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**RESEARCH ARTICLE**

# Long-term data on reproductive output and longevity in captive female common marmosets (*Callithrix jacchus*)

HAYLEY ASH AND HANNAH M. BUCHANAN-SMITH
*Behaviour and Evolution Research Group and Scottish Primate Research Group, Psychology, School of Natural Sciences, University of Stirling, Stirling, Scotland*

Short title: Reproduction and longevity in marmosets

*Correspondence to: Hannah Buchanan-Smith, Psychology, School of Natural Sciences, University of Stirling, Stirling, FK9 4LA, Scotland

Email: h.m.buchanan-smith@stir.ac.uk

Tel: +44 (0)1786 467674

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**ABSTRACT**

The common marmoset (*Callithrix jacchus*) is widely used in biomedical research, with many housed for breeding purposes world-wide. Significant variation in reproductive output among females has been found compared to other anthropoid primates. The present study explores this reproductive variation, focusing on potential predictors of dam longevity and litter size, as well as changes over time. Back-record analysis was conducted, yielding litter information and reproductive summaries of 360 dams housed at three UK marmoset colonies over 4 decades (1970s-2000s). Results revealed differences among the colonies, as well as within colonies over decades, suggesting environment may play an important role. Cox proportional hazards regression analyses revealed significant effects of mean litter size and yearly production on dam longevity. Decade, mean inter-birth interval and mean dam weight were found to be significant factors explaining dam longevity when looking at colonies individually. The most commonly recorded cause of death was 'poor condition'. Linear regression models found that no reproductive variable was useful in explaining mean litter size, except dam weight at conception, data which was only consistently recorded at one colony. While triplets were common at all three colonies, these larger litters were consistently associated with higher infant mortality, despite human intervention to improve survival. This study increases our understanding of marmoset reproduction, and possible improvements to practical aspects of colony management to enhance survival and welfare are discussed.

**Key words: reproduction; dam longevity; litter size; colony management; marmosets**

## INTRODUCTION

### Reproduction in the common marmoset

The common marmoset (*Callithrix jacchus*) is widely used as a non-human primate model in biomedical research [Buchanan-Smith, 2010; Hart et al, 2012]. Combined with their small body size (usually <400g), relative ease of handling, and absence of many zoonoses [Tardif et al, 2011], marmosets are inexpensive to keep compared to the larger macaques (*Macaca* spp.). They also have the highest potential fecundity of any anthropoid primate [Smucny et al, 2004; Tardif et al, 2003], and can be bred in sufficient numbers to meet research requirements [Poole and Evans, 1982]. These factors make them one of the most frequently used New World primates in research and testing [Home Office 2011, Council of Europe 2008, USDA, 2007]. Many more are also currently housed for breeding purposes.

Callitrichidae (i.e. marmosets and tamarins) produce more offspring per delivery, with more variation in litter size, than any other anthropoid primate [Smucny et al, 2004]. There are routinely multiple ovulations per cycle. Twins are the norm, although triplet litters are also common. Inter-birth intervals (IBIs) are also often short (approximately 5 months), with females able to conceive again shortly after birth [Smucny et al, 2004]. This means they can produce two litters a year [Tardif et al, 2008]. However, their high fertility is accompanied by high rates of pregnancy losses and infant mortality [Jaquish et al, 1991]. There can therefore be significant variation in reproductive output per year, as well as over a female’s lifetime [Smucny et al, 2004].

An overview, combining data from published literature and a large American multi-colony database, reported that breeding females had an average longevity of 5-7 years and a maximum of 16.5 years [Tardif et al, 2011]. Animals had a reproductive life span in captivity of around 2 years [Smucny et al, 2004]. However, in a report of another colony, maintained at the University of Cambridge [Ridley et al, 2006], 80% of breeders (males and females) were alive at 10 years of age. These animals were allowed to live out their optimum captive lifespan, only being euthanized for welfare reasons. Due to difficulties acquiring data, there is little known about longevity in wild common marmosets. Results from a wild population, followed for 10 years at a field site in Northeastern Brazil, suggest that early life mortality is relatively high compared to other age groups (66.7% infant survival). Females began reproducing around 4.5-5 years, and continued until they were 8-9 years old. Tenure therefore averaged 3.5 years. Females can breed until relatively close to their maximum life span, with a rather abrupt reproductive decline, associated with follicular depletion, or inability to maintain behavioural dominance [Tardif et al, 2008]. Whilst longevity and infant survival may be expected to be higher in captivity than in the wild, as captive marmosets are protected from predators and dominance competition, as well as have ample food provided, this may not be true for some common marmoset breeding colonies.

**Litter size and dam longevity in captivity**

Few studies have looked at variables that can influence the number of infants born per reproductive attempt in callitrichids [Bales et al, 2001]. Jaquish et al [1996)] found that there was low heritability of litter size, with only husbandry changes significant in the common marmoset. Increased cage volume and complexity, combined with increased protein content in the diet, were associated with a greater number of triplets. A good quantity of usable space has also been found to maximise well-being and breeding success in cotton-top tamarins [Savage, 1995]. Maternal body weight is also known to be important in marmosets, influencing ovulation number, losses during gestation and born litter size [Tardif et al, 1997]. Bales et al [2001] also found that higher pre-pregnancy body mass was associated with a greater number of live births (wild golden tamarins of known age, for 162.5 female-seasons).

However, the most important factor in infant survival is litter size [Tardif et al, 2003]. Several studies following the production of a single captive breeding colony over a number of years report that litter sizes have increased since establishment [Box and Hubrecht, 1987; Poole and Evans, 1982]. However, larger litters generally result in higher infant mortality [Jaquish et al, 1991]. The likelihood of all triplet infants surviving is greatly increased if one or all infants are partially or completely hand-reared [Hearn and Burden, 1979]. However, the welfare consequences and effect on subsequent scientific output of these rearing practices have been questioned [Buchanan-Smith, 2010].

It is also important to examine factors affecting dam longevity in captive colonies. Longevity in the current study is defined as the animals' life span in the colony, which often involves decisions to euthanize due to health or breeding management. In previous studies, Cox proportional hazards regression analysis revealed dam longevity to be significantly affected by number of litters, age at first parturition and site [Smucny et al, 2004]. Dams first reproducing later in life (4 years and over) tended to live longer than those first reproducing at younger ages. Although it may expected that larger litters would be associated with high energetic cost [Tardif et al, 1993] and reductions in life span, there is no evidence that this is the case [Jaquish et al, 1991; Smucny et al, 2004]. Changes in longevity over time have however been found at an American captive colony. Average life span extended from 4.82 years during colony establishment, to 7.07 years when the colony was stable. Mortality however increased with associated changes to the colony, including new animals and housing conditions [Tardif et al, 2011]. With greater experience of colony management and husbandry practices, as well as increases in basic biological knowledge and cage sizes, one might expect improved welfare and less infant mortality from colony establishment to present day.

