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Comparative analyses of life-history strategies in Asiatic and African wild asses using a demographical approach

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Abstract. Trade-offs such as the ones between reproduction and longevity or present and future reproduction are believed to shape reproductive patterns. We here used zoo data to investigate trade-offs and life histories in four taxa of Asiatic (*Equus hemionus* ssp.) and African wild asses (*Equus africanus* ssp.). All taxa showed even in captivity peak birth rates during the periods of highest food availability in their natural environments. Sex-specific survival rates with females living longer than males were evident in kulan and onager but not in kiang and Somali wild ass, pointing towards different life-history strategies even among closely related taxa. Females achieved their highest reproductive output earlier in life than males, which is typical for polygynous mating systems. Offspring number and longevity were positively rather than negatively correlated. Taken together evidence for reproductive trade-offs was weak, though the length of the reproductive period was negatively related to birth rates within the reproductive period. Birth intervals increased with female age, probably reflecting detrimental effects of senescence. Despite several limitations, zoo data seem to be useful to better understand the reproductive biology of endangered, rare or cryptic species.

Key words: life-history, trade-off, post-reproductive phase, reproductive phase, birth interval

Introduction

Life histories comprehend all life stages of an individual from birth to death, including age- or stage-specific patterns of reproduction, survival and death. A major objective is to understand how these traits were formed by natural selection in an evolutionary comparative way (Stearns 1989, Roff 2002, Flatt & Heyland 2011). Key life history traits are for instance longevity, age at first reproduction, number and quality of offspring or parental care (Stearns 1989, Roff 2002, Flatt & Heyland 2011). All these traits are thought to be constrained by trade-offs, as limited resources can only be allocated once and, consequently, augmenting one feature will have negative effects on others (Roff 2002, Stearns 1989, Zera & Harshman 2001, Flatt & Heyland 2011).

A classical trade-off is the one between present and future reproduction, meaning that an increase in present reproduction can only be achieved at the expense of reduced future reproduction opportunities, for instance because it reduces longevity (Stearns 1989, Zera & Harshman 2001, Roff 2002). Longevity, however, may strongly affect individual fitness especially in iteroparous, long-lived species due to positive correlations with reproductive output (Newton 1989, Stearns 1989, Zera & Harshman 2001). Hence, longevity and reproduction are expected to be traded off against each other, although positive correlations have been repeatedly found as high-quality individuals may be able to strongly invest into both (Bell & Koufopanou 1986, Clutton-Brock 1988, Newton 1989). Thus, the above trade-off warrants an optimal distribution of reproductive events throughout lifetime, including birth intervals and birth rates. Birth intervals are regarded as an indicator of the mother's performance, with high-quality females being able to afford short intervals (Duncan et al. 1984). Resource-allocation trade-offs may further be modulated by other factors such as population density. This is because density increases competition, typically reducing food availability and storage reserves in turn reducing reproductive potential (Fowler 1987, Stewart et al. 2005).

Though understanding life-history trade-offs is obviously important, appropriate data are often not

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available. This is especially true for cryptic, rare or endangered species. Against this background we here make use of zoo data gathered for four highly endangered equids, for which hardly any other data are available. We investigate three Asiatic wild ass subspecies (kulan, *Equus hemionus kulan*, onager, *E. h. onager*, and kiang, *E. h. holdereri*) and the African Somali wild ass (*Equus africanus somalicus*) to get some insights into their life histories. Striking advantages of zoo data are their accuracy and their availability even for endangered, non-domestic species (e.g. Pohle 1971-2014, Pohle 1973-2014, Pelletier et al. 2009). Using such data may not only enhance our general understanding of life-history trade-offs, but also breeding protocols and thus offspring production aiding reintroduction or conservation projects for these highly endangered equids (Nowak 1999, Bahloul et al. 2001, Feh et al. 2001, Moehlmann 2005).

Specifically, we address the following questions here: 1) Do births show age-specific variation and seasonal patterns even under beneficial zoo conditions? 2) Are reproduction and longevity traded-off against each other or are they positively correlated? 3) Are there sex differences in survival patterns, which may reflect differential investment into reproduction? 4) Are high offspring numbers/birth rates associated with lower offspring quality? 5) Do birth intervals dependent on female age as a matter of ongoing senescence, or the sex of the previous offspring due to differential maternal investment?

Material and Methods

Study organisms

We here studied three Asiatic wild asses (*Equus hemionus*), namely kulan (*E. h. kulan* Groves & Mazak, 1968), onager (*E. h. onager* Boddaer, 1785), and kiang (*E. h. holdereri* Moorcroft, 1841), as well as the African Somali wild ass (*Equus africanus somalicus* Sclater, 1885). Asiatic wild asses live in (semi-)desert and steppe habitats of Russia, Turkmenia and Kazakhstan (kulan), Iran (onager), and Southern China (kiang; Groves & Mazak 1968, Nowak 1999, Oakenfull et al. 2000). Concomitantly, they are able to survive extended periods of time with minimum food and water supply (Klingel 1998, Nowak 1999). Adult females and immatures live in groups of up to 400 individuals and are led by an old female, while adult males tend to live alone (Klingel 1998, Nowak 1999). Kulan and onager are highly endangered due to poaching, habitat destruction, and competition with

