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Demography of feral horses (*Equus caballus*): a long-term study in Tornquist Park, Argentina

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Abstract

Context. All over the world, invasive alien mammals present conservation problems. Feral horses are invasive in many countries and their management is challenging.

Aims. To determine the demography of feral horses in Tornquist Park, Argentina, so as to develop a quantitative basis for their management.

Methods. Ground counts of individually identified female horses were conducted monthly from 1995 to 1997 and from 2000 to 2002, and seasonally in 1998 and 1999. We calculated the age structure, foaling and survival rates of mares and analysed the effects of adult density and rainfall on demographic parameters. The population trend was calculated by fitting a logistic equation to annual adult mare counts.

Key results. The foaling rate averaged 0.55 annually and the survival rate in females averaged 0.89 for adults, 0.91 for juveniles, 0.87 for yearlings and 0.94 for foals. We found adult density, rainfall and the previous year's rainfall to have a significant effect on fecundity but no effect on adult, juvenile and foal female survival rates. Adult density had a significant negative effect on female yearling survival; however, the effect is probably trivial. The logistic equation parameters gave $r = 0.327$ and carrying capacity (K) = 240 adult mares.

Conclusions. A density-dependent response is suggested. The population growth is mainly limited by low fecundity, with the reduced adult female survival probably also playing a minor role.

Implications. It is expected that the present long-term demographic study will contribute to the understanding of feral ungulate ecology and improve the management of feral populations.

Introduction

Invasive alien mammals are present worldwide and deemed by some sectors of society to be a serious biodiversity conservation problem (Lever 1994; Long 2003; White *et al*. 2008). Invasive feral ungulates constitute a highly successful group and the management of their populations has motivated considerable effort and investment in many countries, including Australia (Bradshaw *et al*. 2007), New Zealand (Parkes and Murphy 2003) and USA (Douglas and Leslie 1996; Witmer *et al*. 2007).

Feral horses (*Equus caballus*) are large herbivorous mammals considered invasive in many countries (Lever 1994; Long 2003). They are especially abundant in Australia and the western USA and at high population densities have an impact on the environment through overgrazing and trampling, although this has been poorly quantified (Dobbie *et al*. 1993; Beever and Brussard 2000; Dawson *et al*. 2006). Demographic data are crucial to the successful management of feral horse populations (National Research Council 1980; Eberhardt *et al*. 1982; Berger 1986; Duncan 1992) and has been collected since the 1970s. However, most existing studies are short-term and are based mainly on aerial counts (Feist and McCullough 1975; Welsh 1975; Frei *et al*. 1979; Wolfe 1980; Garrott *et al*. 1991). Some long-term studies based on aerial censuses do exist (Eberhardt *et al*. 1982). The literature covering individually identified horses over a period of five or more years is very sparse (e.g. Berger 1986; Garrott and Taylor 1990; Duncan 1992; Goodloe *et al*. 2000; Turner and Morrison 2001; Linklater *et al*. 2004; Grange *et al*. 2009; Tatin *et al*. 2009).

There are many feral horse populations in Argentina, especially in the Patagonia and Cuyo regions, although their size and precise geographic range have not been documented. The pampas region, known worldwide for its grasslands, is one of the most transformed ecosystems under the impact of anthropic activities, with natural protected areas being very few and relatively small. Tornquist Park, a hilly grassland reserve in south-western Buenos Aires province, has the largest known feral horse population in the country (Scorolli 1999), reaching a density as high as 22 horses km^{-2} in 1995. Although no official management strategy currently exists, the control of feral horses is considered to be an essential component of efforts to conserve the biodiversity of this extremely valuable grassland area and to minimise any eventual damage. The aim of the present study was to determine the long-term demography of the Tornquist Park feral horse population and explore the relationships among demographic parameters, population density and

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rainfall so as to develop a scientific basis for an adequate management program.

Materials and methods

Study area

Ernesto Tornquist Provincial Park (ETPP) is located in the south of the Province of Buenos Aires, Argentina, between 38°00′ and 38°07′S and 61°52′ and 62°03′W. This natural reserve was established in 1938 and covers 67 km^2 of hilly grassland, with heights ranging between 450 and 1175 m asl. The climate is temperate and humid (Burgos 1968), with a mean annual rainfall of 800 mm. Rains fall mainly in spring, with a second peak in autumn. Snowfalls are occasional and, in general, light. The typical vegetation is grassland steppe dominated by species of the genera *Stipa* and *Piptochaetium* (Cabrera 1976; Frangi and Bottino 1995).

