

# **Selective breeding in the Quagga Breeding Program – the effect of translocations and inbreeding on Plains zebra reproduction**

## **Final report**

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## **Selective breeding in the Quagga Breeding Program – the effect of translocations and inbreeding on Plains zebra reproduction**

### **Executive Summary**

Plains zebra (*Equus quagga burchellii*) have been selectively bred in the Quagga Breeding Program for more than 20 years, producing a number of fourth generation individuals with reduced striping, resembling the extinct quagga. Inbreeding (which can reduce fitness and lead to inbreeding depression) is a common issue in such breeding programs. This report therefore assesses whether the ‘successful’ quagga-like phenotype is being achieved without an increasing degree of inbreeding in the population, and factors affecting reproduction were also investigated.

The following three questions were specifically addressed: 1) Does the degree of relatedness (inbreeding) increase with increasing quagga resemblance? 2) How is reproduction (age at first foaling, inter-foaling-interval and fecundity) influenced by a) inbreeding, b) female age, c) herd location, d) rainfall, e) a change in herd stallion and f) translocations. 3) What factors affect reproductive sex allocation? - e.g. herd location, rainfall, previous foal sex etc. The coefficient of inbreeding, generation number and degree of quagga resemblance (mean stripe score) was calculated for each individual.

The mean degree of quagga resemblance increased with each generation, yet there was no relationship between the coefficient of inbreeding and mean stripe score i.e. quagga resemblance was achieved in fourth generation individuals without a compromise in genetic integrity. The level of inbreeding recorded was generally low (10 % at its peak in the third generation) and had no measurable effect on female reproductive success (fecundity), yet this is most likely due to the small sample size of inbred individuals at reproductive age.

The combined effect of a change in location and a change in herd stallion had the most significant negative effect on inter-foaling-intervals and the age at first foaling (for young females joining a herd with at least two unfamiliar mares already present). A change in stallion alone also increased inter-foaling-intervals, but not as significantly. Management interventions therefore result in immediate costs to reproductive rates.

In the Wellington area, the proportion of male births peaked during summer when total birth number was also highest (between November and February) and was lowest over winter, except for a second peak in June, when rainfall was highest (i.e. winter rainfall area). Foal sex ratios therefore appear to be related to the combined effect of the factors determining resource abundance, namely rainfall and temperature (summer versus winter). Results are also in accordance with expectations from the Trivers-Willard Hypothesis, which states that females in good condition (expected during periods of high resource availability) are likely to produce more sons.

Foal sex ratios were unaffected by the sex of the previous foal and no bias was recorded for females foaling for the first time or following translocation. There was, however, a location effect, as a female foal bias was recorded at Boland Landbou and a male bias at Kranskop. Interestingly, Boland Landbou also had a low mean fecundity while female fecundity at Kranskop was high, suggesting that resource availability was low and high at these two locations, respectively.

## Introduction

The quagga project comprises a selective breeding programme of plains zebra *Equus quagga burchellii* with the intention of producing zebra with the coat colour pattern of the extinct quagga *E. q. quagga* (Harley *et al.* 2009). This breeding programme has been underway for over 20 years and has produced a number of 4<sup>th</sup> generation individuals. This report comprises an assessment of the extent of inbreeding within this programme.

One issue common to captive breeding programs is the risk of inbreeding, which can reduce fitness and lead to inbreeding depression (Keller and Waller 2002). Most breeding programs that are focussed on conservation select individuals for breeding to maximise the retention of generic variation (Ballou & Foose 1996). However, this is not necessarily the case in the quagga breeding program, as individuals are instead selected according to their appearance (they could subsequently be more closely related than random individuals). The risk of inbreeding in this program is therefore particularly high. It would therefore be important to look at whether the ‘successful’ quagga phenotype is being achieved without an increasing degree of inbreeding in the population. This will also be important to ensure there is no decline in the overall fitness in the population.

To test this, the reproductive success of inbred individuals can be compared to non-inbred individuals, although very large sample sizes are required (Lacy 1997). Furthermore, additional factors influencing reproduction can be investigated, such as herd location and management actions e.g. changing of the herd stallion.

Apart from reproductive rates, another factor which can have a significant effect on breeding programs is a bias in the production of male or female offspring. Such a bias in offspring sex ratio has been reported for a number of mares in the quagga breeding program (pers. comm. M. Knight). Theories explaining variation in sex allocation between species and populations are numerous and widely debated (e.g. Silk 1983; Sheldon & West 2004), yet the Trivers-Willard hypothesis (TWH), which states that high quality mothers should produce more sons (Trivers and Willard 1973), is still the most generally accepted. Factors affecting female condition (Cameron *et al.* 1999), such as social

rank, rainfall, population density etc. can therefore all influence the production of male or female offspring (Cassinello & Gomendio 1996).

*Research questions:*

- 1) Does the degree of relatedness (inbreeding) increase with increasing quagga resemblance (i.e. decreased stripes)?
- 2) How is reproduction (age at first foaling, inter-foaling-interval and fecundity) influenced by a) inbreeding, b) female age, c) herd location, d) rainfall, e) a change in herd stallion and f) translocations.
- 3) What factors affect reproductive sex allocation? - e.g. herd location, rainfall, previous foal sex etc.

## **Methods**

*Inbreeding versus stripe score*

The coefficient of inbreeding was calculated for each individual using Wright's equation (Wright 1969):

$$F_X = \sum \left[ \left( \frac{1}{2} \right)^{n+1} (1 + F_A) \right]$$

The generation number (F) was calculated for each individual, according to the method described by Harley *et al.* (2009). The mean degree of inbreeding was then calculated for each generation (1-4).

A measure of quagga resemblance was determined for each individual, by calculating the mean stripe score from the hindbody, forelegs and hindlegs combined, as these are the

three most relevant body areas where striping decreases (Harley *et al.* 2009). The lower the mean score, the higher the quagga resemblance.