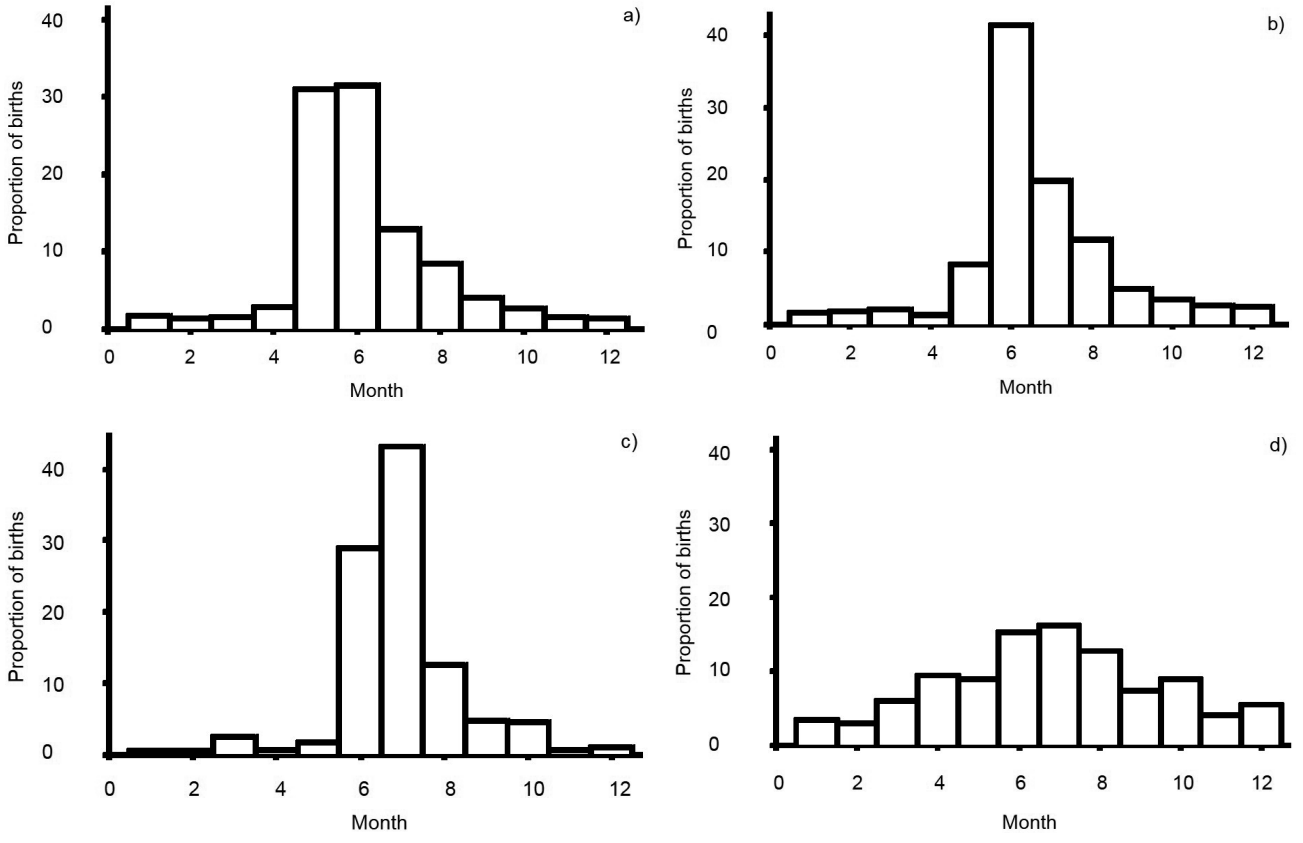


Fig. 1. Frequency distributions of births (% of all births) in relation to month of the year in kulan, a) n = 1605; onager, b) n = 837; kiang, c) n = 343; and Somali wild ass, d) n = 426.

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domestic animals (Dathe 1971, Saltz & Rubenstein 1995, Bahloul et al. 2001, Moehlmann 2005). Kulans mainly persist in (semi-)wild populations in central Asia, and onagers are nowadays restricted to a few protected sites in Iran (Klingel 1998, Bahloul et al. 2001, Moehlmann 2005). Compared with both above taxa, the kiang seems to be less endangered (Nowak 1999, Moehlmann 2005). Historically, *Equus africanus* was distributed throughout northern Africa, but is now critically endangered and restricted to Ethiopia, Eritrea, and Somalia (Lang & Lehmann 1972, Dathe 1973, Gippoliti 2014). The Somali wild ass also inhabits (semi-) arid bush- and grassland.

Data acquisition and analyses

Because of their high endangerment, the World Association of Zoos and Aquaria decided to establish international studbooks for Asiatic (Pohle 1971-2014) and African wild asses (Pohle 1973-2014). These studbooks include data on > 1800 kulan, 900 onager, 350 kiang, and 620 Somali wild ass individuals. The extant zoo populations were founded by 130 kulan, 55 onager, 10 kiang, and 11 Somali wild asses (Pohle 1971-2014, Pohle 1973-2014). The data collected in the studbooks include sex, date of birth, date of death, transfer dates, locations, and the identity of parents for all individuals kept in zoos at a global scale. These data form the basis for all further analyses (cf. Table 1). We calculated lifespan as the period between birth and death, and post-reproductive phase as the period between the birth of the last offspring and the individual's death. Only data from animals that 1) had already died, 2) originate from the northern hemisphere (because of possible climatic and light cycle influences on mortality rates), and 3) from institutions where no management, culling