This Natural Protected Area is very important for biodiversity conservation as it includes many endemic plant and animal species (Kristensen and Frangi 1995). In 1942, a small group of 5–10 horses was introduced into ETPP, eventually becoming feral. In 1995, the 450 descendents of the original group occupied a fenced-off sector of ~20 km^2 (Scorolli 2007). The horses were of Creole breed, similar to all other feral horse populations in Argentina, originating from Spanish and Andalusian horses of essentially African barb ancestry and brought to South America by colonisers during the XVI century (Cabrera 1945).

The feral horse population during the study period comprised between 40 and 66 harem-bands (Scorolli 2007) whose mean home-range area from 1995–1997 was 4.3 km^2 (Scorolli 1999). Their impact on biodiversity in Tornquist Park has not been fully quantified, although some research has suggested that feral horses have modified the composition of the plant and animal community in the area (Zalba and Cozzani 2004; Loydi and Zalba 2009). The convenience of implementing a feral horse management strategy emerged from discussions among rangers, biologists and government authorities.

Census protocol

The feral horses were observed with the aid of binoculars (×10), by walking a fixed path that covered almost the entire 20-km^2 study area over two consecutive days. Data were taken monthly from 1995 to 1997 and 2000 to 2002, and seasonally (four times a year) from 1998 to 1999.

In January–March 1995 female feral horses were individually identified on the basis of coat colour and face and leg markings (Berger 1986; Linklater *et al*. 2004). The individuals were assigned a numerical identification code and their data registered on cards.

The small size of the study area and hilly topography with grassland vegetation provided good visibility, thus facilitating total counts of the female segment of the population. The foals born were registered monthly between August and April and their individual marks recorded. Males in bachelor bands were not registered because these groups were highly unstable and usually located at the periphery and on hilltops.

For operational reasons, it was decided to study the female segment of the population. Mares were classified on the basis of their body size, length of tail and mane as adults (Ad: ≥3 years), juveniles (*j*: 2–3 years old), yearlings (*y*: 1–2 years old) and foals (*f*: 0–1 year old).

The exact adult sex ratio is unknown; however, a mean estimate based on data over 4 years is 0.9 males per female. Population density was calculated as twice the total female count divided by the total area (20 km^2); adult density was calculated in the same manner, but using adult female counts.

Demographic parameters

The foaling season in Tornquist Park extends from August to April, with most foals being born in October, November and December (Scorolli 1999). The biological year runs from the median birth date, 1 November of year t to 31 October of the year $t+1$. The foaling rate (F) was calculated by dividing the total number of foals by the number of adult mares (≥3 years old). Because it is possible that some foals were born and died without being registered, the foaling rates are taken as minimum estimates. The foals born between August and November were considered members of the cohort t.

The survival rate was calculated by dividing the total number of mares in every age class in the November census of year $t+1$ by the number in the census at year t. A horse was assumed to have died if it was registered in one census but not in the remaining censuses in a biological year. Taking into account undetected neonatal mortality, the actual foal survival rate is likely to be lower that the calculated rate. The estimated probability of 'recapture' for individual horses from one month to the next was high, with a minimum estimated value of 0.95 in 1995. Parameter estimates and factors are presented in the text as mean ± standard error. All tests were performed with a selected significance level of $\alpha = 0.05$.

The percentage of adult mares in the total female population and foaling and survival rates were compared with the chi-squared test of equal proportions with the R software package (Crawley 2005, 2007).

We explored the possible effects of adult population density and rainfall on foal, yearling and juvenile female survival by using generalised linear models (GLM) and on adult female survival and fecundity by using generalised linear mixed models (GLMM) (Zuur *et al*. 2009), including an identification code in the model as a random effect to take into account the fact that many individuals were measured repeatedly. The demographic data for survival and fecundity were coded as binary variables, as follows: '1' for survive and '0' for not survive and '1' for adult mare with a foal and '0' for adult mare without a foal. The selected level of significance for retaining a parameter in the model was $P < 0.05$ and models were selected on the basis of the Akaike information criteria (AIC) (Burnham and Anderson 2002). We also tested the possible correlation between factors by means of simple correlation.