### Aim

The present study examined reproductive information from three large well-established UK captive *Callithrix jacchus* colonies, each using different infant-rearing practices, over a period of four decades. Patterns of change between establishments and over time in litter size, infant mortality and dam longevity were determined to increase our understanding of reproductive variation, particularly factors affecting dam longevity and born litter size. This has the potential to aid in the management of captive common marmoset colonies [Smucny et al, 2004], many of which are housed for breeding purposes to provide models for biomedical research [Hart et al, 2012].

## METHOD

### Population Description

Reproductive information was obtained from records of marmoset dams used for breeding or in reproductive studies at three UK colonies. One colony was a commercial breeder, the other two bred marmosets primarily for use on site. The first dams in the records, which began breeding early in each decade, were selected. Data were collected from 120 dams at each site. At Colony A (CA), 30 dams in each of four decades (1970s, 1980s, 1990s and 2000s) were selected. As there were no data available from the 1970s at Colony B (CB) and Colony C (CC), data from 40 dams in each of three decades (1980s, 1990s and 2000s) were collected from these sites. This yielded information from 360 dams. Fifteen wild-caught and fifteen in-house bred animals were sampled in the 1970s at CA (no difference was found between the two in number of litters ($t=0.00$ (28), $p=1.00$) and litter size born in captivity ($t=1.14$ (134), $p=0.256$)). All other animals were bred in-house. This produced data from 2712 litters (CA 527; CB 1237; CC 967 litters). Loss of archived data at CB meant that born litter size was lost from all files in the 1980s, although weaned litter size could still be extracted. The data therefore consisted of dam information for 5588 born infants (CA 1287; CB 2004; CC 2297 infants). Lack of records during the early 1980s at CC also meant that survived litter size could not be extracted. Data were collected between February 2011 and February 2013, and were approved after review by the Stirling University Psychology Ethics Committee and by each facility involved. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

Two sets of back-record data were examined for each colony. The breeding file contained litter information for each dam, and the stock file contained individual dam life histories (including dates of birth and death, and manipulations for experimental or management purposes). These data sets were cross-referenced to provide a full account of each female's life in the colony. Dams euthanized at the end of an experiment were not included, although many sampled at CA were manipulated for non-terminal studies (e.g. given implants, injected with hormones and bled periodically).

**Litter Information**

Litter information consisted of data from each particular dam, regarding dates of birth for each litter, litter size, sex ratio and inter-birth intervals. Survival of each infant at birth (CA, CB and CC) and to weaning age (6 months; CB and CC) was recorded. Data for the first litter following intentionally aborted pregnancies or contraception administration were excluded when calculating mean IBI. Contraception was generally only used once or twice towards the end of a female's breeding life, usually if there was a health problem. If contraception was stopped, females did occasionally become pregnant again.

**Reproductive Summaries**

Reproductive history was also summarised for each female. Reproductive output variables included mean litter size born, mean litter size survived, number of litters produced and mean IBI. Longevity, age at first parturition, reproductive life span (calculated as the years between a dam's first and last birth), lifetime production, lifetime survived production, production per reproductive year and survived production per reproductive year (calculated by dividing lifetime production or survived production by (reproductive life span + 0.67)). The figure 0.67 years represents the average in utero investment in the first litter (5 months), plus the lactation investment in the last litter (time until weaning (3 months)) [Smucny et al, 2004]. Table 1 shows the number of dams sampled for each variable at each colony.

**Infant-rearing practices**

At CA, one infant from each triplet litter was either fostered or hand-reared in the 1970s. In later years, no intervention was carried out when triplets were born. At CB, infants from triplet litters were rotationally hand-reared (one was removed for 8 hrs/day from the family and given supplementary food), in an attempt to improve survival. Triplets were also fostered if an appropriate dam was available, or completely hand reared if the family rejected or abused their young. At CC, triplets were supplementary fed, in which all infants were removed from the family for 2 hours twice a day for hand feeding. Very light infants (<27g) were routinely euthanized at day 1.

**Maternal body weight and number in dam litter**

As all animals are weighed every month at CC, this information was available on individual records. Weights at likely conception dates or early in pregnancy, approximately 5 months prior to the birth date, before significant gain from the fetuses [Tardif and Jaquish, 1997; Bales et al, 2001), were recorded and used in analysis. Mean dam weight ranged from 366.06g ± 49.39 for singleton litters (N=47) and 373.80g ± 41.57 for twins (N=489), to 396.49g ± 45.74 (N=376) for triplets and 391.20g ± 40.16 for quadruplets (N=10). The number of infants in the dam's litter at her birth was also recorded at CC, and so this was included to look at any potential genetic influence in mean litter size. Neither weights nor dam's own litter size was recorded consistently at CA or CB.

**Statistical analysis**

Data were summarised and analysed using SPSS statistical software. Descriptive statistics were carried out to summarise the reproductive output of the 120 dams at each colony. The percentages of each born litter size and their associated losses, as well as changes in litter size and dam longevity over time were also examined.

Descriptive statistics were also conducted to summarise cause of death over all three colonies (n=356). These were divided into 'euthanized', 'died naturally', or 'not stated' (some within this category gave a cause of death, but did not specify whether the animal was euthanized or died naturally of the problem). This was further divided into 'health' or ‘breeding management’ reasons for death, as well as if this was ‘not stated’ (in some cases it was recorded that the animal was euthanized or died naturally, but the reason was unknown).

**Mean litter size**

Multi-linear regression procedures using the Enter method were performed on 258 dams for whom we had complete data on all independent variables (IVs), to describe the amount of variation in the dependent variable (DV) mean litter size. Preliminary Spearman’s Rank correlations were first used to look for potential multicollinearity between variables. Number of litters was not included in the analyses, due to the strong correlation with dam longevity ($r=0.89$, $p < 0.001$), although no other variable was highly correlated ($r > 0.60$) with another. $R^2$ change values for each additional variable entered in the regression model were used to describe the variance explained by each IV. The criterion for entry into the model was $p<0.05$. Although DVs were not normally distributed, models can still be used to make valid conclusions from this sample [Field, 2009]. Colony and decade were regression control variables. Independent variables of longevity, mean IBI, age at first parturition and yearly production [following Smucny et al, 2004] were entered into the model.