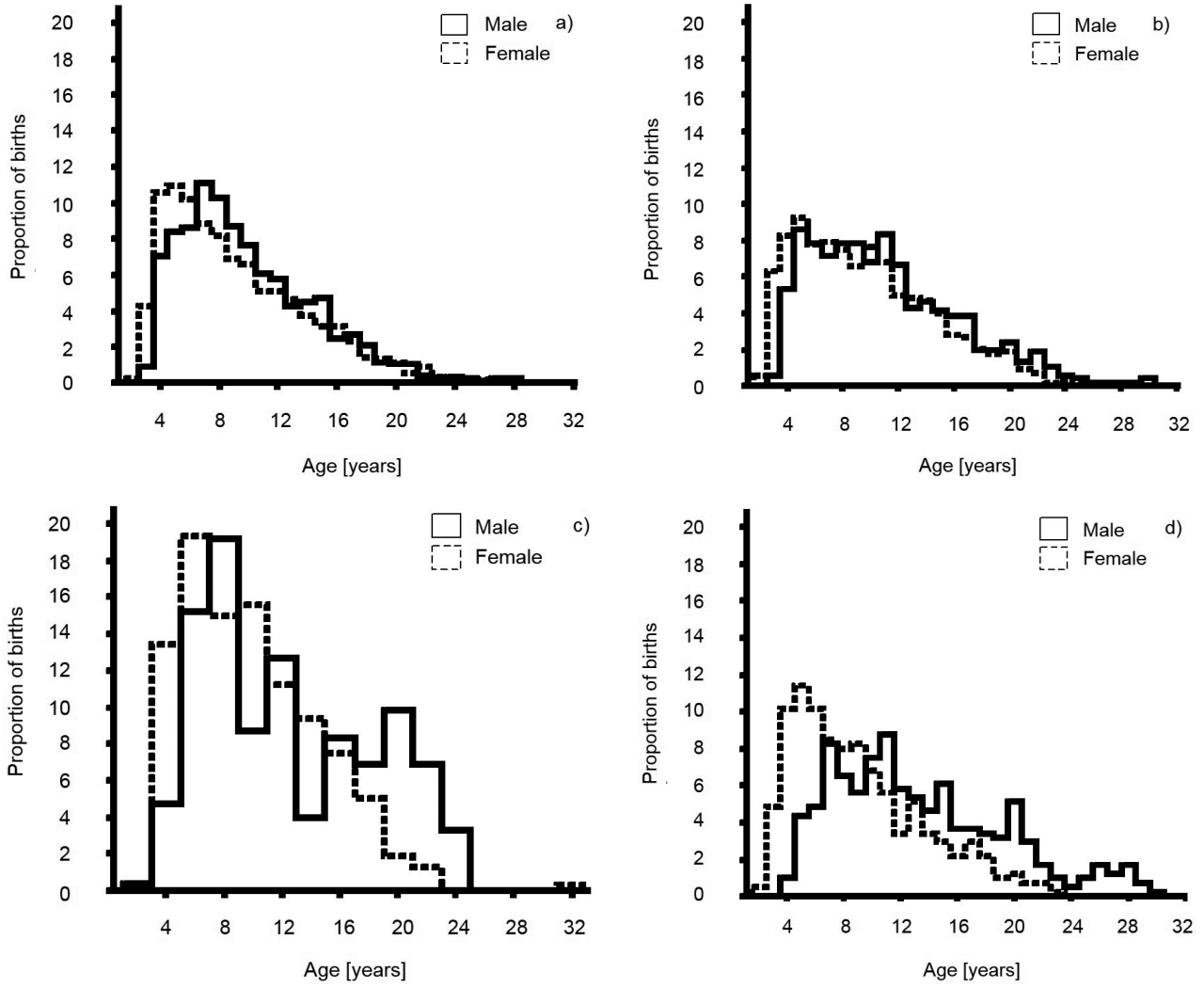


Fig. 2. Frequency distributions of births (%) in relation to male and female age for kulan, a) n_{males} = 1496, $n_{females}$ = 1351; onager, b) n_{males} = 756, $n_{females}$ = 749; kiang, c) n_{males} = 276, $n_{females}$ = 321; and Somali wild ass, d) n_{males} = 413, $n_{females}$ = 413.

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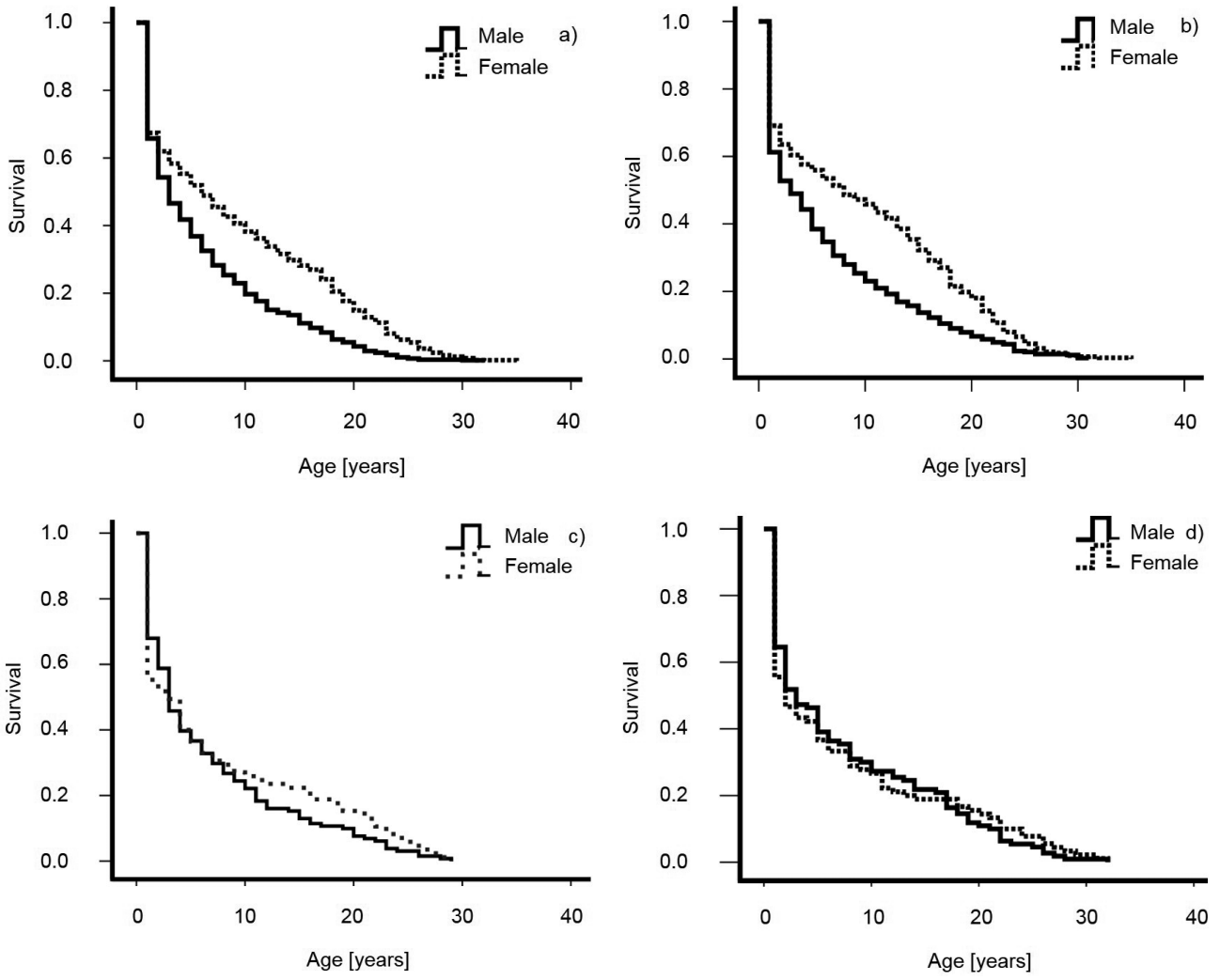


Fig. 3. Cumulative survival in relation to age in male and female kulan, a) n = 1915; onager, b) n = 899; kiang, c) n = 353; and Somali wild ass, d) n = 432.

or contraception as it was the case in the past were applied were included in subsequent analyses. Note that most of the data presented here stem from 1955-1995 i.e. the period during which males and females were typically kept together and unconstrained reproduction was allowed.

Table 1. Summary of parameters (including categories and units) used to investigate life-history patterns in Asiatic and African wild asses.

Parameter	Categories/units
Sex	male, female
Longevity	(days)
Age at first reproduction	(days)
Length of reproductive phase	(days)
Length of post-reproductive phase	(days)
Offspring number	number
Birth interval	(days)
Birth rate per year throughout the entire lifespan	(number/year)
Birth rate per year throughout the reproductive phase	(number/year)
Percentage of offspring surviving > 100 days	(%)
Mean longevity of offspring	(days)

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Table 2. Results of parent-offspring regressions to estimate the heritability of longevity. Heritabilities were estimated as the slope of mid-parents versus mid-offspring linear regressions. Only *P*-values < 0.025 are significant after applying a sequential Bonferroni correction.