The population trend was analysed by fitting the logistic equation to the adult mare count data by means of non-linear least-squares, as suggested by Eberhardt *et al*. (2008).

We used the following equation:

$$N(t) = \mathrm{K}/1 + ce^{-rt}, \quad c = \mathrm{K}/N_0 - 1,$$

where $N(t)$ is population size in year t, K is carrying capacity, r is maximum growth rate and c a constant that includes N_0, the initial population size. For comparative purposes we fitted the same equation to the 8-year data on the Camargue feral horse population reported by Grange *et al*. (2009).

All statistical analyses were performed with the R software package (http://cran.r-project.org, verified 9 April 2010). Rainfall data were obtained from a meteorological database owned by Tornquist Park administrators.

Results

The percentage of adult mares was constant from 1995 to 1998 at 48–55% ($\chi^2 = 2.702$, d.f. = 3, $P = 0.439$), increased up to 64% by 2002 ($\chi^2 = 3.918$, d.f. = 1, $P = 0.048$) and then decreased again to 60–65% ($\chi^2 = 2.231$, d.f. = 3, $P = 0.526$). Over the study period as a whole, foals, yearlings and juveniles together made up between 35 and 52% of the total mare population (Fig. 1).

In 1996, 1997, 2000 and 2001 foals were born between August and April, mostly (~80%) in October–December (Fig. 2), coinciding with late spring. The foaling rate showed no clear trend during the study period, with a mean of 0.55 (Table 1); it was above the mean in 1995 (0.81), then decreasing in 1996 (0.61; $\chi^2 = 9.563$, d.f. = 1, $P = 0.002$), remaining constant until 1998 ($\chi^2 = 2.438$, d.f. = 2, $P = 0.295$), decreasing again in 1999 (0.27; $\chi^2 = 23.413$, d.f. = 1, $P < 0.001$), increasing in 2000 (0.46; $\chi^2 = 15.144$, d.f. = 1, $P < 0.001$) and then remaining constant until 2002 ($\chi^2 = 5.007$, d.f. = 2, $P = 0.082$). The sex ratio of foals was 1 : 1 in all 8 years of the study ($\chi^2 = 5.261$, d.f. = 7, $P = 0.628$) ($n = 692$).

The survival rate of females averaged 0.886 ± 0.026 for adults ($\chi^2 = 7.689$, d.f. = 7, $P > 0.360$), 0.907 ± 0.003 for juveniles ($\chi^2 = 2.981$, d.f. = 7, $P > 0.880$), 0.866 ± 0.052 for yearlings ($\chi^2 = 7.023$, d.f. = 7, $P > 0.426$) and 0.936 ± 0.023 for foals ($\chi^2 = 2.351$, d.f. = 7, $P > 0.938$) (Fig. 3), with little variation among the years (χ^2, $P > 0.05$).

Effects on survival

The GLMM analysis carried out on the 1340 adult mares studied between 1995 and 2002 showed their survival to be unaffected by adult density (slope = 0.017 ± 0.035, $P = 0.614$) and rainfall (slope = -0.00004 ± 0.001, $P = 0.939$). The best-fit model corresponded to a constant adult mare survival of 0.886 ± 0.026

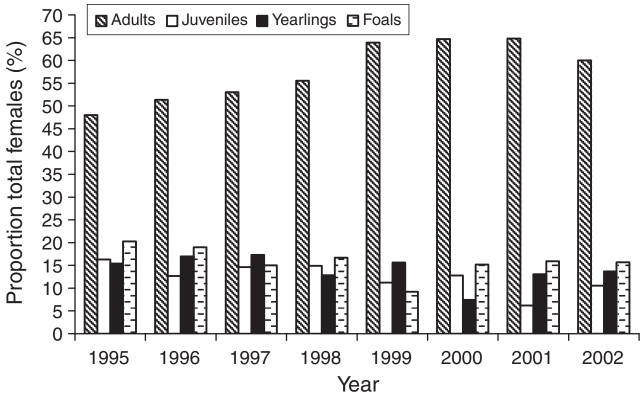

Fig. 1. Age structure as percentage frequency of the female population of feral horses in Tornquist Park during the 1995–2002 period.