### *Reproduction*

Age at first foaling, inter-foal-intervals (IFIs) and female fecundity was determined for all adult females where possible (age at first foaling and female age at each foaling event was unknown for the founder individuals). Female fecundity (foals produced per year) was determined from the age of 16 months (this was youngest age at first foaling recorded in the program was and therefore considered as the potential age of first foaling for females) for each adult female and only foals surviving more than 12 months were included in analyses (i.e. foals raised successfully to independence)

Potential ‘disruptions’ to breeding females, caused by management interventions through selective breeding, were identified as changes in the stallion associated with a female, as well as the translocation of a female to a different population. The effect of these changes on the subsequent IFI was therefore investigated. The treatment was either ‘no change’, ‘stallion change’ or ‘location and stallion change’. There was only one case with a change in location but the same stallion was retained, hence this scenario was excluded from these analyses.

The effect that the translocation of young females had on the subsequent age of first foaling was investigated. Furthermore, the number of adult females already in a herd at the time of joining a herd was included in the analyses, as age and herd joining are known to usually influence social rank (Pluháček *et al.* 2006). Herd joining order was grouped into two classes, namely first or second female to join a herd (1-2) and third or fourth female (3-4).

A one-way ANOVA test was used to test for significant differences between situations and a *post-hoc* Tukey test then determined where differences lay (Tukey 1953). IFI data was not normally distributed and was therefore Log transformed to achieve normality.

Mean female fecundity was determined for each sub-population (excluding those with less than five births) to test for significant differences between sub-populations i.e. a location effect. Initial fecundity subsequent to a change in stallion or translocation was also excluded.

The distribution of foal births through the year was determined for populations in the Wellington area, by combining all births from Elandsberg, Bontebok Ridge and Kranskop (Arc en Ciel and Vlakkenheivel had too few births, i.e. <5, and were therefore excluded), for the entire duration of the breeding program. The Three Month Running Mean (3MRM) was then determined, as was the 3MRM of rainfall (for which Elandsberg data from 2005-2011 was used). The relationship between births and rainfall distribution within the year was then investigated. The distribution of births within a year is assumed to be an indicator of when conditions are most favourable e.g. resources are most abundant (Ogutu *et al.* 2008; Nuñez *et al.* 2009).

#### *Foal sex ratios*

The male proportion of foals born each month of the year was established for the three relevant Wellington-area populations combined (for the duration of the breeding program). The 3MRM was then compared to the distribution of total births (3MRM) throughout the year to see if there was an increase in the proportion of male or female births with increasing total birth number i.e. when conditions are most favourable. Similarly, the distribution of 'proportion male foals' (3MRM) within the year was compared to rainfall (3MRM), another potential indicator of resource availability. Multiple regression was used to evaluate the effect of both rainfall and total births on male foal proportion.

Additionally, a potential bias in foal sex for the following situations was investigated: 1) females foaling for the first time, 2) the translocation of a female prior to her first foal, 3) social rank at the time of a female's first foal (assumed to be related to the order at which she joins the herd) and 4) previous foal sex. Lastly, an individual or location effect on foal sex ratio was investigated (for individuals or locations with at least five foals). For each situation, Chi-squared goodness-of-fit analyses were used to determine whether there were more male or female foals than expected (Zar 1996).

## Results

### *Inbreeding versus stripe score*

The degree of inbreeding was significantly different between generations ( $\chi^2 = 117$ ,  $df=3$ ,  $P<0.01$ ). Generations two, three and four were all significantly more inbred than the founder population, with the highest level in generation three (~10%, Fig. 1). The highest level of inbreeding in an individual was 28%. The drop in the level of inbreeding in generation four is likely due to the translocation of individuals between populations, as Bowland *et al.* (2001) recommend the translocation of individuals every five years in order to maintain genetic heterogeneity in small zebra populations (9 individuals).

Mean stripe score per generation decreased with increasing generation (Fig. 2), i.e. the degree of quagga resemblance increased with each generation. There was, however, no relationship between the coefficient of inbreeding and mean stripe score for individuals (Fig. 3). Inbreeding did therefore not increase with an increase in quagga resemblance.



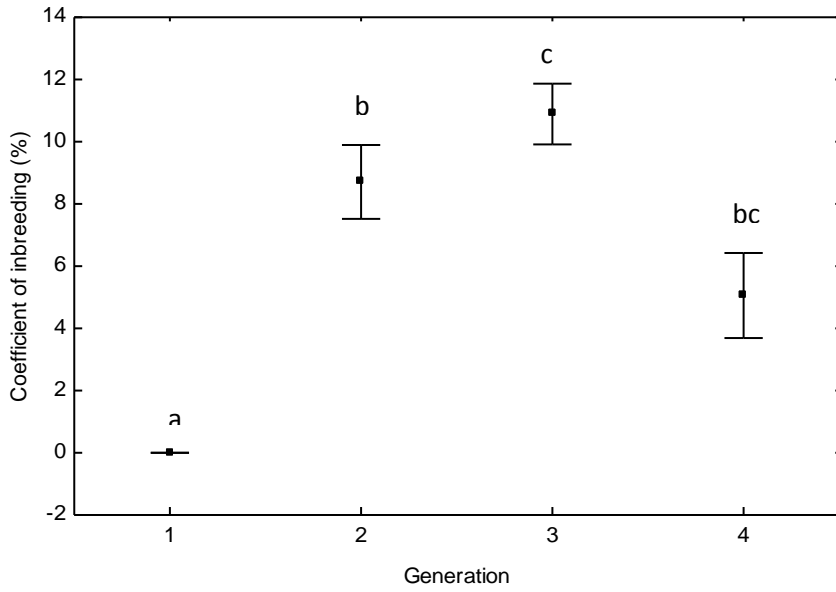


Figure 1. Mean ( $\pm$  SE) coefficient of inbreeding for all individuals in each generation. Unlike letters (a, b and c) indicate significant differences.