It became clear from comparions that the colonies showed different patterns. There were also different issues that arose, including data from wild-caught animals in the 70s at CA, missing data in the 80s at CB and CC, and no weights or dam litter size recorded at CA and CB. Each colony was therefore also analysed separately, to prevent important information being lost. An ANOVA was conducted to look at differences in weight between litter sizes at Colony C.

### Survival analysis

Cox proportional hazards regression was performed to investigate which reproductive output variables could affect dam longevity. This is appropriate as it can be used to evaluate the effect of two or more continuous or categorical variables on whole-life survivorship. It also handles censored cases, so animals without a completed lifespan can be included [Jaquish et al, 1991].

Survival analysis was conducted for 262 dams of known birthdates, using the Enter method, with covariates of mean litter size, mean IBI, age at first parturition and yearly production. Site and decade were included as control variables. Each colony was also analysed separately, with decade as a control variable. Additional covariates of number of dam litter and dam weight at likely conception were included for CC. For dams with known date of death, longevity was the time of death. For dams still alive in the colonies (n=4), longevity was the age at censor date. This was defined as the date of the last update in the colony records.

## RESULTS

### Variation in reproductive output

Reproductive output variables for the dams of the three colonies (combined decades) are summarised in Table 2. The values represent grand mean and medians calculated from the mean values of all dams. For CA data, no measured parameter was normally distributed (>0.05) and so median values are most appropriate. For CB data, ‘yearly production’ and ‘yearly survived production’ were normally distributed, and for

CC, longevity and weight at conception were normally distributed, and so mean values are most appropriate for these.

### Changes in mean litter size and dam longevity

Figures 1 and 2 display median dam longevity and median of the mean litter size, for each colony over the decades. These graphs reveal the different patterns of change over the decades between the sites.

### Litter sizes and associated losses

Figures 3 displays the percentage of births at Colonies A, B and C. Compared to twins, triplet births were equally as common at CA, more common at CB and a little less common at CC, when data from all four decades were combined. Table 3 shows the total percentage of mortality (number of infants) associated with each litter size at each colony at birth, within 6 months and in total. In the majority of cases, these were by natural causes or euthanasia due to poor growth. Infant mortality was highest in quadruplet and quintuplet litters.

### Dam cause of death

Descriptive statistical analysis was carried out on 356 dams from all three colonies. Table 4 shows the number of animals that were euthanized or died naturally, as well as when this was not stated, and the associated percentages of each cause of death (health, breeding management or unknown). Where this information was recorded, the most common cause of death was euthanasia due to poor condition.

### Mean litter size

A linear regression model of mean litter size was estimated ($R^2$ =0.45), explaining 44.8% of the variance in mean litter size for the combined colonies. Two hundred and fifty eight cases were included in the analysis. Control variables for decade, and colony were included in the model. Significant differences in mean litter size were found between colonies (explaining 45%), with CC having significantly lower mean litter size than CA and CB. CA and CB were not significantly different. A significant difference was also found between decades (explaining 42%). Mean litter size in the 90s was significantly higher than in the 80s. No other comparisons were significant. Net of the control variables, yearly production had the highest explanatory value (44.7%, positive effect) followed by longevity (9.8%, positive), with all being significant.

A linear regression model of mean litter size was estimated for each colony. For CA, 80 cases were included, and 45.9% of the variance was explained. Control variables for decade were included in the model (explaining 23.6%). Mean litter size in the 70s and 80s were significantly lower than in both the 90s and 2000s. Net of the control variables only yearly production was significant (22.3%, positive effect).

For CB, 75 cases were included, and 47.8% of variance was explained for mean litter size. As all cases in the 1980s were incomplete, only those in the 1990s and 2000s were included. Mean litter size was significantly higher in the 90s than the 2000s. Net of the control variables (explaining 13.1%), only yearly production was significant (34.6%, positive effect).

For CC, 102 cases were included, and 55.7% of the variance in mean litter size was explained. No decade was significantly different to another. Net of the control variables yearly production had the highest explanatory value (51.3% positive effect), followed by mean dam weight (21.7%, positive effect), with both significant. A one-way ANOVA revealed a significant difference in dam weight at likely conception between born litter sizes ($F(3, 918) = 21.61$, $P<0.001$), with post hoc tests showing dam weight to be higher in triplet births than twin ($P<0.001$) and singleton births ($P<0.001$). No difference was however found in quad births. While dam's own litter size was included in analysis, this was not found to contribute significantly to the model. Table 5 summarises the results of the Multiple Linear Regression from combined and separate colony analysis.

**Survival analysis**

A whole-life survivorship analysis revealed that colony, mean litter size and yearly production were significant ($P<0.05$) factors affecting dam longevity. CA had significantly lower survival than CC and CB, although CB and CC were not significantly different. Decades 80 and 90 were significantly higher than in the 2000s, although no other comparison was significant. Increases in mean litter size and yearly production were both significantly associated with higher longevity.

Analysis of individual colonies revealed that only mean IBI had a significant relationship (positive) with dam longevity at CA. Dams with longer mean IBI demonstrated higher longevity than those with shorter mean IBI. There were no significant differences in longevity between the decades at CA. Only decade was significant at CB. Females breeding in the 90s lived for longer than those breeding in the 2000s. At CC, mean litter size (positive), yearly production (positive), mean IBI (negative) and mean weight (positive) were all significant factors affecting dam longevity. Females with higher mean litter size, higher yearly production, shorter mean IBI and higher weight showed greater longevity. No significant differences in longevity were found between decades at CC. While dam's own litter size was included in analysis, this was not found to contribute significantly to the model. Table 6 summarises the results of the Cox Proportional Hazards Regression from combined and separate colony analysis.

## DISCUSSION

### Reproductive output and dam longevity

The present study summarised the reproductive output of captive marmosets housed at three UK colonies over 4 decades. Overall, many values are similar to those previously described [Smucny et al, 2004; Tardif et al, 2003; Box and Hubrecht, 1987], although several are greater in the UK colonies. These higher UK values appear to be due to the lifetime production and number of litters at CB in particular, where there was also the highest reproductive lifespan and shortest IBIs. While some females had a reproductive life span of only one or two litters, others had consistently high production over many years. There was therefore considerable variation between female common marmosets. Table 7 provides comparative data from previous research.