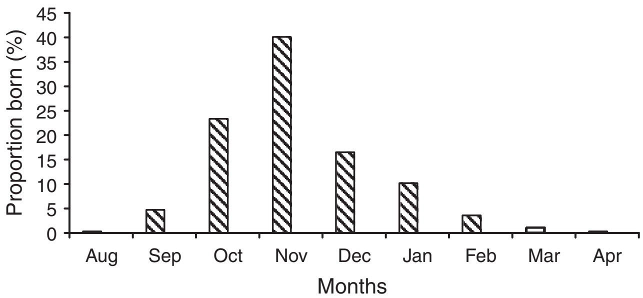

Fig. 2. Percentage of foals born by month in the feral horse population at Tornquist Park in the years 1996, 1997, 2001 and 2002.

Similarly, GLM analysis of the 278 juvenile mares monitored over the same period showed adult density (slope = -0.019 ± 0.073, $P = 0.791$) and rainfall (slope = -0.001 ± 0.001, $P = 0.672$) to have no significant effect on survival. The selected model was that of constant juvenile female survival (0.907 ± 0.033).

In the case of the 321 yearling mares studied over this same period, however, the GLM analysis revealed highly

Table 1. Total number of foals, adult mares, foaling rate, density and total annual rainfall at Tornquist Park during the 1995–2002 period

N, number of adult females; F, foaling rate

Year	Foals	*N*	F	Adult density (no. of horses km^{-2})	Rainfall (mm)
1995	88	109	0.81	10.9	725
1996	80	130	0.62	13.0	903
1997	78	141	0.55	14.1	1236
1998	98	160	0.61	16.0	847
1999	50	188	0.27	18.8	940
2000	89	192	0.46	19.2	914
2001	103	208	0.50	20.8	1480
2002	120	210	0.57	21.0	1244
Mean ± s.e.	86.5 ± 20.20	167 ± 37.90	0.55 ± 0.05	16.73 ± 3.79	1036 ± 90.10

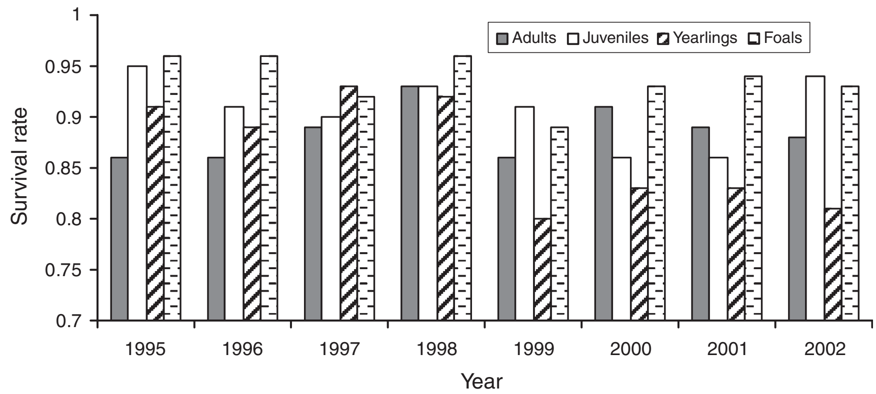

Fig. 3. Survival rate for the different age classes of females at Tornquist Park during the 1995–2002 period.

significant negative effects of adult density on survival (slope = –0.130 ± 0.049, *P* = 0.008) and no significant effect of rainfall (slope = 0.001 ± 0.001, *P* = 0.429). The selected model includes only adult density, and the explanatory power based on the proportion of deviance was 3%.

Adult density (slope = –0.047 ± 0.083, *P* = 0.568) and rainfall (slope = –0.00002 ± 0.001, *P* = 0.987) had no significant effect on survival according to the GLM analysis carried out on the 360 foals covered in the study. The best-fit model was that of constant foal female survival (0.936 ± 0.023).