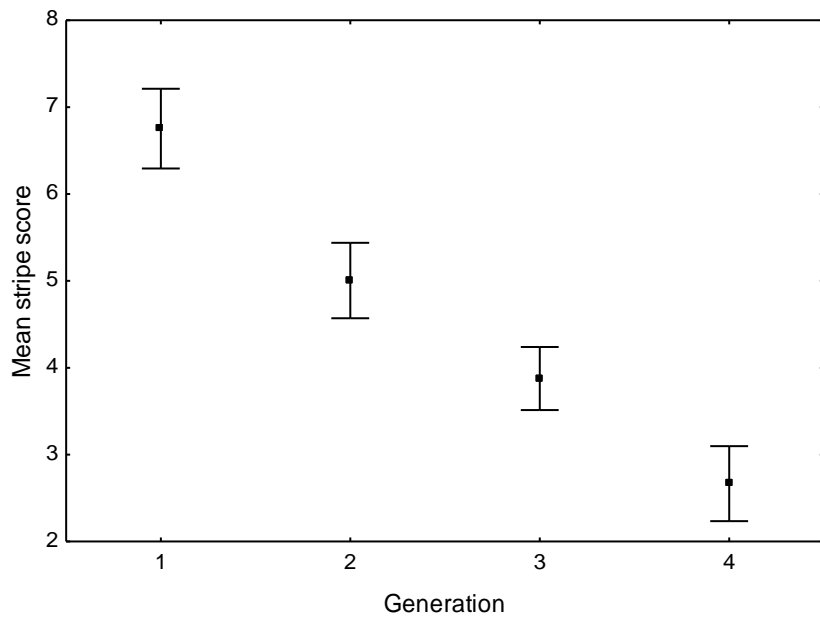


Fig. 2. Mean ( $\pm$  SE) stripe score (from hindbody, forelegs and hindlegs) of all individuals in each generation.

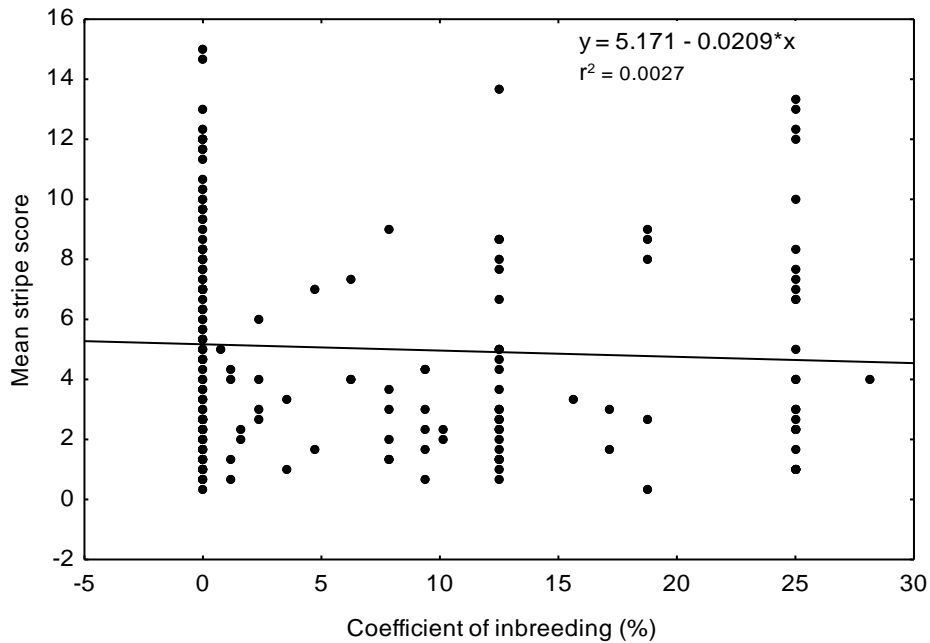


Fig. 3. Mean stripe score versus the coefficient of inbreeding for all individuals (including founder individuals).

### *Reproduction*

Data for 224 foal births was obtained from 62 breeding mares and 34 breeding stallions, for the duration of the breeding program (1987-2012).

Translocation and/or a change in the breeding stallion had a significant negative effect on the subsequent IFI of females. While a change in stallion resulted in the mean IFI increasing significantly from 15.9 months to 18.7 months, the increase was far more dramatic after a change in location and stallion, rising to a mean of 38.9 months (Fig. 4).

Translocation of young females had no negative effect on the age at which they first foaled if they were one of the first two females in the breeding herd. Similarly, the order of joining a herd had no effect when females remained in their natal population. If, however, translocated females were the third or fourth to join their new herd (i.e. were lower ranking), the age at first foaling increased markedly (although not significantly, Fig. 5). Familiarity

between females in a herd therefore appears to play an important role in their stress/harassment levels (which affects reproduction; Rubenstein & Nuñez 2009), rather than rank alone.

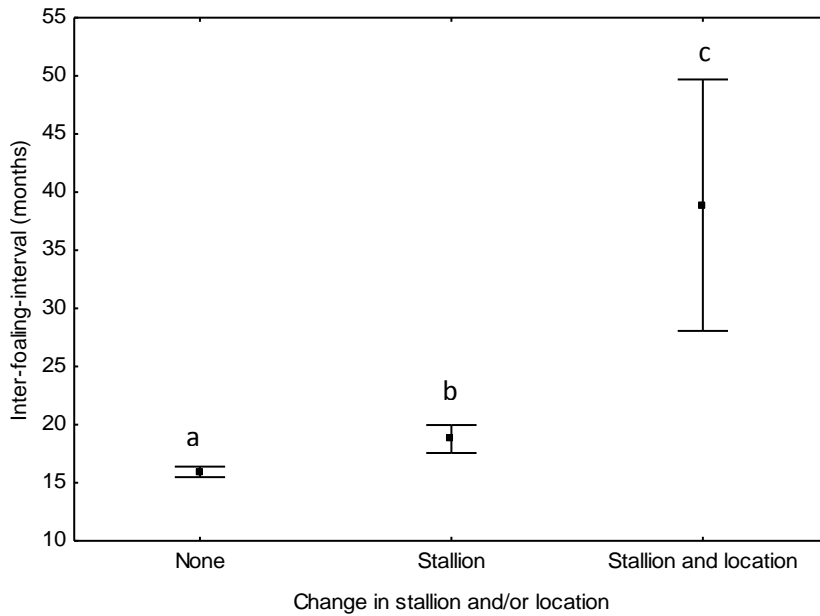


Fig. 4. Mean ( $\pm$  SE) inter-foaling-intervals for females subjected to either 1) no change in herd stallion or location, 2) a change in herd stallion or 3) a change in herd stallion and a change in location i.e. translocated. Unlike letters (a, b and c) indicate significant differences.