Over all three colonies, average longevity was approximately 6 years in the UK. This is similar to other establishments from the 1980s [Box and Hubrecht, 1987] to the 2000s [Smucny et al, 2004]. It appears that while the majority of animals was euthanized, rather than died naturally, this was due to health and welfare reasons, most commonly ‘poor condition’. More detailed records would however be beneficial, including a more specific cause of death. Management decisions can also be made regarding which animals are most suitable to keep in breeding, and so longevity could be related to production [Essl, 1998]. However, only a very small portion, of those with adequate records, were euthanized due to breeding management. Dam health and longevity is therefore a concern. While one may expect increased longevity in captivity compared to the wild, as predators and food shortage are not constraints, this does not appear to be the case at some colonies.

**Factors affecting dam longevity**

A whole-life survivorship analysis, combining data from all three UK colonies, found that site, decade, yearly production and mean litter size were all significant predictors of dam longevity. Dam longevity and lifetime productivity at CA, where experimental manipulations were often carried out for reproductive studies, was the lowest of the three colonies, and very similar to those obtained by Smucny et al [2004]. Average longevity was 5.31 years, which was relatively similar in each decade. However, many animals were placed on terminal experiments in the 2000s, which did limit the available sample in this decade. Dam longevity and lifetime productivity at CB, a commercial facility in which breeding pairs were rarely disturbed, was the highest. Average longevity was 9.58 years in the 1990s, which is similar to the University of Cambridge [Ridley et al, 2006]. However, this significantly decreased in the 2000s, after a change in diet and moves between buildings. Differences in housing and husbandry could therefore be important factors in dam longevity between colonies. Results from CC, an establishment that bred for purpose, fell between those obtained at the other two sites. Longevity remained at around 6 years over the decades, which is similar to data published by Tardif et al [2003]. This suggests that longevity in captivity does not appear to have improved significantly, despite increased understanding of the species' biological and psychological needs and concurrent improvements in their care. While there were insufficient details to investigate which specific environmental factors are most important, it appears that appropriate housing and particularly a diet that meets nutritional needs is necessary, as is a stable, closed colony with minimal disturbance [Tardif et al, 2011].

Although the costs of high reproduction might be expected to reduce condition and longevity [Tardif et al, 2008], there was no evidence that this was the case. In fact, dams with larger mean litter sizes, producing more infants per year, tended to have higher longevity. Previous research [Jaquish et al, 1991; Smucny et al, 2004] has found no relationship between litter size and dam longevity. Although larger litters did not appear to be detrimental to physical health, there is evidence that they may be stressful for parents. Tardif et al. [2002] found that dams spent less time carrying and nursing triplet infants, compared to twin infants. There was also a higher frequency of triplet-infant initiated interactions, associated with increased harassment by mothers, than for twins. These findings suggest that dams could only tolerate a limited amount of time with their young, and that larger litters seem to disrupt maternal behaviour [Tardif et al, 2002].

Only mean IBI was significant in explaining dam life span at CA, with dams experiencing longer inter-birth intervals surviving longer. Mean IBI was also significant at CC, although a negative association was found at this colony. Instead, heavier dams survived for longer at CC, where weight was recorded. This may be because lactation is relatively costly for marmosets, with small mothers experiencing substantial mass loss and high risk of mortality following twin litters [Tardif et al, 2002]. While, it is possible that the constant high energetic demand of pregnancy and lactation could reduce longevity, and so increasing time between births may give females time to recover body condition, this effect does not span all three colonies and so no robust conclusions can be made. However, this could be interesting area for future research to explore.

Although results from previous studies suggest that delaying the onset of breeding in captivity may increase longevity [Jaquish et al, 1991], with early age at first reproduction having detrimental health consequences, no association was found between age at first parturition and dam longevity in the present study. However, age at first parturition was generally around 2.0 years, with very few after this time. Perhaps if more females had begun breeding after 4 years, a similar result to Smucny et al [2004] would be found. This may be another interesting area of future research, and a possible consideration in the management of breeding marmosets. While it is important to consider age-related pathologies, marmosets could be managed to survive for longer before degeneration occurs [Tardif et al, 2011].

**Litter size and infant mortality**

Litters larger than two accounted for approximately half of the births examined in each colony. However, these larger litters did have considerably greater perinatal mortality than in twins, ranging from 30% of infants from triplet litters to 65% from quintuplets. High infant mortality has been reported previously in captive colonies [Jaquish et al 1991], primarily due to the large proportions of triplets born.

As marmoset families are rarely able to rear more than two infants at a time [Poole and Evans, 1982], these young are unlikely to survive without some form of human intervention. While CA did not intervene when triplet litters were born in later decades, CB and CC both consistently carried out supplementary feeding of triplet infants. Despite hand rearing, large litters still resulted in higher mortality than twins. While it was rare for all three triplets in a litter to die, there was often one infant loss within the first few weeks.

These rearing practices also involve removal from the family for extended periods of time, which has been associated with adverse developmental outcomes [Dettling et al, 2002; Pryce et al, 2004]. Although triplet losses at birth were higher at CC than CB, due to routine euthanisia of very light infants, losses at 6 months were lower. This suggests that their practice of rotational hand-rearing may have been more successful, as litter mates remained together and were separated from the family for shorter periods of time. Due to our ethical obligation to ensure good welfare, as well as the importance of raising animals that are 'fit for purpose', potential factors affecting mean litter size were also studied.

**Factors affecting born litter size**

A linear regression model, combining data from all three UK colonies, found that 44.8% of variance in mean litter size born was explained by site, decade, yearly production and dam longevity. CC had the lowest mean litter size of the three colonies. Differences over time were also found at CA, where births changed from predominantly twins in the 70s and 80s to predominantly triplets in the 90s and 2000s. Litter size fell significantly in CB, although remained similar at CC.

Inspection of colonies separately showed that only yearly production was significant at CA and CB. However, these findings are somewhat obvious or unavoidable, and so are not useful predictors. They are therefore of little interest, as they will not contribute to Refinements. Mean dam weight at likely conception was a significant predictor of mean litter size at CC, with heavier dams producing larger litter sizes. Dam weight was also significantly higher prior to triplet births compared to twin or singleton births. Tardif and Jaquish [1997] also showed that higher weight was associated with higher number of ovulations. However, mothers that lose mass during pregnancy can reabsorb fetal material, leading to litter size reduction in utero [Tardif and Jaquish, 1997]. Litter size could therefore change from date of conception, which may explain why this factor did not explain more of the variation.