Longevity	Slope	F	*P*	n
Kulan	0.11	8.0	**0.005**	333
Onager	0.20	17.0	**< 0.001**	216
Kiang	0.20	4.2	0.047	46
Somali wild ass	0.05	0.2	0.656	43

Statistical analyses

All statistical tests have been computed using SPSS 13.0 or Minitab 16. The distribution of births in relation to season (month, Fig. 1) and in relation to male and female age across species and sexes (Fig. 2) were tested against each other using Kolmogorov-Smirnov tests. Survival curves of males and females were statistically compared with Wilcoxon-Gehan tests (Fig. 3). Heritability of longevity was estimated as the slope of mid-parent versus mid-offspring regressions (Table 2). To

Table 3. Linear mixed models for the effects of offspring number and birth rate, respectively, on breeding male and female longevity in kulan, onager, kiang, and Somali wild ass. Offspring number reflects the absolute number of offspring sired (for males) or born (for females) throughout the entire lifespan, and birth rate the number of offspring sired or born divided by the respective individual's longevity. For each factor, a separate model was constructed owing to strong correlations among traits. Data were tested for normality and transformed if necessary. The respective reproductive parameter was included as fixed covariate, and individual ID, keeping, and density as random variables. Parameters not shown in the table have been removed during model construction due to redundancy. Only *P*-values < 0.001 are significant after applying a sequential Bonferroni correction.

	Effects	Estimate ± 1 SE	df	F	Wald Z	*P*
Kulan	Intercept	5633.0 ± 546.0	1, 38	106.5		**< 0.0001**
Males	Offspring number	95. 5 ± 20.1	1, 155	22.6		**< 0.0001**
n = 157	ID (random)	2.7 ± 4.0			0.7	0.4997
	Keeping	71.2 ± 126.5			0.6	0.5734
	Density	621.9 ± 1196.9			0.5	0.6034
Kulan	Intercept	6550.7 ± 520.9	1, 8	158.2		**< 0.0001**
Males	Birth rate (lifespan)	–224.5 ± 309.4	1, 133	0.2		0.4694
n = 157	ID (random)	4.1 ± 6.0			0.7	0.4949
	Keeping	5.8 ± 38.6			0.1	0.8814
	Density	945.7 ± 1803.3			0.5	0.6000
Kulan	Intercept	6943.7 ± 525.6	1, 79	174.5		**< 0.0001**
Females	Offspring number	175.0 ± 43.3	1, 200	16.3		**0.0001**
n = 214	ID (random)	2.6 ± 4.1			0.6	0.5202
	Keeping	206.6 ± 435.5			0.5	0.6352
Kulan	Intercept	7734.8 ± 450.6	1, 205	294.1		**< 0.0001**
Females	Birth rate (lifespan)	–2897.9 ± 1018.7	1, 211	8.1		0.0049
n = 213	ID (random)	5.7 ± 8.5			0.7	0.5037
	Keeping	395.3 ± 704.9			0.6	0.5904
Onager	Intercept	6186.4 ± 722.1	1, 96	73.4		**< 0.0001**
Males	Offspring number	129.6 ± 30.3	1, 94	18.3		**< 0.0001**
n = 96	ID (random)	13.0 ± 19.5			0.7	0.5050
	Keeping	7999.0 ± 11947.9			0.7	0.5032
	Density	30419.2 ± 50482.8			0.6	0.5468
Onager	Intercept	8055.9 ± 782.3	1, 81	10.3		**< 0.0001**
Males	Birth rate (lifespan)	–471.1 ± 579.0	1, 89	-0.8		0.4181
n = 93	ID (random)	21.2 ± 31.4			0.7	0.4982
	Keeping	10865.0 ± 16248.8			0.7	0.5037
	Density	13104.5 ± 29998.0			0.4	0.6622
Onager	Intercept	5451.5 ± 488.9	1, 109	124.3		**< 0.0001**
Females	Offspring number	383.3 ± 63.1	1, 142	63.1		**< 0.0001**
n = 144	ID (random)	10.8 ± 16.5			0.7	0.5134
Onager	Intercept	9081.5 ± 538.3	1, 113	284.6		**< 0.0001**

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Females	Birth rate (lifespan)	–3026.9 ± 1314.0	1, 142	5.3		0.0227
n = 145	ID (random)	41.2 ± 59.4			0.7	0.4881
	Keeping	412.4 ± 836.1			0.5	0.6218
Kiang	Intercept	9329.3 ± 856.7	1, 22	118.6		**< 0.0001**
Males	Offspring number	79.5 ± 47.7	1, 20	47.7		0.1110
n = 22	ID (random)	499.8 ± 782.3			0.6	0.5229
	Density	27088.5 ± 40958.4			0.7	0.5084
Kiang	Intercept	9747.8 ± 846.5	1, 21	132.6		**< 0.0001**
Males	Birth rate (lifespan)	943.0 ± 1043.4	1, 20	0.8		0.3768
n = 22	ID (random)	632.5 ± 969.6			0.7	0.5142
	Density	28112.4 ± 42721.0			0.7	0.5105
Kiang	Intercept	7057.8 ± 1078.1	1, 21	42.9		**< 0.0001**
Females	Offspring number	227.9 ± 161.1	1, 21	2.0		0.1719
n = 21	ID (random)	472.4 ± 723.7			0.7	0.5139
Kiang	Intercept	10387.2 ± 1170.2	1, 20	78.8		**< 0.0001**
Females	Birth rate (lifespan)	–5524.2 ± 3561.8	1, 19	3.4		0.1372
n = 20	ID (random)	1633.1 ± 2455.1			0.7	0.5059
Somali wild ass	Intercept	13864.6 ± 2130.5	1, 7	42.4		**< 0.0001**
Males	Offspring number	91.1 ± 24.2	1, 21	14.1		**< 0.0001**
n = 23	ID (random)	449.0 ± 734.8			0.6	0.5412
	Density	55232.7 ± 95744.7			0.6	0.5640
Somali wild ass	Intercept	15911.7 ± 2443.4	1, 15	42.4		**< 0.0001**
Males	Birth rate (lifespan)	1502.6 ± 691.2	1, 20	4.7		0.0416
n = 23	ID (random)	738.6 ± 1146.4			0.6	0.5194
	Density	50406.0 ± 94400.9			0.5	0.5934
Somali wild ass	Intercept	5086.7 ± 1195.2	1, 14	18.1		**0.0009**
Females	Offspring number	689.1 ± 99.1	1, 31	48.4		**< 0.0001**
n = 32	Keeping (random)	2328.4 ± 7277.6			0.3	0.7490
	Density	84183.3 ± 184242.3			0.5	0.6477
Somali wild ass	Intercept	10014.9 ± 2551.4	1, 19	15.4		**0.0009**
Females	Birth rate (lifespan)	2555.2 ± 3770.8	1, 30	0.5		0.5031
n = 32	ID (random)	384.0 ± 692.7			0.6	0.5794

investigate effects of 1) reproductive traits on longevity (Table 3), 2) reproductive traits on the length of the reproductive and post-reproductive phase, respectively (Table 4), and 3) the impact of age at reproduction on birth intervals (Table 5) we used linear mixed models including individual identity (ID), keeping and density (if applicable) as random (or repeated) covariates. We calculated "individual density" as the median group size experienced by a given individual during its entire life span, keeping as the location where the animal lived the majority of its lifespan and ID as the identity number of a certain individual.