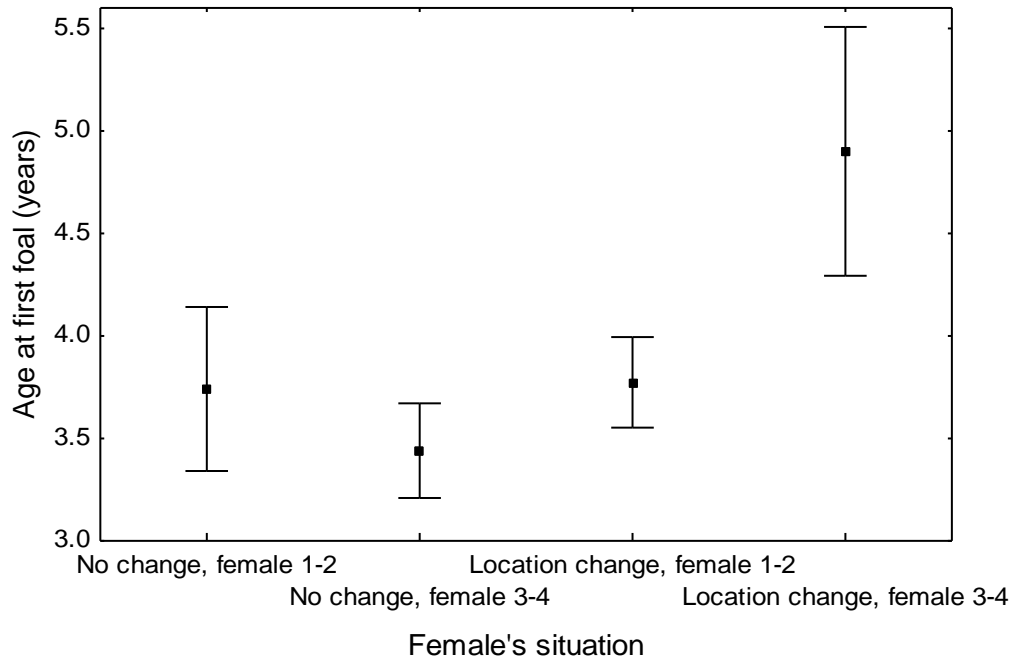


Fig. 5. The mean ( $\pm$  SE) age of females foaling for the first time after translocation (prior to first foaling) and/or after being one of the first two mares to join a herd versus the third or fourth mare joining.

Female fecundity was not related to the coefficient of inbreeding of her offspring (Fig. 6). Even though nearly half of all foals born into the program were inbred to some degree (130 not inbred versus 115 inbred), only 12 inbred mares reproduced during the duration of the project, producing 28 foals. The sample size of foals per inbred mare was therefore too small to pick up any effects of a mare's inbreeding on her fecundity. It was not possible to look at the effect of inbreeding on age at first reproduction, as only four inbred females, foaling for the first time, had not been translocated to a new sub-population prior to foaling, i.e. a translocation effect could not be excluded.

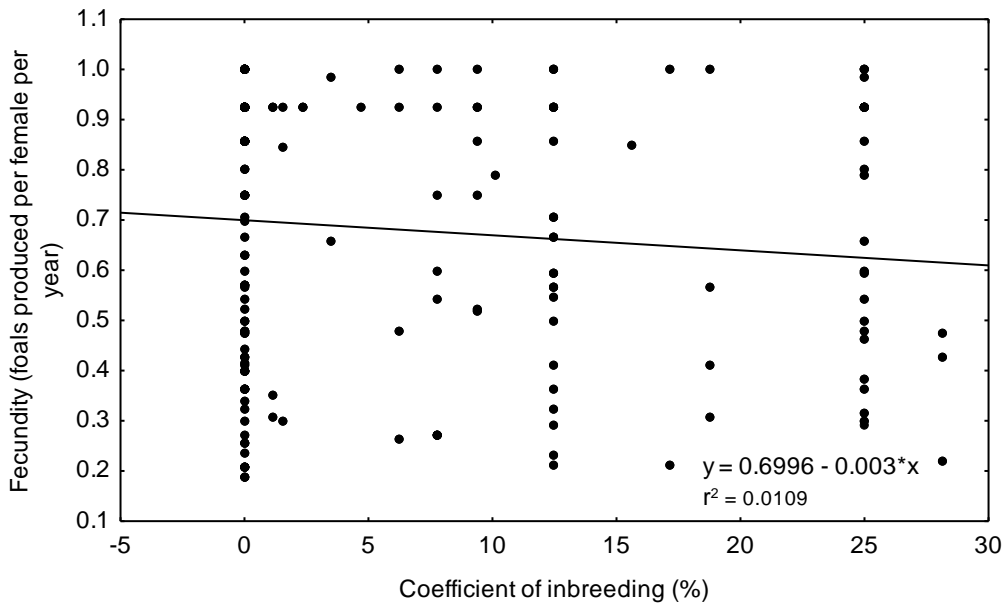


Fig. 6. Female fecundity versus the coefficient of inbreeding of the corresponding offspring, excluding births directly after a change in stallion or location.