The dam's own litter size was not significant in predicting litter size, a finding reported by previous authors [Tardif and Jaquish, 1997; Jaquish et al, 1991], and so genetic variance does not appear to play a major role. Tardif and Jaquish [1997] found that much variation in number of ovulations was seen within, rather than between, females. Low repeatability of final litter size per dam has also been discovered [Jaquish et al, 1991]. It is therefore unlikely that selecting breeding females who were born to twin litters themselves would be a successful way of promoting twin births in captive colonies. Litter size instead appears to be flexible [Jaquish et al, 1996], determined by environmental variables affecting energy availability, such as diet or physical activity. Captive animals can weigh as much as 600g [Poole and Evans, 1982], compared to their wild counterparts weighing around 330g, which may account for captive females producing more larger litters than their wild counterparts. Maintaining dams at lower weights, may help to reduce larger litters, which are associated with higher infant mortality. This must be applied carefully, as heavier dams also seem to have greater longevity.

## Conclusion

The present study provides interesting information on reproduction and life history in female marmosets housed at UK breeding colonies, in comparison to similar international establishments. Areas of concern include high rates of infant deaths and dam health. Potential predictors of mean litter size and dam longevity were therefore examined, and possible ways of aiding with practical aspects of managing these animals discussed. Maintaining a colony of experienced breeders, with longer healthy life spans and an increased incidence of twin births could have far-reaching implications to improve the quality of life for marmosets in breeding facilities. This is especially important given the considerable number bred for use in a wide range of biomedical research around the world.

## CONFLICT OF INTEREST

The authors of this manuscript have no conflict of interest that would inappropriately bias this research.

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FIGURE 1: Median dam longevity (N= 105 CA; 120 CB; 115 CC) for each colony over four decades. Median: solid line; 25 and 75 percentiles: dotted line; Individual dams: open circles

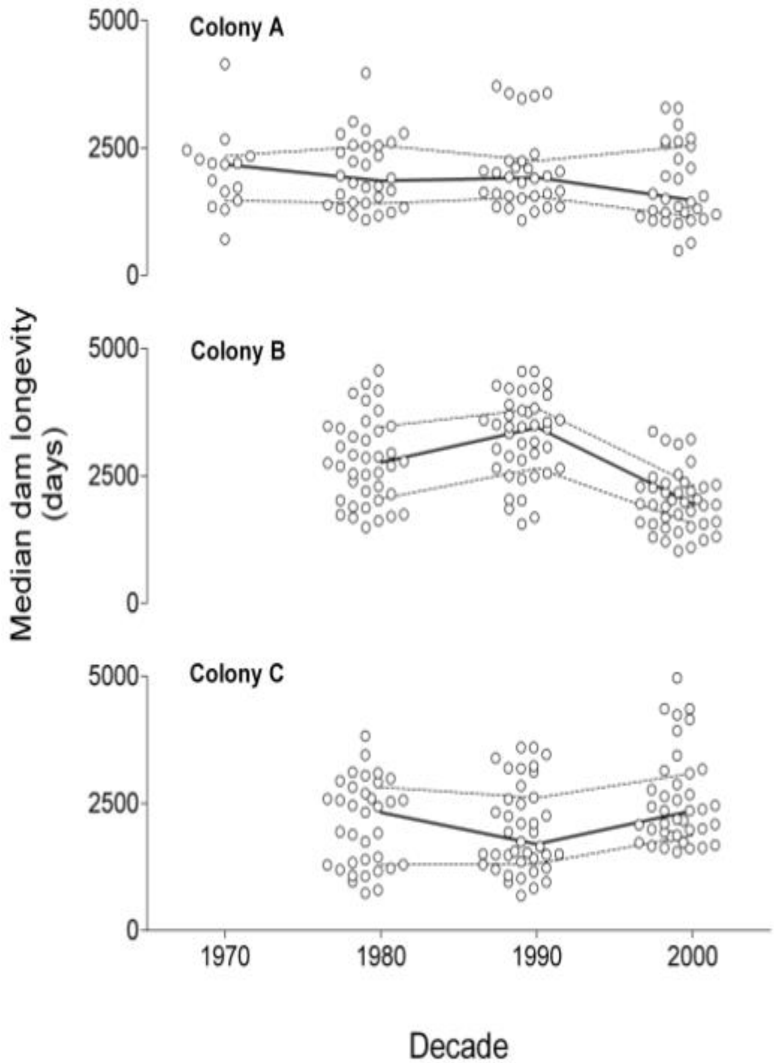

Figure 2

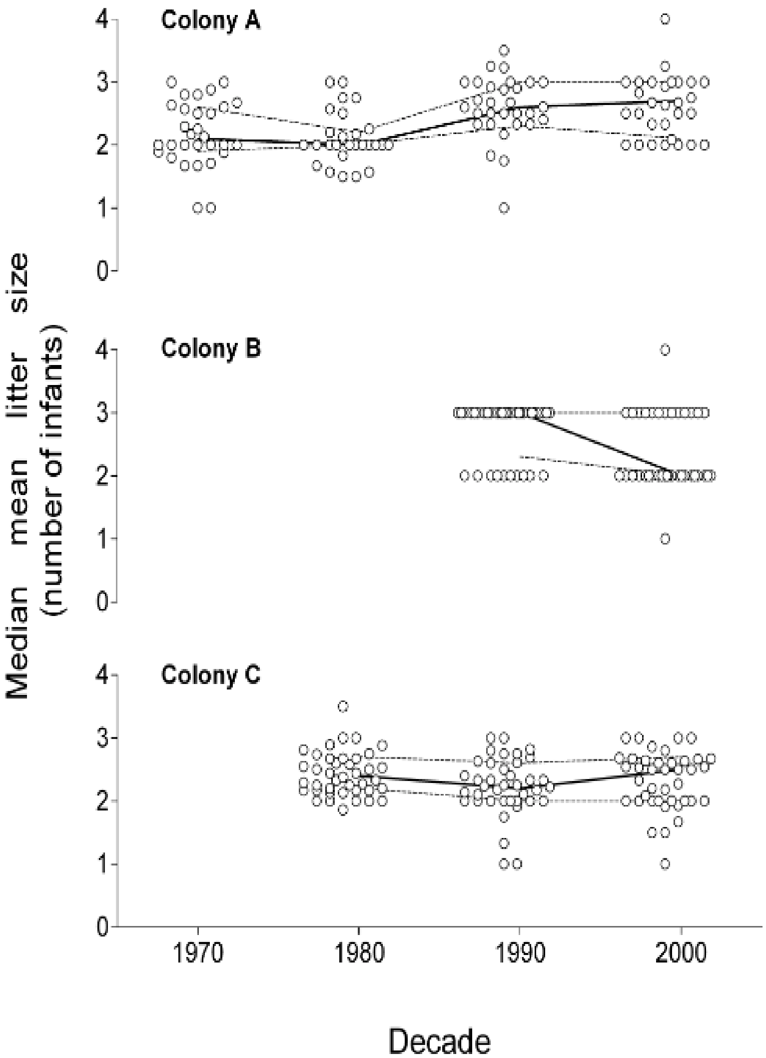


**FIGURE 2: Median of mean litter size (N= 120 CA; 80 CB; 120 CC) for each colony over four decades. Mean litter size calculated as sum of number of infants in each litter, divided by total number of litters, for each dam. Median: solid line; 25 and 75 percentiles: dotted line; Individual dams: open circles**