Effects on fecundity

GLMM analysis of the data for 1340 adult mares showed adult density, rainfall and the previous year's rainfall to have a highly significant effect on fecundity (Table 2). Adult density was not significantly correlated with rainfall (*r* = 0.654, d.f. = 7, *P* = 0.078) or with the previous year's rainfall (*r* = 0.472, d.f. = 7, *P* = 0.237). The selected model includes adult density, rainfall and the previous year's rainfall.

Table 2. Estimated effect of adult density, rainfall and previous-year rainfall on adult fecundity calculated using generalised linear mixed models (GLMM) at Tornquist Park during the 1995–2002 period
$*P < 0.1$, $**P < 0.05$, $***P < 0.001$

Parameter	GLMM estimate	s.e.	*Z*-value	*P*-value
Intercept	0.667	0.3952	1.688	0.0913
Adult density	–0.1680	0.0240	–6.974	3.08e–12***
Rainfall	0.0007	0.0003	2.524	0.0116*
Previous-year rainfall	0.0015	0.0002	5.854	4.79e–09***

Population trend

The size of the population, calculated on the basis of adult mare counts, increased steadily from 109 in 1995 to 210 in 2002 (Table 1). The logistic curve fitted the Tornquist Park and Camargue data well (Fig. 4). The parameters estimated for the Tornquist Park population were as follows: *r* = 0.327 ± 0.062, carrying capacity K = 239.990 ± 17.406 and the constant *c* = 1.699; those for the Camargue population were calculated

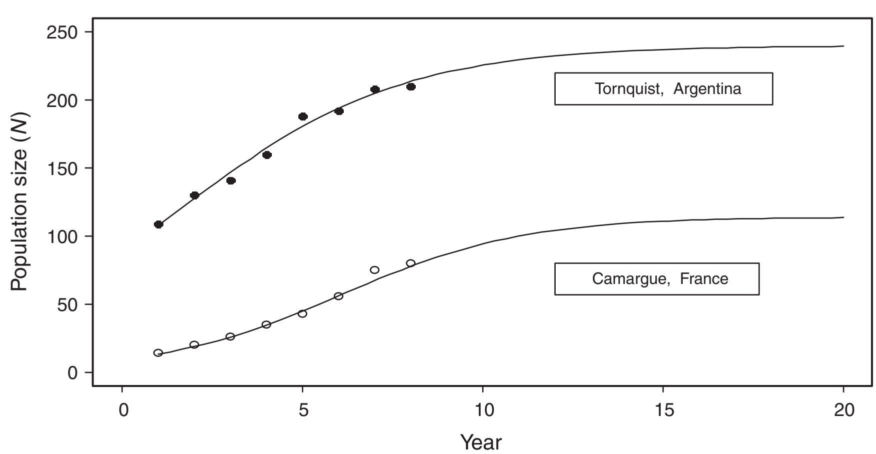

Fig. 4. Logistic curves for the feral horse population of Camargue, France, and Tornquist Park, Argentina. *N* = number of horses.

as $r = 0.399 \pm 0.033$, carrying capacity $K = 113.564 \pm 11.371$ and constant $c = 11.403$

Discussion

The current study is the first study presenting data on feral horse demography in Argentina and constitutes one of the few long-term (>5 years) studies of individually identified feral horses in the manner of the reports by Berger (1986), Garrott and Taylor (1990), Goodloe *et al*. (2000), Linklater *et al*. (2004) and Grange *et al*. (2009). Our results suggested that the feral horse population of Tornquist Park has probably approached carrying capacity and that fecundity and probably also adult survival are density-dependent. Our results were comparable to the values reported for non-managed feral horse populations whose growth is limited by lack of adequate food resources (Goodloe *et al*. (2000) in Cumberland Island, USA, Walter (2002) in the Australian Alps, Australia, Linklater *et al*. (2004) in Kaimanawa ranges, New Zealand, and Grange *et al*. (2009) in the Camargue, France). The observed age structure, with a relatively high and constant ratio of adult mares, suggested that population growth during the study period was slow, as reported by Cameron *et al*. (2001) for a slowly increasing population and Berman (1991) for a decreasing population.