Reproduction appears to be optimal when females are about eight to ten years old, as inter-foaling-intervals were lowest for this age group (Fig. 8). Longer IFIs (>14 months) for this age group were mostly greater than 24 months, suggesting that undetected deaths could be responsible for these long intervals (24 months is sufficient time for two pregnancies of 12 months each i.e. two births), unlike for the younger age group where a large number of IFIs were in the 12-24 month range. Short IFIs (12-15 months) were also common for young females (<8 years old), but all except one IFI were longer than 16 months for females above 12 years (Fig. 8).

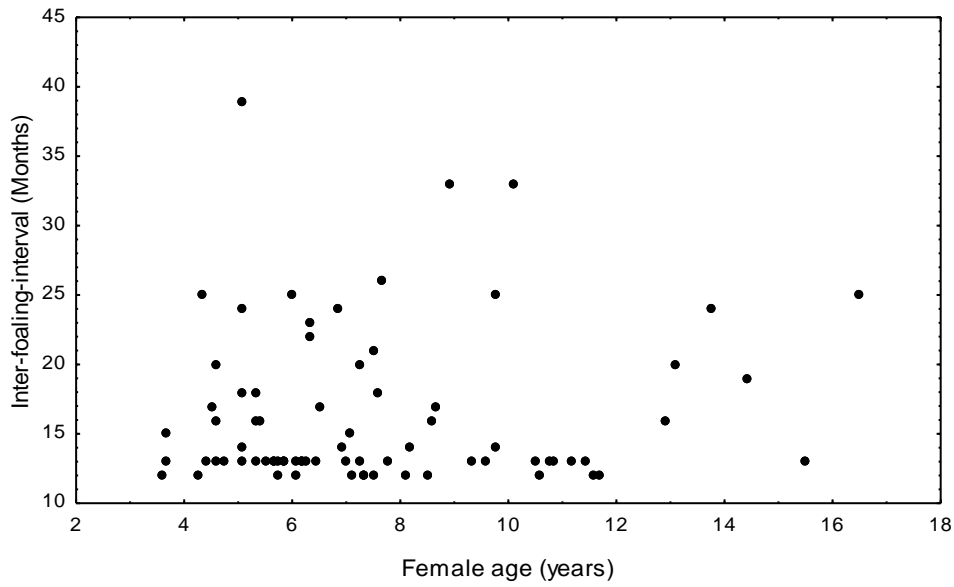


Fig. 7. Inter-foaling-intervals versus female age, excluding the initial interval after a change in stallion or location.

Mean female fecundity for sub-populations ranged from 0.54 to 0.88 foals born per female per year (surviving >12 months; Fig. 8). The difference between sub-populations was, however, not quite significant ( $\chi^2 = 14.35$ ,  $df = 8$ ,  $P = 0.07$ ). Location, therefore, did not have a significant effect on female fecundity.

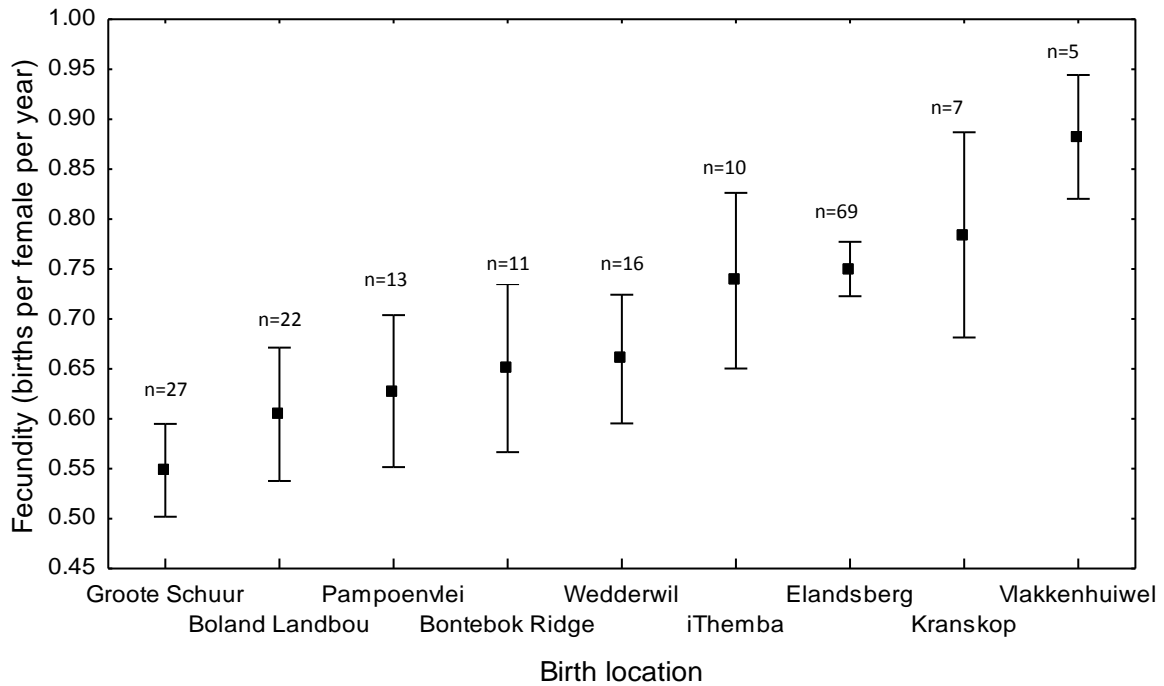


Fig. 8. Mean ( $\pm$  SE) fecundity of females at each location (sub-population), for sub-populations with at least five births, ranked from lowest to highest to enable easy identification of the low versus highly fecund populations (n = number of foals).

Births in the Wellington area (Elandsberg, Bontebok Ridge and Kranskop – the three populations with a foal birth sample size  $\geq 5$ , peaked in the summer months, between November and February and were at their lowest in winter, around May-June (Fig. 9). Rainfall, however, was highest during the winter months of May-August and lowest from December to March (Fig. 9). Foaling season was therefore not dependant on rainfall, but instead perhaps on temperature, as vegetative productivity would be reduced by cold winter temperatures, despite the high winter rainfall (Poincelot 1980) i.e. reduced resource abundance.