**Figure 3**

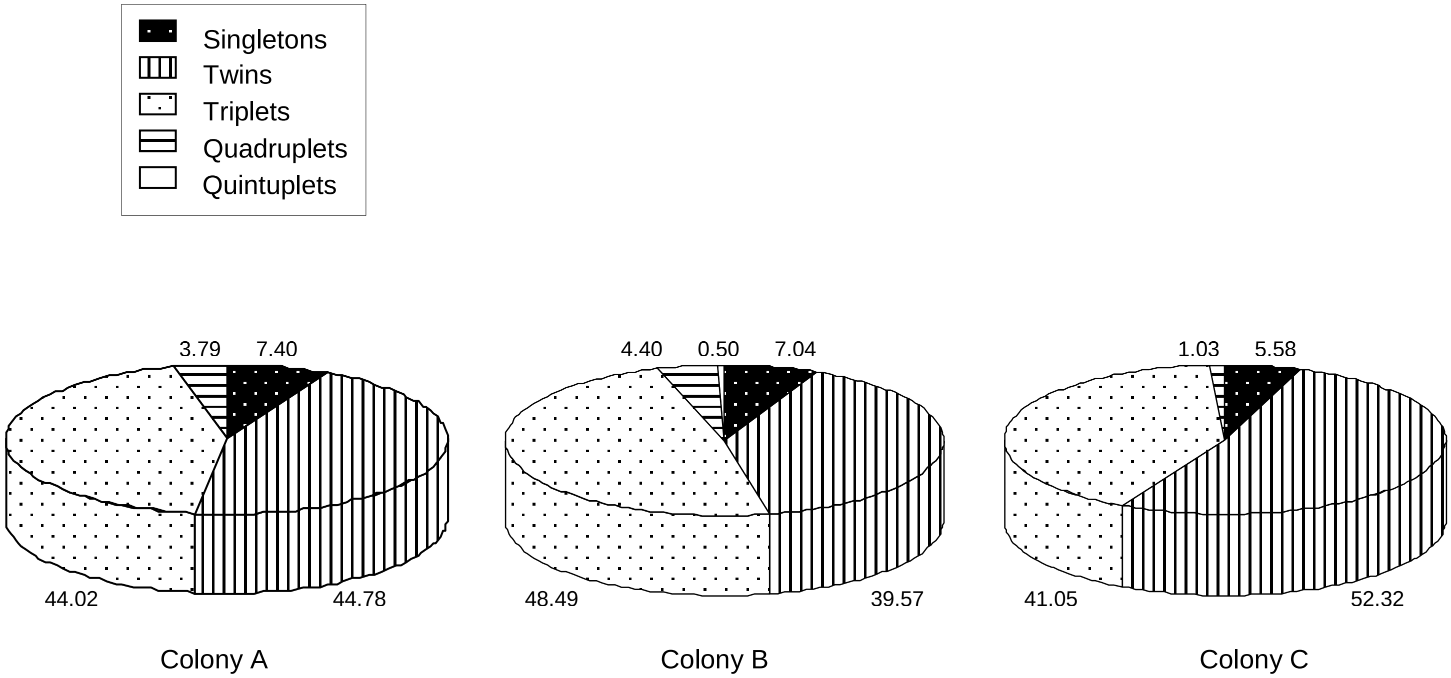


FIGURE 3: Percentage of litter sizes at birth at Colonies A (N= 527), B (N= 796) and C (N= 967)

**TABLE 1: Number of dams included for each variable in each colony**

| Variable | Colony A | Colony B | Colony C |
|---|---|---|---|
| **Dam longevity** | 105<br>(Ex 15 wild caught in 70s) | 120 | 115<br>(Ex 4 ex breeders still alive in 2000s and 1 purchased in 80s) |
| **IBI** | 93<br>**(**Ex 27 primiparous) | 115<br>(Ex 5 primiparous) | 108<br>(Ex 12 primiparous) |
| **Age at 1st parturition** | 105<br>(Ex 15 wild caught- may have had previous litters) | 120 | 119<br>(Ex 1 purchased in 80s) |
| **Lifetime production** | 105<br>(Ex 15 wild caught) | 80<br>(Ex 40 in 80s- no record of born litters) | 119<br>(Ex 1 purchased in 80s) |
| **Survived production** | 105<br>(Ex 15 wild caught) | 120 | 80<br>(Ex 40 in 80s- no record of losses) |
| **Production/yr** | 120 | 80<br>(Ex 40 in 80s) | 120 |
| **Survived production/yr** | 120 | 120 | 80<br>(Ex 40 in 80s) |
| **Reproductive life span** | 80<br>(Ex 40 wild caught and primiparous) | 115<br>(Ex primiparous) | 107<br>(Ex primiparous and 1 purchased in 80s) |
| **Litter size** | 120 | 80<br>(Ex 40 in 80s) | 120 |
| **Survived litter size** | 120 | 120 | 80<br>(Ex 40 in 80s with missing data) |
| **Number of litters** | 105<br>(Ex 15 wild caught) | 120 | 119<br>(Ex 1 purchased in 80s) |
| **Maternal body weight at conception** | 0 | 0 | 118<br>(Ex 2 in 80s with missing data) |
| **Number in dam litter** | 0 | 0 | 118<br>(Ex 2 in 80s with missing data) |

