E)) proportions of synchronisation and κ coefficients of synchronisation

		P(A)	P(E)	κ	Var(κ)	z
Overall	1994 pre-release	0.744	0.360	0.593	0.00053	25.75
	1994 post-release	0.747	0.367	0.600	0.00056	25.00
	1996	0.617	0.338	0.421	0.00031	23.39
Graze	1994 pre-release	0.426	0.279	0.204	0.00059	8.37
	1994 post-release	0.448	0.292	0.221	0.00064	8.84
	1996	0.318	0.217	0.129	0.00034	7.01
Move	1994 pre-release	0.047	0.008	0.039	0.000006	16.25
	1994 post-release	0.104	0.027	0.108	0.000024	22.04
	1996	0.049	0.019	0.031	0.000015	8.16
Stand	1994 pre-release	0.072	0.014	0.059	0.000012	17.20
	1994 post-release	0.036	0.006	0.030	0.000010	30.00
	1996	0.018	0.006	0.012	0.0000032	6.67
Rest	1994 pre-release	0.184	0.059	0.133	0.000068	16.12
	1994 post-release	0.158	0.042	0.121	0.000046	18.06
	1996	0.231	0.096	0.149	0.000110	14.33
Other	1994 pre-release	0.015	0.0006	0.014	0.00000033	23.33
	1994 post-release	0.002	0.0003	0.001	0.00000200	0.93
	1996	0.001	0.0001	0.001	0.00000004	3.00

Table 5 provides the κ statistics overall and by behaviour. With the exception of the 'other' behavioural category, all κ coefficients were significantly different from zero, indicating that synchrony was greater than expected by chance. Synchrony was highest for grazing and resting behaviours. The level of synchrony was very similar pre- and post-release in 1994, but behaviour was generally less synchronised in 1996. When scans during which there was only one adult out of synchrony were examined, the stallion was the only outlier more frequently than predicted by chance in all 3 years.

3.5. Body condition scores

The body condition of every adult in Khaan's harem was scored as a 0, both in June 1994 before release, and in July after release. A score of 0 indicates normal body condition (Van Dierendonck et al., 1996) and is roughly equivalent to a score of 4 under the system of Bos (1999). In 1996 scores ranged from 4.1 to 4.5, with a June average of 4.26 and a July average of 4.42, which is descriptively translated as being "Fat" (Carroll and Huntington, 1988).

4. Discussion

Behavioural synchrony among social ungulates may reflect both environmental and social influences (Côté et al., 1997). These takhi were brought together for the first time on

arrival in Mongolia. Van Dierendonck et al. (1996) reported full synchronisation during 53–75% of the observations of this harem in 1992 and 1993. During our observations in 1994, they continued to display considerable group synchrony, which was unaffected by release. Their level of synchrony is considerably higher than reported for domestic sheep (Rook and Penning, 1991). This may reflect the permanent harem social structure of takhi, (social influence) as compared with the more fluid associations of sheep, or it may be a response to the exposure of these takhi to natural predators (wolves) in Hustain Nuruu (environmental influence). Synchrony was highest during grazing and resting, when vigilance is necessarily lower than during standing or moving. According to Jarman (1974) it is important for group cohesion that all members graze and rest synchronously, while synchronisation of other activities is not as necessary for group cohesion. Moving behaviour was more synchronised immediately after release as the takhi began sustained treks through their new environment.

In 1996 the degree of synchrony declined for all but resting behaviour. The reasons for this decline are unknown, but a possible combination of factors include: (1) the immigration of a new adult mare in 1996 who may not have been well integrated into the group, although the number of times she was an outlier did not exceed that predicted by chance; (2) the presence of more subadults in 1996, creating a matriline consisting of a mare and her offspring showing higher intragroup synchrony than the harem as a whole, i.e. subgroup synchrony may supercede group synchrony; (3) the increase in harem size from 9 animals in 1994 to 12 in 1996. In muskoxen, the degree of synchrony declined with group size (Côté et al., 1997), and Clutton-Brock et al. (1982) found that red deer more than 50 m apart (presumably more likely in large groups) were less synchronised then those within 50 m of one another. The decline in group synchrony by 1996 presaged the disintegration of Khaan's harem. In early 1998 the matriline was picked up by a young stallion and by the fall of 1998 Khaan had lost all his mares to rivals.

Khaan's foals were all 1 month old (1994 pre-release) or 2 months old (1994 post-release, 1996) at the time of observation. As has been recorded for captive takhi, these foals spent less time grazing than did adults, probably because a significant portion of their nutritional needs came from their mother's milk. The increase in time spent grazing by the 1994 foals after release (and the similar amount of time spent by 1996 foals) is probably maturational. By this time the foals were 2 months old, and during the second month of life, captive takhi foals exhibit a sharp increase in foraging behaviour (Boyd, 1988b).

Freed from the need to spend as much time grazing, foals moved, stood, and rested more than did the adults. Again, maturational effects were apparent as the amount of time spent resting declined by the second month of age, as has been reported in captive foals (Boyd, 1988b). When compared to captive foals, the percentage of time the 1-month-old foals spent grazing and moving was within 5%, while amount of time spent standing was 8% lower and resting 14% higher than for captive foals. As free-ranging 2 months old, the foals spent 10% less time grazing, about the same amount of time standing, 8% more time moving immediately after release, and 10% more time resting than captive foals. These are likely minimised differences in that the captive foals studied by Boyd (1988b) were observed between the hours of 08:00 and 18:00, so that grazing time might have been

underestimated and resting time overestimated, given the typical distribution of these behaviours across the day (see below).