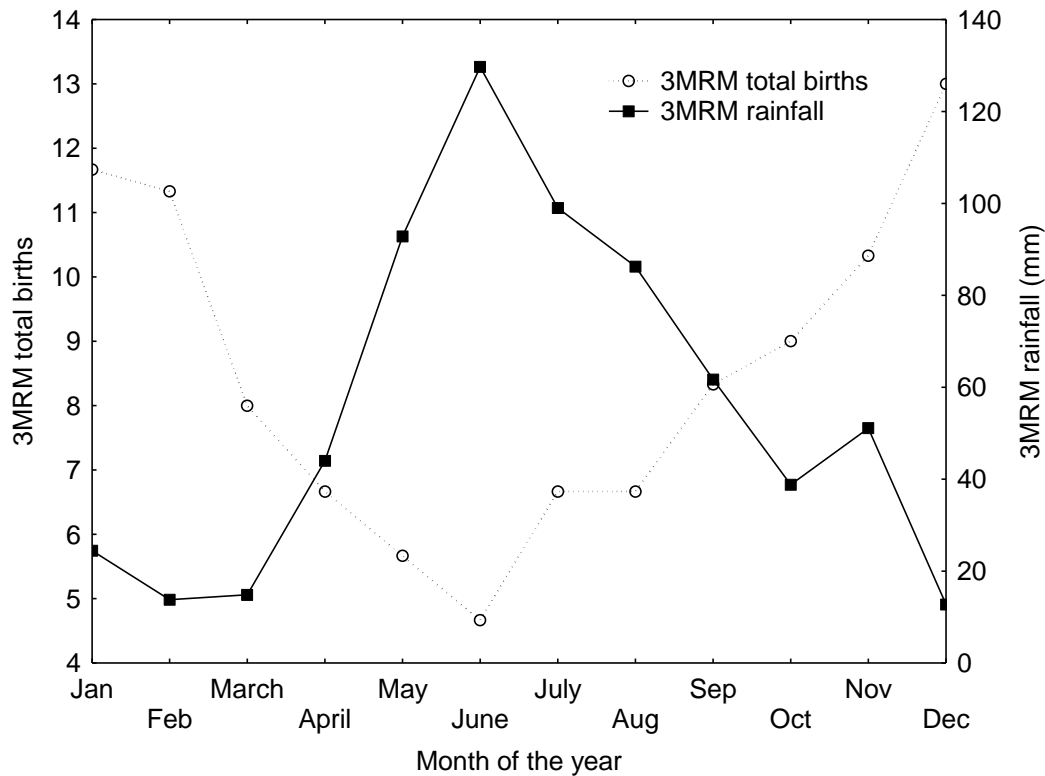


Fig. 9. The monthly (three month running mean) distribution of births (1987-2012) and rainfall (2008-2011) for populations in the Wellington area.

#### *Foal sex ratios*

The proportion of male births was highest during the summer months (December to February), during the peak foaling season (Fig. 10). There was, however, another peak in male births in winter, coinciding with the high rainfall months of June-July (Fig. 11). Reproductive sex allocation therefore appears to be related to the combined effect of rainfall and birthing season (both indicators of resource availability), yet this combined effect was not significant ( $F_{1,12} = 1.32$ ,  $P < 0.32$ ,  $R^2_{adj} = 0.05$ ).

There was no bias towards male or female births for females foaling for the first time ( $\chi^2 = 0.21$ ,  $df = 1$ ,  $P = 0.64$ ). Translocation of a female before her first foal also had no effect on the sex of her first foal ( $\chi^2 = 0.05$ ,  $df = 1$ ,  $P = 0.83$ ). Similarly, the number of females in a herd at the time of a young female joining the herd, had no effect on the sex of her first foal (first or second:  $\chi^2 = 0.0$ ,  $df = 1$ ,  $P = 1$ ; third or fourth:  $\chi^2 = 0.36$ ,  $df = 1$ ,  $P = 0.54$ ).



Foal sex was not influenced by the sex of the previous foal, as there was no bias for either sex following a male ( $\chi^2 = 0.53$ ,  $df = 1$ ,  $P = 0.47$ ) or female birth ( $\chi^2 = 0.01$ ,  $df = 1$ ,  $P = 0.91$ ).