* Ex= excluding

**TABLE 2: Variation in dam reproductive variables (Colonies A, B and C, combined decades)**

| Variable | Mean and SD | | | Median, min- max | | |
|---|---|---|---|---|---|---|
| | A | B | C | A | B | C |
| Dam longevity (yrs) | 5.31± 2.06 | 7.39± 2.60 | 6.04± 2.47 | 4.98 (1.31- 11.34) | 6.99 (2.80- 16.20) | 5.76 (1.88- 13.59) |
| Inter-birth interval (days) | 229.17± 81.71 | 190.87 ± 39.22 | 192.05± 81.85 | 206.00 (151.00- 669.00) | 180.00 (151.00- 337.00) | 170.20 (149.67- 754.00) |
| Age at first parturition (yrs) | 2.68± 0.82 | 2.32± 0.68 | 2.30± 0.63 | 2.49 (1.19-5.17) | 2.19 (1.14-6.69) | 2.13 (1.33-5.62) |
| Lifetime production (no of infants born) | 10.77± 9.16 | 25.05± 17.10 | 18.88± 13.72 | 9.00 (1.00-42.00) | 21.00 (1.00-59.00) | 16.00 (1.00-59.00) |
| Survived production (no of infants) | 9.74± 8.61 | 19.05± 12.68 | 13.45± 11.54 | 8.00 (0.00-42.00) | 16.00 (1.00-53.00) | 10.50 (0.00-46.00) |
| Production/year (infants born/ yr of RL) | 3.84± 1.19 | 4.67± 1.31 | 4.32± 1.05 | 3.62 (1.49-7.71) | 4.60(1.49-7.74) | 4.42 (1.49-6.48) |
| Survived production/year (infants/yr of RL) | 3.34± 1.29 | 3.39± 0.88 | 2.99± 1.47 | 3.24 (0.00-6.58) | 3.39 (0.76-5.49) | 3.43 (0.00-5.44) |
| Reproductive lifespan (yrs) | 2.61± 1.91 | 4.75± 2.26 | 3.77± 2.39 | 2.15 (0.42-9.06) | 4.61 (0.63-13.36) | 3.58 (0.41-11.68) |
| Litter size (no of infants born) | 2.37± 0.53 | 2.55± 0.55 | 2.32± 0.43 | 2.33 (1.00-4.00) | 3.00 (1.00-4.00) | 2.33 (1.00-3.50) |
| Survived litter size (no of infants) | 2.06± 0.65 | 1.87± 0.37 | 1.56± 0.71 | 2.00 (0.00-3.23) | 2.00 (1.00-3.00) | 1.75 (0.00-3.00) |
| Number of litters (litters/dam) | 4.37± 3.37 | 10.31± 6.15 | 7.93± 5.49 | 3.00 (1.00-14.00) | 9.00 (1.00-30.00) | 7.00 (1.00-23.00) |
| Weight at conception (g) | | | 373.39± 43.44 | | | 369.13 (283.00-503.00) |
| Number in dam litter | | | 2.42± 0.53 | | | 2.00 (1.00-4.00) |

*Reproductive life span (RL) is summarised for multiparous females only. Survival age and age at first birth were calculated for dams born into the colony, and so exclude wild caught animals. Inter-birth intervals were calculated excluding abortions and after a change of mate.
*For CA, medians are most appropriate for all values. For CB 'yearly production' and 'yearly survived production', and CC 'dam longevity' and 'dam weight at conception' mean values are most appropriate.

TABLE 3: Percentage of each litter size, together with their associated mortality (all three colonies)

| | **Singletons** | | | **Twins** | | | **Triplets** | | | **Quadruplets** | | | **Quintuplets** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Colony** | A | B | C | A | B | C | A | B | C | A | B | C | A | B | C |
| Number of litters born | 38 | 56 | 54 | 235 | 315 | 506 | 228 | 386 | 397 | 20 | 35 | 10 | 0 | 4 | 0 |
| Number of Infants born | 38 | 56 | 54 | 470 | 630 | 1012 | 684 | 1158 | 1188 | 80 | 140 | 40 | 0 | 20 | 0 |
| Number of infant losses at birth | 3 | 3 | 5 | 38 | 17 | 45 | 82 | 54 | 104 | 6 | 20 | 8 | 0 | 0 | 0 |
| % losses at birth | 7.89 | 5.36 | 9.25 | 8.09 | 2.70 | 4.45 | 11.99 | 4.66 | 8.75 | 7.50 | 14.29 | 20.00 | 0.00 | 0.00 | 0.00 |
| Number of infant losses at 6 months | N/A | 9 | 3 | | 84 | 44 | | 302 | 205 | | 43 | 6 | | 13 | 0 |
| % losses at 6 mnths | N/A | 16.07 | 5.55 | | 13.33 | 4.34 | | 26.08 | 17.26 | | 30.71 | 15.00 | | 65.00 | 0.00 |
| Total number of infant losses | N/A | 12 | 8 | | 101 | 89 | | 356 | 309 | | 63 | 14 | | 13 | 0 |
| % total losses | N/A | 21.43 | 14.81 | | 16.03 | 8.79 | | 30.74 | 26.01 | | 45.00 | 35.00 | | 65.00 | 0.00 |

*NA= no data on infant mortality after the day of birth

**Table 4: Percentages of each cause of death when animals were either euthanised, died naturally or when this was not recorded (N=356)**

| | **Euthanised** (N= 274) | **Natural death** (N=22) | **Not stated** (N=60) |
|---|---|---|---|
| **% Health** | **65.69** | **27.27** | **48.33** |
| Gastrointestinal | 1.45 | 4.55 | 1.67 |
| Injury | 1.82 | 0 | 0 |
| Neurological | 2.19 | 0 | 1.67 |
| Poor condition | 44.90 | 13.64 | 33.33 |
| Reproductive | 7.30 | 9.09 | 10 |
| *Respiratory* | *3.28* | *0* | *1.67* |
| Surgical complications | 1.09 | 0 | 0 |
| Tumour | 3.28 | 0 | 0 |
| Optic | 0.36 | 0 | 0 |
| **% Breeding management** | **1.82** | **0** | **0** |
| Removed from breeding | 1.09 | 0 | 0 |
| Not breeding | 0.36 | 0 | 0 |
| Infanticide | 0.36 | 0 | 0 |
| **% Unknown** | **32.48** | **72.72** | **51.67** |