Results

Births in relation to season and age

In terms of the distribution of birth rates across the season, all four taxa showed similar patterns with peaks between May and July (Fig. 1). In Somali wild asses, though, births appeared to be more scattered throughout the season than in the other three taxa. Sex differences, with birth rates peaking at a later age in males than in females, were significant in all four taxa (Kolmogorov-Smirnov test: all P-values < 0.001; Fig. 2). Accordingly, first reproduction took place at an age of three years in kulan males, two years in kulan females, three years in onager males, two years in onager females, two years in kiang males, three years in kiang females, four years in male and two years in female Somali wild asses. Birth distributions in relation to age for males were very similar across species, the only significant difference occurring between kiang and Somali wild ass (Z = 5.6, P <

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Table 4. Reproductive parameters and the length of the reproductive phase and the post-reproductive phase. Effects of various reproductive parameters (cf. Table 1) on the length of the reproductive phase and the post-reproductive phase, respectively, using linear mixed models for kulan, onager, kiang, and Somali wild ass females. For each factor, a separate model was constructed owing to strong correlations among traits. Data were tested for normality and transformed if necessary. The respective reproductive parameter was included as fixed covariate, and individual ID, keeping, and density as random variables. Parameters not shown in the table have been removed during model construction due to redundancy. Only *P*-values < 0.0005 are significant after applying a sequential Bonferroni correction.

Repro-ductive phase	Effects	Estimate ± 1 SE	df	F	Wald Z	*P*
Kulan	Intercept	–66.6 ± 370.4	1, 202	< 0.1		0.8575
Female	Female longevity	0.4 ± < 0.1	1, 212	89.9		**< 0.0001**
n = 212	ID (random)	1.3 ± 2.0			0.7	0.5063
	Density	1881.2 ± 2763.1			0.7	0.4960
n = 212	Intercept	3232.8 ± 284.7	1, 160	128.9		**< 0.0001**
	Post-reproductive phase	–0.2 ± 0.1	1, 210	8.1		0.0049
	ID (random)	4.3 ± 6.3			0.7	0.4960
	Keeping	112.6 ± 248.2			0.5	0.6501
	Density	1100.9 ± 1702.0			0.6	0.5177
n = 212	Intercept	1478.3 ± 242.3	1, 133	37.2		**< 0.0001**
	Offspring number	291.9 ± 27.3	1, 212	114.7		**< 0.0001**
	ID (random)	0.7 ± 1.1			0.6	0.5231
n = 211	Intercept	1167.6 ± 314.0	1, 138	13.8		**0.0003**
	Birth rate (lifespan)	6016.3 ± 722.6	1, 209	69.3		**< 0.0001**
	ID (random)	1.3 ± 2.1			0.6	0.5259
	Keeping	56.0 ± 157.1			0.4	0.7215
n = 163	Intercept	5252.4 ± 232.6	1, 161	509.8		**< 0.0001**
	Birth rate (reproductive phase)	–2667.1 ± 226.5	1, 160	138.6		**< 0.0001**
	ID (random)	3515.3 ± 225.5			0.7	0.5012
	Density	–209.3 ± 58.7			0.7	0.5064
n = 212	Intercept	4329.6 ± 566.4	1, 206	58.4		**< 0.0001**
	Percentage offspring surviving > 100 days	–1791.6 ± 613.0	1, 208	8.5		0.0039
	ID (random)	3.8 ± 5.7			0.7	0.4985
	Keeping	78.3 ± 199.6			0.4	0.6948
	Density	1803.6 ± 2690.9			0.7	0.5027
n = 212	Intercept	3668.8 ± 356.6	1, 199	105.8		**< 0.0001**
	Age at first reproduction	–0.4 ± 0.1	1, 210	10.6		0.0013
	ID (random)	3.6 ± 5.4			0.7	0.4986
	Keeping	128.2 ± 269.6			0.5	0.6345
	Density	927.5 ± 1459.1			0.6	0.5250
Onager	Intercept	1684.0 ± 456.4	1, 84	13.6		**0.0004**
Female	Female longevity	0.5 ± 0.1	1, 133	107.6		**< 0.0001**
n = 140	ID (random)	3.5 ± 5.6			0.6	0.5345
n = 140	Intercept	6646.1 ± 355.3	1, 45	349.8		**< 0.0001**
	Post-reproductive phase	–0.2 ± 0.1	1, 138	8.2		0.0048
	ID (random)	28.8 ± 41.5			0.7	0.4883
	Keeping	251.1 ± 541.1			0.5	0.6426
n = 138	Intercept	2781.2 ± 332.6	1, 47	69.9		**< 0.0001**
	Offspring number	506.0 ± 43.5	1, 121	135.2		**< 0.0001**
	ID (random)	2.3 ± 4.0			0.6	0.5545
n = 137	Intercept	5104.0 ± 464.7	1, 83	120.6		**< 0.0001**