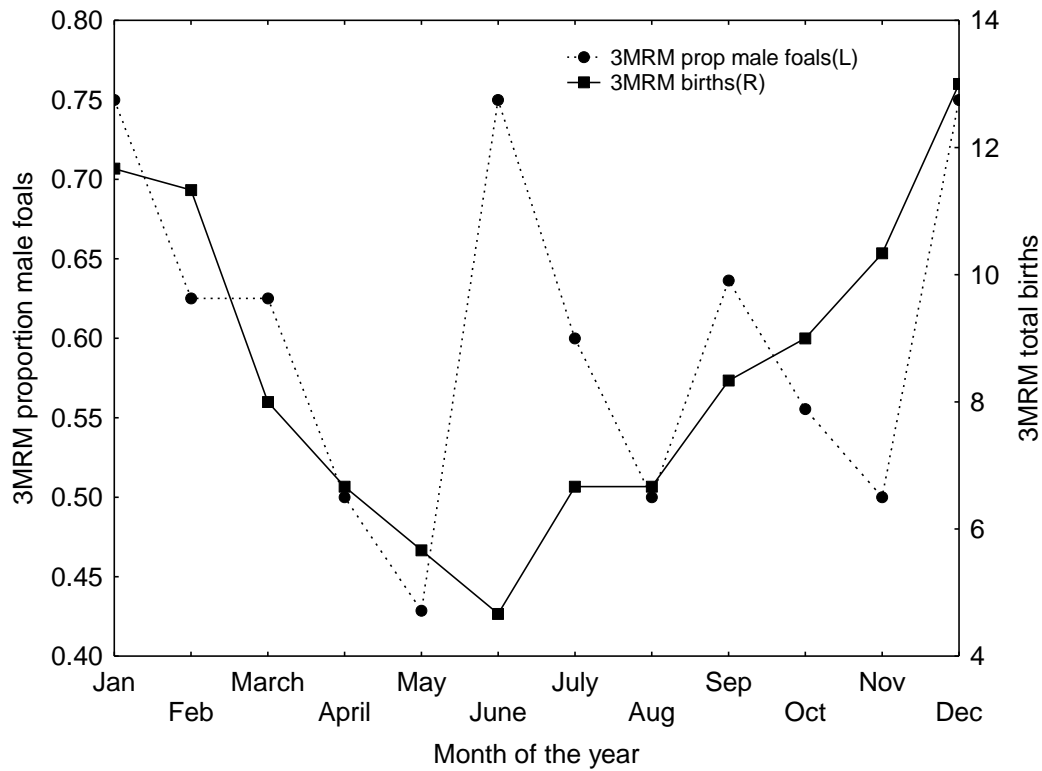


Fig. 10. Monthly (three month running mean) distribution of the proportion male births in that month and the total number of births.

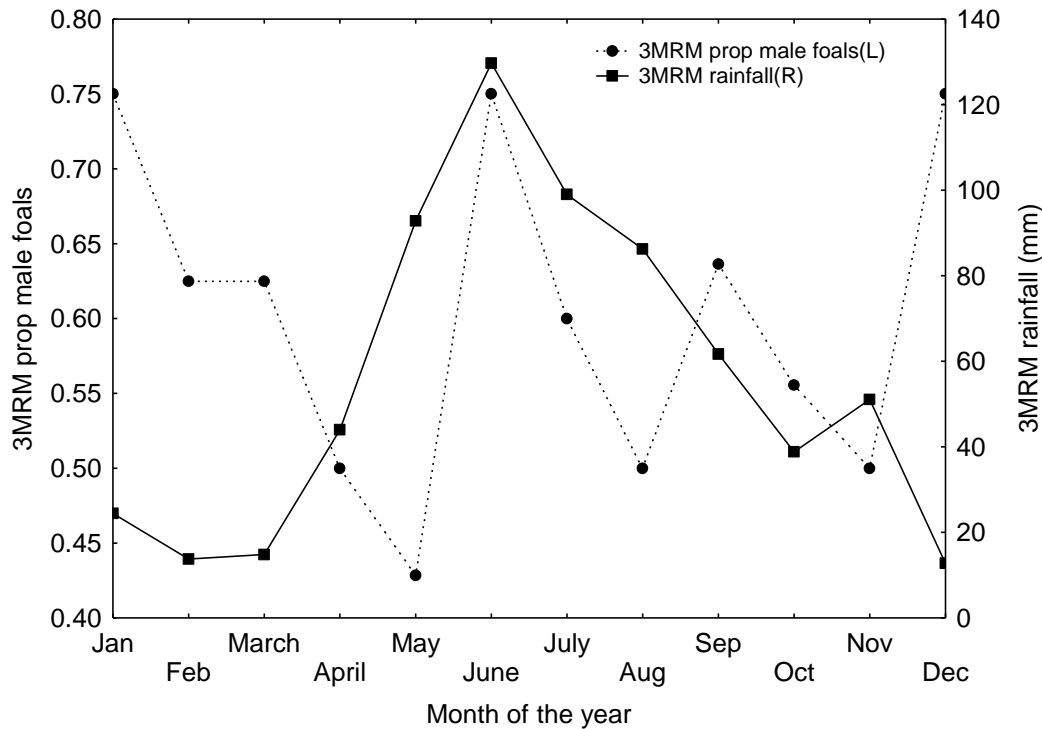


Fig. 11. Monthly (three month running mean) distribution of the proportion of male births and rainfall.

Only two stallions and one mare showed a significant bias in the sex of their offspring. The stallions known as Allan and Ike produced significantly more male and females foals, respectively (Table 1), while the mare Ricky produced significantly more males (Table 2). Two locations had a significant bias in the sex of foals, namely Boland Landbou (female bias) and Kranskop (male bias; Table 3). It is not certain whether the bias for female foals at Boland Landbou and males at Kranskop is location or individual dependant, but when looking at the mean fecundity values for these sites, it seems it may be location dependant. Boland Landbou had the second lowest mean fecundity and had a female foal bias, whereas Kranskop had one of the highest mean fecundities and had a male foal bias. These results are in accordance with the Trivers-Willard hypothesis and expectations for plains zebra (based on unpublished data by H. Hrabar), where females in favourable conditions (and hence good body condition) produce more male offspring. This suggests that

conditions at Boland Landou are generally resource limited, while Kranskop is resource abundant. The correlation (although not significant) between the two resource dependant reproductive traits, namely fecundity and foal sex ratios is shown in Figure 12.

The stallion Allan appears to be the main determinant of his male foal bias, as his foals were produced by five different females in Elansdberg, where no overall foal sex bias was found.

Table 1. Male versus female foals produced by herd stallions (with at least five known-sex foals).

Stallion	Female number	foal	Male foal number	Total foals	Proportion male foals	Bias in foal sex
Albert	8	6		14	0.43	NS
Alex	14	11		25	0.44	NS
Allan	2	11		13	0.85	Sig
Etienne	6	5		11	0.45	NS
Fanie	1	6		7	0.86*	NS
George	4	8		12	0.67	NS
Ike	16	4		20	0.20	Sig
Luke	9	10		19	0.53	NS
Megavolt	4	3		7	0.43	NS
Mike	3	2		5	0.40	NS
Nico	4	1		5	0.20*	NS
Paul	4	6		10	0.60	NS
Ryan	1	5		6	0.83*	NS
Shaun	8	5		13	0.38	NS
Ziggi	1	4		5	0.80*	NS

\*A marked difference in the number of male versus female foals, yet difference is not significant.

Table 2. Male versus female foals produced by each adult female (with at least 5 known-sex foals).