In captivity, subadults are usually removed from the harem, so the harem composition at Hustain Nuruu presented an unusual opportunity to compare subadult time budgets to that of adults, particularly in 1996 when several subadults were present. The time budget of subadults proved to be similar to that of the adults, with the exception that the two subadults whose dam was present were still suckling.

Release of the horses most greatly affected the amount of time they spent moving. Immediately after release, the amount of time spent moving doubled for all age classes. This increase might represent a sign of stress ('agitation'), exploration of a novel environment, or trekking between favoured sites. In their 1992 observations of this harem just a month after arrival in Mongolia, Van Dierendonck et al. (1996) recorded a frequency of moving only 3% below the post-release values reported here. In later months, percentage of time spent moving declined during their observations to closely match the pre-release values recorded for the harem in 1994. Extensive exploration and trekking were not possible, given the size of the enclosure, so the most likely explanation for the initial results of Van Dierendonck et al. (1996) is mild agitation resulting from stress due to travel, harem formation (the harem was newly formed on arrival), and a new environment. Our 1994 post-release observations were conducted between 2 and 4 weeks after release. In the week immediately after release this harem twice left the Reserve (Boyd, 1998), lending credence to the exploration hypothesis as an explanation for the large increase in time spent moving after release in 1994. Subsequently, Khaan's harem established a home range near its former enclosure and remained within this home range and therefore, within the Reserve. By 1996 the amount of time spent moving declined significantly from immediate post-release levels, but was still significantly higher than prior to release. The free-ranging takhi spent more time moving than when they were captive, or than their counterparts in captive harems are known to spend (Boyd, 1988a). This is most likely due to trekking between water and grazing or resting sites. Whereas in their enclosures the takhi had never been more than 0.5 km from the stream, after release they ranged more widely from water. During observations the takhi would typically leave their morning grazing site, travel 1–2 km to water, and then travel another 2 km to seek shade or heights which were favoured places to rest. After another 2 km trek to the stream in the evening, they returned to favoured grazing sites (see also King, this volume). Housing takhi in spacious enclosures is insufficient to permit them to duplicate this aspect of their wild time budget.

The increased amount of time spent moving did not come at the expense of time spent grazing, which was virtually unchanged in the weeks after release. However, with the exception of the foals, members of Khaan's harem spent less time grazing in 1996 than in 1994, although the difference was not statistically significant. Although the foals did not show a decline in the amount of time spent grazing in 1996, they were still spending at least 10% less time grazing than captive peers studied by Boyd (1988b). It could be that trekking between known favourable sites in 1996 allowed takhi to select better forage than had been present in their enclosure, so they could meet their nutritional needs in less time. Or it may be that weather conditions in 1996 produced better forage so that less grazing time was needed. Regardless, the fact that the takhi could improve body condition while spending

less time foraging implies successful acclimatisation to free-ranging conditions. The fact that 1- and 2-year-old subadults were being allowed to nurse also implies that the takhi experienced excellent nutritional status in 1996 (Boyd, 1991).

Amount of time spent in recumbent rest is relatively inflexible, but typically occurs prior to 06:00 when these observations began (Bubenik, 1961; Boyd, 1988a). The rest recorded here is largely standing rest, which appears to be more labile. Immediately after release, when large amounts of time were spent moving, although the amount of time spent grazing was unchanged, the amount of time spent resting declined significantly. When takhi have "extra time" they evidently rest. The horses rested more prior to release, and again in 1996 and 1998 (King, this volume) when less time was spent grazing.

Release did not appear to affect the distribution of behaviours across the day. Moving and standing behaviours were evenly distributed throughout the day. The horses moved between water, resting sites, mineral licks, and grazing sites, punctuating these bouts with periods of standing. However, grazing and resting behaviour showed strong time-of-day effects correlated with the typical change in ambient temperature that occurs during these hours. Between 06:00 and 08:00 h the horses spent the majority of their time grazing. As the sun rose higher and the temperature increased, the horses moved to resting sites, and resting behaviour occupied the majority of the middle hours of the day. As soon as the sun began to sink and the temperature started to fall, by about 18:00 h, the horses were again spending most of their time grazing. This summer-time crepuscular feeding on either side of a midday resting period has been reported previously for captive takhi (Boyd et al., 1988) and these animals in particular (Van Dierendonck et al., 1996), and it probably represents avoidance of thermal stress and insect harassment by the many flies present in Hustain Nuruu during the summer (Keiper and Berger, 1982). That these patterns were present prior to release and persisted subsequent to release suggests that the takhi were not so stressed by reintroduction as to disrupt their daily routine.

5. Conclusion

Upon release the most pronounced change to the time budget of the takhi was an increase in the amount of time spent moving. While initially a component of exploration may have been involved, persistence of the increase 2 years later suggests that some other explanation is needed. It is believed that the takhi are spending time trekking between favoured sites. Time budgets of foals prior to release were similar to those of captive peers. Upon release, the time budgets of all age classes were similarly affected. The time budget of the 1- and 2-year olds was more similar to that of adults than of foals, indicating their approaching adulthood. Crepuscular grazing and midday resting were typical, regardless of the date relative to reintroduction. The amount of time spent in standing rest appears to be labile; when the takhi moved more immediately after release, resting was the behaviour that correspondingly declined in frequency. When the takhi spent less time grazing in 1996, there was a corresponding increase in the amount of time spent resting. Successful acclimatisation to the wild is indicated by the takhi spending less time grazing, having "leisure time" to spend in rest, and having sufficient nutrition to nurse subadults while maintaining or improving body condition.

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