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	Birth rate (lifespan)	3710.9 ± 1123.6	1, 136	10.9		0.0012
	ID (random)	21.8 ± 31.7			0.7	0.4914
	Keeping	197.2 ± 462.0			0.4	0.6695
n = 138	Intercept	6480.5 ± 537.0	1, 103	145.6		**< 0.0001**
	Birth rate (reproductive phase)	–534.6 ± 1078.1	1, 137	0.2		0.6208
	ID (random)	28.4 ± 41.1			0.7	0.4893
	Keeping	293.1 ± 610.6			0.5	0.6312
n = 212	Intercept	4329.6 ± 566.4	1, 206	58.4		**< 0.0001**
	Percentage offspring surviving > 100 days	–1791.6 ± 613.0	1, 208	8.5		0.0039
	ID (random)	3.8 ± 5.7			0.7	0.4985
	Keeping	78.3 ± 199.6			0.4	0.6948
	Density	1803.6 ± 2690.9			0.7	0.5027
n = 139	Intercept	6576.7 ± 421.7	1, 83	243.2		**< 0.0001**
	Age at first reproduction	–0.2 ± 0.1	1, 137	2.5		0.1197
	ID (random)	26.7 ± 38.6			0.7	0.4898
	Keeping	159.9 ± 424.4			0.4	0.7064
Kiang	Intercept	–557.9 ± 729.1	1, 21	0.6		0.4526
Female	Female longevity	0.6 ± 0.1	1, 21	41.8		**< 0.0001**
n = 21	Intercept	5371.9 ± 785.7	1, 6	46.7		0.0005
n = 21	Post-reproductive phase	< 0.1 ± 0.3	1, 18	< 0.1		0.8990
	ID (random)	225.3 ± 359.0			0.6	0.5303
	Density	6661.0 ± 20379.1			0.3	0.7438
n = 21	Intercept	1467.5 ± 668.8	1, 21	4.8		0.0396
	Offspring number	483.5 ± 118.2	1, 21	16.7		0.0005
n = 20	Intercept	5421.9 ± 1242.9	1, 20	19.0		0.0022
	Birth rate (lifespan)	1879.5 ± 3203.8	1, 19	0.3		0.5642
	Density (random)	36798.7 ± 60164.6			0.6	0.5408
n = 19	Intercept	5732.0 ± 424.5	1, 19	182.3		**< 0.0001**
	Birth rate (reproductive phase)	-2587.0 ± 641.7	1, 19	16.3		0.0007
n = 20	Intercept	3741.2 ± 1118.1	1, 19	11.2		0.0034
	Percentage offspring surviving > 100 days	3956.3 ± 1522.5	1, 19	6.8		0.0176
	Density (random)	78183.1 ± 116382.9			0.7	0.5017
n = 21	Intercept	8572.8 ± 944.6	1, 20	82.4		**< 0.0001**
	Age at first reproduction	–1.8 ± 0.4	1, 20	18.3		**0.0004**
	ID (random)	497.0 ± 723.6			0.7	0.4922
Somali wild ass	Intercept	–420.9 ± 601.1	1, 31	0.5		0.4890
Female	Female longevity	0.5 ± 0.1	1, 31	34.8		**< 0.0001**
n = 31	Intercept	2575.7 ± 505.7	1, 31	25.9		**< 0.0001**
n = 31	Post-reproductive phase	0.1 ± 0.2	1, 31	0.1		0.7037
n = 31	Intercept	–215.3 ± 319.1	1, 31	0.5		0.5048
	Offspring number	564.9 ± 50.2	1, 31	126.5		**< 0.0001**
n = 29	Intercept	–291.6 ± 344.0	1, 29	0.7		0.4036
	Birth rate (lifespan)	21532831.8 ± 2028108.4	1, 29	112.7		**< 0.0001**
n = 24	Intercept	6979.2 ± 1751.2	1, 20	15.9		0.0007
	Birth rate (reproductive phase)	–2388.1 ± 558.7	1, 16	18.3		0.0006
	ID (random)	188.4 ± 408.3			0.5	0.6445
	Keeping	189.8 ± 6478.3			< 0.1	0.9766

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	Density	69082.0 ± 143337.9			0.5	0.6298
n = 31	Intercept	5329.9 ± 2286.2	1, 6	5.4		**0.0003**
	Percentage offspring surviving > 100 days	–473.4 ± 1478.2	1, 28	0.1		0.7511
	ID (random)	125.7 ± 300.5			0.4	0.6757
	Density	12566.7 ± 62398.5			0.2	0.8404
n = 31	Intercept	3632.2 ± 951.3	1, 31	14.6		0.0006
	Age at first reproduction	–0.5 ± 0.5	1, 31	1.2		0.2752
Postrepro-ductive phase	Effects	Estimate ± 1 SE	df	F		*P*
Kulan	Intercept	–1175.1 ± 329.5	1, 126	12.7		0.0005
Female	Female longevity	0.5 ± < 0.1	1, 212	136.3		**< 0.0001**
n = 215	ID (random)	0.3 ± 0.6			0.6	0.5603
	Density	522.1 ± 821.2			0.6	0.5250
n = 230	Intercept	2163.7 ± 187.7	1, 208	132.9		**< 0.0001**
	Number of offspring	-64.5 ± 30.2	1, 216	4.6		0.0337
	Density (random)	373.1 ± 664.9			0.6	0.5748
n = 213	Intercept	3817.8 ± 286.5	1, 136	177.6		**< 0.0001**
	Birth rate (lifespan)	–6065.1 ± 683.3	1, 213	78.8		**< 0.0001**
	Density (random)	0.6 ± 1.0			0.6	0.5316
n = 163	Intercept	1714.1 ± 156.7	1, 78	119.7		**< 0.0001**
	Birth rate (reproductive phase)	–26.1 ± 54.6	1, 163	0.2		0.6326
	Density (random)	319.9 ± 569.8			0.6	0.5745
n = 230	Intercept	1258.5 ± 494.7	1, 229	6.5		**< 0.0001**
	Percentage offspring surviving > 100 days	822.6 ± 555.6	1, 229	2.2		0.1401
	Density (random)	804.0 ± 1259.5			0.6	0.5232
n = 214	Intercept	1834.9 ± 326.2	1, 180			**< 0.0001**
	Age at first reproduction	0.1 ± 0.1	1, 214			0.5264
	Density (random)	717.7 ± 1152.6			0.6	0.5335
Onager	Intercept	–1733.0 ± 460.2	1, 85	14.2		**< 0.0001**
Female	Female longevity	0.5 ± 0.1	1, 137	74.5		**< 0.0001**
n = 147	ID (random)	3.4 ± 5.4			0.6	0.5355
n = 147	Intercept	1793.3 ± 241.7	1, 147	55.0		**< 0.0001**
	Number of offspring	–56.2 ± 49.5	1, 147	1.3		0.2586
n = 145	Intercept	3726.9 ± 353.5	1, 90	111.1		**< 0.0001**
	Birth rate (lifespan)	–6599.1 ± 945.5	1, 145	48.7		**< 0.0001**
	ID (random)	2.6 ± 4.3			0.6	0.5440
n = 162	Intercept	1608.4 ± 266.6	1, 155	36.4		**< 0.0001**
	Birth rate (reproductive phase)	109.1 ± 277.0	1, 161	0.2		0.6944
	Density (random)	332.6 ± 588.2			0.6	0.5718
n = 147	Intercept	1464.1 ± 351.9	1, 147	17.3		**0.0001**
	Percentage offspring surviving > 100 days	141.7 ± 441.7	1, 147	0.1		0.7488
n = 141	Intercept	1438.8 ± 301.0	1, 141	22.8		**< 0.0001**
	Age at first reproduction	0.1 ± 0.1	1, 141	0.2		0.6943
Kiang Female	Intercept	–1198.2 ± 558.8	1, 22	4.6		0.0433
n = 22	Female longevity	0.3 ± 0.1	1, 22	21.0		**0.0001**
n = 21	Intercept	572.5 ± 586.9	1, 21	1.0		0.3405
	Number of offspring	133.7 ± 103.8	1, 21	1.7		0.2117