Mare	Female number	foal	Male foal number	Total foals	Proportion male foals	Bias in foal sex
Stelza	4	1		5	0.20*	NS
Tracy	2	4		6	0.67	NS
Marjean	2	3		5	0.60	NS
Melanie	5	7		12	0.58	NS
Marilyn	7	2		9	0.22*	NS
Monica	2	6		8	0.75	NS
Jeanetta	3	5		8	0.63	NS
Mariette	7	3		10	0.30*	NS
Brenda	4	1		5	0.20*	NS
Charlene	5	6		11	0.55	NS
Lulu	5	6		11	0.55	NS
Marcelle	5	3		8	0.38	NS
Ricky	1	8		9	0.89	Sig
Sokkies	4	1		5	0.20*	NS
Tandi	3	3		6	0.50	NS
Try-Me	5	2		7	0.29	NS

\*A marked difference in the number of male versus female foals, yet difference is not significant.

Table 3. The number of male versus female foals born at each location (for those locations with at least 5 known-sex births).

Location	Female number	foal	Male foal number	Total foals	Proportion male foals	Bias in foal sex
Boland Landbou	17	6		23	0.26	Sig
Bontebok Ridge	4	7		11	0.64	NS
Elandsberg	29	42		71	0.59	NS
Groote Schuur	22	19		41	0.46	NS
Ithemba Labs	5	7		12	0.58	NS
Kranskop	1	9		10	0.90	Sig
Pampoenvlei	1	6		7	0.86*	NS
Vlakkenhuiwel	4	1		5	0.20*	NS
Vrolikheid	3	2		5	0.40	NS
Wedderwil	11	4		15	0.27*	NS

\*A marked difference in the number of male versus female foals, yet difference is not significant.

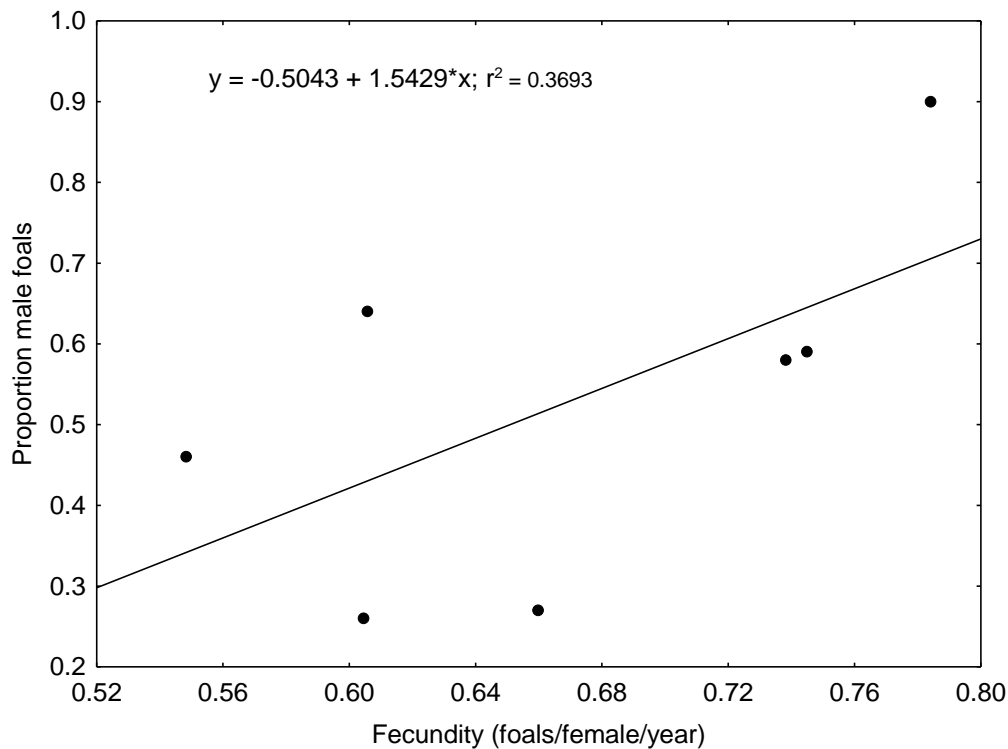


Fig. 12. The relationship between the mean proportion of male foals born at each location (with at least 10 known-sex foals) and the mean fecundity of females at the location ( $F_{1,5} = 2.93$ ,  $P = 0.15$ ,  $R^2_{adj} = 0.24$ ).

## Conclusions

- The level of quagga resemblance achieved in fourth generation individuals was achieved without an apparent compromise in genetic integrity, yet the degree of inbreeding needs to be compared to natural populations to confirm this.
- Inbreeding had no measurable effects on female reproductive success (fecundity) in this study. This is likely due to the low level of inbreeding in the population, but the number of foals produced by inbred mares was also very small (28) and this sample size is probably insufficient to detect any effects (Lacy 1997).
- The immediate costs of human intervention (a metapopulation approach to management and selective breeding) on reproductive rates are made apparent by this

study. Translocations between sub-populations (where females also changed their breeding stallion) resulted in significantly longer inter-foaling-intervals as well as an increase in the age at first foaling (for young females joining a herd with at least two unfamiliar mares already present). A change in stallion alone also increased inter-foaling-intervals, but not as significantly.

- Prime female reproductive years appear to be from about eight to ten years old, as inter-foaling-intervals were lowest for this age group.
- Foal sex ratio appears to be related to indicators of resource availability, namely birth season and rainfall (although these two factors do not coincide with one another in the winter-rainfall area of Wellington). The increased proportion of male foals during peak birth months and again during high rainfall months is in accordance with expectations from the Trivers-Willard Hypothesis, which states that females in good condition (expected during periods of high resource availability) are likely to produce more sons.
- The positive relationship between the proportion of male births and female condition/resource abundance was confirmed through the location effect. Boland Lanbou had a female foal bias and low mean female fecundity (also negatively affected by low resource availability), while Kranskop had a male foal bias and a high mean female fecundity.
- Foal sex ratios were unaffected by 1) first time foaling, 2) translocation of females or 3) previous foal sex.

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