**TABLE 5: Summary of regression results for mean litter size born age (combined, n=258 and separate colony analysis)**

| Model variables | $R^2$ | Adjusted $R^2$ | $R^2$ change | Significance of added variable |
|---|---|---|---|---|
| **COMBINED COLONIES (n=258 complete cases)** | | | | |
| **Whole model r2=.448, adjusted .432** | | | | |
| Site | 0.045 | 0.037 | 0.045 | P<0.01 |
| Site AvC | | | | P<0.05 |
| Site BvC | | | | P=0.001 |
| Decade | 0.042 | 0.030 | 0.042 | P<0.05 |
| Decade 90v80 | | | | P<0.01 |
| Yearly production | 0.447 | 0.434 | 0.373 | P<0.001 |
| Dam longevity | 0.098 | 0.077 | 0.024 | P<0.01 |
| **COLONY A (n=80 complete cases)** | | | | |
| **Whole model r2=.459, adjusted .43** | | | | |
| Decade | 0.236 | 0.206 | 0.236 | P<0.001 |
| Decade 70v100 | | | | P=0.01 |
| Decade 80v100 | | | | P<0.001 |
| Decade 90v70 | | | | P<0.05 |
| Decade 90v80 | | | | P<0.001 |
| Yearly production | 0.459 | 0.430 | 0.223 | P<0.001 |
| **COLONY B (n=75 complete cases)** | | | | |
| **Whole model r2=.478, adjusted .463** | | | | |
| Decade | 0.131 | 0.120 | 0.131 | P=0.001 |
| Decade 90v100 | | | | P=0.001 |
| Yearly production | 0.478 | 0.463 | 0.346 | P<0.001 |
| **COLONY C (n=102 complete cases)** | | | | |
| **Whole model r2 = .557, adjusted .539** | | | | |
| Mean dam weight | 0.255 | 0.232 | 0.217 | P<0.001 |
| Yearly production | 0.551 | 0.537 | 0.513 | P<0.001 |

**Table 6: Cox Proportional Hazard Regression Coefficients for Whole-Life Survivorship Analysis of dams**

| Covariate | Estimate | SE | Wald statistic | df | P | Relative risk | Lower 95% CI for relative risk | Upper 95% CI for relative risk |
|---|---|---|---|---|---|---|---|---|
| **COMBINED COLONIES (n= 262)** | | | | | | | | |
| Whole model ($X^2$=43.923) | | | | | | | | |
| Site | | | 18.289 | 2 | <0.001 | | | |
| BvA | -0.696 | 0.165 | 17.854 | 1 | < 0.001 | 0.499 | 0.361 | 0.689 |
| CvA | -0.425 | 0.151 | 7.899 | 1 | =0.005 | 1.530 | 1.137 | 2.057 |
| Decade | | | 11.938 | 3 | <0.01 | | | |
| 80v100 | -0.356 | 0.174 | 4.178 | 1 | <0.05 | 0.700 | 0.498 | 0.985 |
| 90v100 | -0.512 | 0.512 | 11.417 | 1 | =0.001 | 0.599 | 0.445 | 0.806 |
| Mean litter size | -0.444 | 0.153 | 8.426 | 1 | <0.005 | 0.641 | 0.475 | 0.866 |
| Yearly production | -0.231 | -0.062 | 13.812 | 1 | <0.001 | 0.794 | 0.703 | 0.896 |
| **COLONY A (n=80)** | | | | | | | | |
| Whole model ($X^2$=5.15) | | | | | | | | |
| Mean IBI | -0.004 | 0.002 | 4.555 | 1 | <0.05 | 0.996 | 0.992 | 1.000 |
| **COLONY B (n=75)** | | | | | | | | |
| Whole model ($X^2$=38.216) | | | | | | | | |
| Decade | | | | | | | | |
| 90V100 | -1.823 | 0.304 | 36.072 | 1 | <0.001 | 0.161 | 0.089 | 0.293 |
| **COLONY C (n=106)** | | | | | | | | |
| Whole model ($X^2$=30.172) | | | | | | | | |
| Mean litter size | -0.688 | 0.334 | 4.250 | 1 | <0.05 | 0.502 | 0.261 | 0.967 |
| Mean IBI | 0.003 | 0.001 | 6.154 | 1 | <0.05 | 1.003 | 1.001 | 1.005 |
| Yearly production | -0.584 | 0.125 | 21.841 | 1 | <0.001 | 0.557 | 0.436 | 0.712 |
| Mean weight | -0.011 | 0.003 | 12.167 | 1 | <0.001 | 0.989 | 0.984 | 0.995 |

**Table 7: A summary of results from previous studies of captive colonies, including combined results from all three sites in the present study**

| Variable | Current study (n=302[1];304[2];305[3];316[4];320[5];340[6]; 344[7] dams) | Smucny et al (2004) (n=272[1];287[2];400[3] dams) | Tardif et al (2003) (n=479 dams) | Box & Hubrecht (1987) (n=543 infants) |
|---|---|---|---|---|
| **Dam longevity (years)** | | | | |
| Mean | 6.29[6] +/- 2.55 | 5.74[3]+/-2.46 | 5.99 +/-2.31 | 6.00 |
| Median | 5.94[6] | | | |
| **IBI (days)** | | | | |
| Mean | 202.54[4] +/- 71.27 | 216.7[1]+/-98.53 | | |
| Median | 181.21[4] | | 162.00 | 158.00 |
| **Age at 1st parturition (years)** | | | | |
| Mean | 2.42[7] +/- 0.73 | 2.91[3]+/-1.16 | | |
| Median | 2.25[6] | | | |
| **Lifetime production (number of infants born)** | | | | |
| Mean | 17.70[2] +/- 14.48 | 8.03[3]+/-7.15 | 7.75 | |
| Median | 14.00[2] | | 6.00 | |
| **Survived production (number of infants)** | | | | |
| Mean | 14.38[3] +/- 11.80 [a] | 4.37[3]+/-4.36 [b] | | |
| Median | 11.00[3] [a] | | | |
| **Production/yr (infants born/yr of RL)** | | | | |
| Mean | 4.23[5] +/- 1.21 | 3.66[3]+/-1.57 | 2.30 | |
| Median | 4.23[5] | | | |
| **Survived production/yr (infants/yr of RL)** | | | | |
| Mean | 3.27[5] +/- 1.21 | 1.87[3]+/-1.29 [b] | | |
| Median | 3.37[5] | | | 4.00 [b] |
| **Reproductive life span** (years) | | | | |
| Mean | 3.84[1] +/- 2.51 | 2.08[2]+/-1.55 | | |
| Median | 3.33[1] | | | |
| **Litter size** (number of infants born) | | | | |
| Mean | 2.40[5] +/- 0.50 | 2.22[3]+/-0.56 | | |
| Median | 2.33[5] | | | |
| Mode | 2.00 | | 2.00 | 3.00 |
| **Survived litter size (number of infants)** | | | | |
| Mean | 1.86[5] +/- 0.61 | 1.87[3]+/-0.68 [b] | | |
| Median | 2.00[5] [a] | | | |
| **Number of litters** (litters/dam) | | | | |
| Mean | 7.67[7] +/- 5.72 | 3.54[3]+/-2.84 | 3.45 | |
| Median | 6.00[7] | | 4.00 | |

a. Survived the day of birth and up to 6 months
b. Survived up to 1 month after birth
+/- SD