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n = 20	Intercept	3619.5 ± 792.5	1, 20	20.9		**0.0004**
	Birth rate (lifespan)	–5817.8 ± 2422.7	1, 19	5.8		0.0265
	ID (random)	466.5 ± 728.2			0.6	0.5218
n = 19	Intercept	2312.0 ± 543.6	1, 19	18.1		< **0.0001**
	Birth rate (reproductive phase)	–622.1 ± 692.5	1, 18	0.8		0.3811
n = 20	Intercept	2020.1 ± 1105.5	1, 19	18.7		0.0836
	Percentage offspring surviving > 100 days	–359.3 ± 1490.5	1, 20	19.9		0.8120
	ID (random)	150.6 ± 309.4			0.5	0.6264
n = 21	Intercept	2230.1 ± 971.5	1, 21	5.3		0.0321
	Age at first reproduction	–0.3 ± 0.4	1, 21	0.3		0.4856
	ID (random)	60.5 ± 109.6			0.6	0.5808
Somali wild ass	Intercept	–1081.9 ± 498.2	1, 32	4.7		0.0374
Female	Female longevity	0.4 ± 0.1	1, 32	27.8		**< 0.0001**
n = 32	Intercept	635.9 ± 548.9	1, 32	1.3		0.2553
n = 32	Number of offspring	110.7 ± 86.6	1, 32	1.6		0.2099
n = 32	Intercept	3230.6 ± 853.3	1, 31	14.3		0.0006
	Birth rate (lifespan)	–4373.2 ± 2183.5	1, 31	4.0		0.0540
	Keeping (random)	5092.0 ± 9385.1			0.5	0.5874
n = 24	Intercept	–0.3 ± 681.0	1, 24	< 0.1		0.9997
	Birth rate (reproductive phase)	1793.7 ± 678.3	1, 24	7.0		0.0142
n = 32	Intercept	2320.8 ± 1623.1	1, 11	2.0		0.1805
	Percentage offspring surviving > 100 days	1441.0 ± 1115.0	1, 30	1.7		0.2061
	Density (random)	78.3 ± 170.7			0.5	0.6463
n = 31	Intercept	3813.2 ± 1500.2	1, 19	6.5		0.0198
	Age at first reproduction	0.5 ± 0.4	1, 30	1.8		0.1909
	ID (random)	179.0 ± 317.4			0.6	0.5728

0.001), with the distribution being more peaked in kiang. The same pattern of a more peaked birth distribution, being significantly different from all other species (all *P*-values < 0.004), also prevailed in female kiang. Furthermore, the distribution of births in kulan females differed from those in onager and Somali wild ass (both *P*-values < 0.001). All other comparisons were non-significant.

Sex- and species-specific variation in survival rates

Mean longevity was 5.1 ± 0.3 and 8.7 ± 0.4 years in kulan males and females, 5.7 ± 0.4 and 9.4 ± 0.5 years in onager males and females, 5.8 ± 0.6 and 6.6 ± 1.0 years in kiang males and females, and 6.8 ± 0.8 and 6.5 ± 1.0 years in male and female Somali wild asses. Accordingly, kulan (Wilcoxon-Gehan: 24.2, df = 1, *P* < 0.001) and onager females (Wilcoxon-Gehan: 20.6, *P* < 0.001) showed significantly higher survival rates than their male counterparts, which was not the case in kiang (*P* = 0.431) and Somali wild ass (*P* = 0.660; Fig. 3). Across species, male survival rates did not differ significantly (all *P*-values > 0.3). In contrast, kulan and onager females had significantly higher survival rates than kiang and Somali wild ass females (kulan *vs.* kiang: Wilcoxon-Gehan: 7.2, *P* = 0.007; kulan *vs.* Somali wild ass: Wilcoxon-Gehan: 5.4, *P* = 0.021; onager *vs.* kiang: Wilcoxon-Gehan: 6.3, *P* = 0.012; onager *vs.* Somali wild ass: Wilcoxon-Gehan: 5.3, *P* = 0.022; all other combinations non-significant: *P* > 0.6). Throughout, mortality rates were not significantly affected by male or female density (after Bonferroni correction; range of *P*-values 0.022 – 0.983, n = 16 analyses). Parent-offspring regressions indicated significant heritability for longevity in kulan and onager and an according tendency in kiang (Table 2).

Reproduction and longevity

Mean offspring number per breeding individual was 7 ± 0.5 in kulan males and 4 ± 0.2 in kulan females, 7 ± 0.6 and 4 ± 0.2 in onager males and females, 7 ± 1.3 and 3 ± 0.3 in kiang males and females, and 9 ± 1.3 and 4 ± 0.3 in Somali wild ass males and females. Maximum offspring number amounted to 42 and 16 in kulan males and females, 36 and 13 in onager males and females, 28 and 10 in kiang males and females, and 38 and 10 in Somali wild ass males and females.

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Table 5. Effects of age at each reproductive event and the sex of the previous offspring on birth interval using linear mixed models. Birth interval was included as fixed covariate, age at first reproduction as covariate, sex of the previous offspring as fixed factor, animal ID as repeated, keeping and density as random variables. Data were tested for normality and transformed if necessary. Parameters not shown in the table have been removed during model construction due to redundancy. Only *P*-values < 0.007 are significant after applying a sequential Bonferroni correction.

	Effects	Estimate ± 1 SE	df	F	Wald Z	*P*
Kulan	Intercept	512.87 ± 69.33	1, 160	54.7		**< 0.0001**
n = 997	Age at reproduction	0.08 ± 0.01	1, 996	74.5		**< 0.0001**
	Sex previous offspring	67.26 ± 30.43	1, 995	4.9		0.0273
	ID (repeated)	230242.82 ± 10306.87			22.3	**< 0.0001**
	Keeping (random)	5.19 ± 8.22			0.6	0.5279
	Density (random)	6.20 ± 12.00			0.5	0.6047
Onager	Intercept	419.21 ± 65.91	1, 564	40.5		**< 0.0001**
n = 564	Age at reproduction	0.10 ± 0.02	1, 564	44.0		**< 0.0001**
	Sex previous offspring	22.83 ± 49.48	1, 564	0.2		0.6447
	ID (repeated)	344962.42 ± 20542.21			16.8	**< 0.0001**
Kiang	Intercept	218.41 ± 87.19	1, 252	6.3		0.0129
n = 252	Age at reproduction	0.13 ± 0.02	1, 252	41.9		**< 0.0001**
	Sex previous offspring	26.92 ± 63.00	1, 252	0.2		0.6695
	ID (repeated)	247931.38 ± 22087.48			11.2	**< 0.0001**
Somali wild ass	Intercept	355.51 ± 60.07	1, 312	35.0		**< 0.0001**
n = 312	Age at reproduction	0.09 ± 0.01	1, 312	33.1		**< 0.0001**
	Sex previous offspring	5.84 ± 46.44	1, 312	< 0.1		0.9000
	ID (repeated)	166274.33 ± 13312.60			12.5	**< 0.0001**

Offspring number was significantly positively related to longevity in kulan males and females, onager males and females, and Somali wild ass males and females, but not in kiang males and females, while birth rate was not significantly related to longevity throughout (Table 3).