Demographic parameters

Fecundity

All foals were born during the 9-month period from August to April, with a clear peak in late spring, in a pattern very similar to that recorded elsewhere in the southern hemisphere by Linklater *et al*. (2004) and Berman (1991) and in the northern hemisphere by Welsh (1975), Boyd (1979), Keiper and Houpt (1984), Berger (1986), Siniff *et al*. (1986) and Duncan (1992). The 1 : 1 sex ratio of foals observed during our study is congruent with the reports of Monard *et al*. (1997), Linklater *et al*. (2004) and Grange *et al*. (2009).

The foaling rate showed a wide range and no clear trend. However, the GLMM analysis revealed a negative effect of adult density on female fecundity and minor positive effects of rainfall, and previous year's rainfall, indicating a clear density-dependent response. The mean foaling rate was moderate (0.55) and similar to that reported for other non-managed or resource-limited feral horses (0.4–0.65) (Boyd 1979; Keiper and Houpt 1984; Siniff *et al*. 1986; Goodloe *et al*. 2000; Walter 2002; Linklater *et al*. 2004).

The highest value registered in 1995 (0.81) is similar to that reported for feral horses (0.7–0.9) by Salter and Hudson (1982), Keiper and Houpt (1984), Berger (1986) and Duncan (1992). The lowest (0.27) in 1999 is comparable to the lowest recorded value for the species (0.26–0.38) by Siniff *et al*. (1986), Kirkpatrick and Turner (1991), Garrott and Taylor (1990) and Greger and Romney (1999). However, we assume our results to be underestimated because the censuses in 1998 and 1999 were conducted seasonally.

We hypothesise that the moderate foaling rates recorded were caused by low pregnancies in mares with low body condition. Although the age classification we used, with all mares >3 years old being considered as adults, did not permit us to analyse this aspect, the low body condition values for adult mares during 2001 and 2002 (Scorolli 2007) lends indirect support to this hypothesis. Kirkpatrick and Turner (1991) found that low fecundity on Assateague Island, USA, was caused by lactational anoestrus. However, we do not consider this to be an important factor in the present study because many foals dispersed when between 1 and 2 years old, and a large number of mares foaled in consecutive years (A. Scorolli, pers. obs.). We cannot rule out the possibility that social factors such as those reported by Linklater *et al*. (2004) and Tatin *et al*. (2009) played a role in the low fecundity observed in the present study.

Survival

Foal female survival (0.94) was high and similar to that recorded by other authors for feral horses (Boyd 1979; Wolfe 1980; Berger 1986; Siniff *et al*. 1986; Duncan 1992; Cameron *et al*. 2001). The expected decrease in foal survival at high density (Eberhardt 1977, 2002; Fowler 1987) was not observed in Tornquist Park, in agreement with the results of Tatin *et al*. (2009) for Przewalski horses, but in contrast with those for the Camargue as reported by Grange *et al*. (2009). At this stage, we have no explanation for the constant and high foal survival rate; however, the moderate fecundity registered suggests that some mares could have traded their reproduction for survival, foaled only when environmental conditions were suitable and so increased the probability of foal survival.

The results of the GLM showed a significant effect of adult density on yearling female survival; however, the explanatory power of the best-fit model was very low (3%) and suggested a trivial effect. Yearlings could have been potentially more vulnerable to resource limitation than were other female age classes because most of them were already weaned, and still actively growing.

Adult density and rainfall were seen to have no effect on foal or juvenile (2 years old) female survival, as was the case in the study by Grange *et al*. (2009).

Adult female survival showed no clear response to density; values were high (0.86–0.89) and constant during the study period, as expected for large mammals (Gaillard *et al*. 1998). However, the observed values were unusual for feral horses and lower than those reported by Berger (1986) (0.95) ($\chi^2 = 11.334$, d.f. = 1, $P < 0.001$) and Garrott and Taylor (1990) (0.97) ($\chi^2 = 27.592$, d.f. = 1, $P < 0.001$), indicating that this parameter could have played some role in limiting population growth. We suspect that the adult female survival rate was already low before the present study commenced in 1995. Turner and Morrison (2001) reported similar adult survival values (0.80) but without mentioning any possible cause.

Grange *et al*. (2009) found that adult mare survival in the Camargue at high population densities decreased from high (0.9–1.0) to low (0.79–0.86) values, similar to our results, and proposed that feral horses trade survival for reproduction. The Camargue population was studied in its initial growth phase after being introduced into a new environment and, in contrast to our moderate rates, Grange *et al*. (2009) registered very high foaling rates (0.9), which they considered to be caused by artificial selection and the recent feralisation. Nevertheless, our unusually low adult female survival rates indicate that perhaps some trade-off has occurred in Tornquist Park, and this parameter can be influenced by density dependence although the evidence is not conclusive.

Density dependence

In large mammals, evidence of density dependence was presented in reviews by Fowler (1987), Sinclair (1989) and Gaillard *et al*. (1998, 2000) although equids were poorly represented. Some authors reported food limitation in populations of feral horses (Welsh 1975; Walter 2002; Grange *et al*. 2009) whereas others proposed that social stress was the main limiting factor (Linklater *et al*. 2004; Tatin *et al*. 2009).

The feral horse population at Tornquist Park grew during the study period from a density of 10.9 to 21 adult horses km^{-2}, being one of the highest known densities for feral horses (23.2–35.4 horses km^{-2}) (Tyler 1972; Welsh 1975; Franke Stevens 1990; Duncan 1992).

The results of the present study showed, for the first time, a feral horse population probably approaching carrying capacity. The observed trend in adult mare counts fits well with a logistic model, suggesting that the Tornquist Park population was near the estimated asymptotic value for population size of 240 adult females, corresponding to a density value of 24 adult horses km^{-2}. Although it is recognised that the data series was shorter than desirable, the results nevertheless provided evidence of a density-dependent process.

The intrinsic estimated population growth rate ($r = 0.327$), the maximum attainable at very low densities, was higher than other results for feral horses ($r = 0.16$–0.30) (Garrott *et al*. 1991; Duncan 1992; Walter 2002; Linklater *et al*. 2004) but lower than the value obtained by fitting the logistic equation to the Camargue feral horse data (0.399). The Camargue population was studied during the initial phase of feralisation, and presented an unusually high fecundity rate (0.9–1.0) that could partly explain this very high intrinsic growth rate.

Growth of the Tornquist Park feral horse population appeared to be limited by low fecundity most likely caused by food availability. The role in the population limitation of the relatively low adult female survival observed remains unclear. Conclusions about this confined and relatively small population should not be extrapolated to feral horses under other conditions. The observed density-dependent response in vital rates, even in the absence of a reduced foal survival rate, is in general agreement with that proposed for large mammals by Eberhardt (1977).

Management implications

Our results suggest that the implementation of the management of feral horse population in Tornquist Park, reducing the population to densities similar to or lower than those recorded in 1995, will lead to an increase in demographic rates. The results of the present study could therefore help model the feral horse population demography under different management scenarios.

In the absence of adequate management, the survival rate of adult and yearling mares in the study area will probably fall, mainly as a result of under-nutrition. The welfare implications of this – certain sectors of society, especially animal rights groups, may find it unethical or unacceptable to let feral horses die from starvation – should be taken fully into account in the context of any eventual management strategy to be implemented by the pertinent authorities.

At the end of the study period in November 2002, a mass mortality occurred during a violent rainstorm in Tornquist Park (Scorolli *et al*. 2006). The number of dead horses registered was 193, and 115 of them were females. The proportions of dead females in each age class were 31% for adults, 58% for juveniles, 48% for yearlings and 41% for foals. Since that date, the population has slowly managed to recover somewhat. Between April 2006 and June 2007, the Tornquist Park authorities implemented a population control program and captured 220 feral horses, ~100 male and 120 female, in a mobile corral. The size of the population in 2007 was down to 200 horses, corresponding to a density of six adult horses per square kilometre, providing an opportunity to investigate demographic responses at lower densities.

Confined, non-managed populations of feral mammals with few or no predators can increase in size until they approach carrying capacity and become limited by low fecundity and survival. Many consider it undesirable to arrive at this point, placing responsibility on managers to take ethical and welfare aspects into account when planning management strategies. Long-term demographic studies, especially of individually identified animals, could contribute to a better understanding of the ecology of feral ungulates, allow more reliable population modelling and improve their management.

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