The length of reproductive phase (Table 4) correlated significantly positively with longevity and offspring number in all taxa, and with birth rate throughout the entire lifespan in two out of four taxa. Reproductive phase tended to be negatively related to post-reproductive phase in kulan and onager, and to birth rate within the reproductive phase in one out of four cases (plus two according tendencies). No significant relations were found between offspring surviving > 100 days and the length of the reproductive phase. Age at first reproduction was significantly negatively related to the length of the reproductive phase in kiang only. Throughout, effects of female identity, keeping, and density had no significant influence.

Similar to above, the length of the post-reproductive phase was significantly positively related to female longevity in all four taxa (Table 4). Additionally, birth rate throughout the entire lifespan was significantly negatively associated with the length of the post-reproductive in kulan and onager. Relationships between other reproductive traits and the length of the post-reproductive were non-significant throughout, as were effects of female identity, keeping, and density.

Birth intervals increased significantly with age in all four taxa, while the sex of the previous offspring had no significant impact (Table 5). Effects of individual ID were significant throughout, while those of keeping or density were not. Regarding the relationship between birth rate throughout the entire lifespan and the percentage of offspring surviving > 100 days, a significantly negative relationship was found in kulan females only ($F_{1,209}$ = 15.8, P < 0.0001; all other P-values > 0.46).

Discussion

Births in relation to season and age

All four taxa showed a seasonal distribution of births peaking in spring and early summer (May to July), though the distribution appeared to be less peaked in Somali wild asses compared with the other taxa. Asiatic wild asses live in Asian regions where rainfalls peak usually in spring. Thus, the majority of young are born 1-2 months after peak rainfall, i.e. within the period of highest food availability (Siegmund 2006). At the same time, females are in good condition within this period of time (Prins 1996). The Przewalski horse (*Equus przewalski*), a related equid with similar biology, also shows a

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peak of births between May and July (Volf 1996). In Somalia and Eritrea, the home of the Somali wild ass, most rain falls in May, October and November, which may explain the more scattered birth pattern. Anyway, our data clearly suggest that the wild asses studied are well synchronized with the ecological conditions within their natural environments, despite being kept under favourable conditions throughout the year. Compared with females, males are typically older when they reproduce for the first time. This pattern is characteristic for polygynous mating systems, in which males compete directly for access to females (sexual bimaturism: Badyaev 2002, Taborsky & Brockmann 2010). Accordingly, males reach their highest reproductive output later than females.

Sex- and species-specific variation in survival rates

In kulan and onager but not in kiang and Somali wild ass, females lived longer than males as has been also found in other mammals and birds (Promislow 1992). This difference is caused by females of both former taxa living longer than their male counterparts as well as kiang and Somali wild ass females, while male longevity did not differ significantly across taxa throughout. A shorter male lifespan may originate from the need to monopolize females, which depends on resource holding potential (i.e. is strength; Klingel 1977, Badyaev 2002, Taborsky & Brockmann 2010). Therefore, males have to accumulate more body mass and, thus, need more energy (Clutton-Brock et al. 1997, Badyaev 2002, Taborsky & Brockmann 2010). Nevertheless, they are typically able to monopolize females in their "best years" only, reducing benefits of living particularly long. In females, in contrast, longevity is often positively related to offspring number (see below). Why kiang and Somali wild ass did not show sexual differences in mortality rates is currently unclear, while the very similar patterns found for onager and kulan may reflect their close relatedness. Both taxa can hardly be distinguished phenotypically and are fully hybridisable (Dathe 1971). Longevity showed a low heritability in kulan and onager and an according tendency in kiang, which is typical for fitness-related traits (Falconer 1981, Kruuk et al. 2000, Åkesson et al. 2008).

Reproduction and longevity

High reproductive investment and longevity are often believed to be traded-off against each other (Clutton-Brock 1988, Newton 1989, Kirkpatrick & Turner 2007). In our study, though, longevity and the length of the reproductive period were positively related (except in kiang for the correlation with longevity). Such patterns of positive rather than negative correlations have been found repeatedly (Bell & Koufopanou 1986, Clutton-Brock 1988, Newton 1989). They presumably reflect that individuals getting older have more time to produce offspring, and that high-quality individuals may afford to strongly invest into both longevity and reproduction (Bell & Koufopanou 1986, Clutton-Brock 1988, Newton 1989). In this context, it should be noted that birth rate was not related to longevity, showing that birth rates were similar in animals differing in lifespan, corroborating the first conclusion above. Additionally, the length of the reproductive period was positively related to birth rate throughout the entire lifespan in two taxa, supporting the second conclusion.

Reproductive and post-reproductive phase jointly contributed to longevity (Cohen 2004, Turbill & Ruf 2010), although the two were negatively correlated in two taxa. A prolonged post-reproductive phase may have, e.g. in humans, benefits for the group (Judge & Carey 2000, Reznick et al. 2006, Lahdenperä et al. 2014), which may also apply to equids (Klingel 1977, 1998, Volf 1996). Interestingly, the length of the reproductive period and birth rate within the reproductive period (i.e. mean birth intervals) were negatively correlated in three taxa, suggesting a trade-off between the two. Thus, it appears that a fixed number of offspring can be produced within a longer or shorter time period, but that high birth rates cannot be sustained over longer periods (Grange et al. 2004, Barnier et al. 2012).

Birth intervals depend mainly on the delay of conception after birth (Puschmann 2003, Barnier et al. 2012). In plains zebra (*Equus quagga* ssp.) a longer birth interval after male than female offspring has been found, indicating that sons may be more costly than daughters (Clements et al. 2011, Barnier et al. 2012), based on a higher demand for food and care (Trivers & Willard 1973, Cameron & Linklater 2000, Barnier et al. 2012). In our study, however, such relationships were not evident throughout. However, birth interval increased with increasing female age, suggesting detrimental effects of ongoing senescence (Clutton-Brock 1984).

Conclusions

We here used zoo-derived data to explore life-history trade-offs and reproductive patterns in four equid taxa. Captive populations experience highly favourable conditions and are largely relieved from seasonal constraints (e.g. food, climate, predators).

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Even though birth rates clearly showed seasonal variation matching the food availability in their natural habitats. We therefore assume that data derived from zoo populations may be at least to some extent useful to understand animal life histories. Interestingly, females lived longer than males in two of the taxa only, indicating divergent life-history strategies even amongst these closely related taxa. Offspring number and longevity were positively rather than negatively correlated, indicating that high-quality individuals can afford to invest into both at a time. Evidence for trade-offs, in contrast, was very weak. As an example, the length of the reproductive period was negatively related to birth rate within the reproductive period. This may suggest that a fixed number of offspring can be produced within a longer or shorter period, but that high birth rates cannot be sustained over extended time periods. Despite several limitations, zoo data seem to be useful to better understand the reproductive biology of endangered, rare or cryptic species.

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