

# Breeding by young-of-the-year female deer mice: Why weight?<sup>1</sup>

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**Abstract:** Female deer mice (*Peromyscus maniculatus*) in the Kananaskis Valley, Alberta seldom breed during the summer of their birth despite having a breeding season which appears to be long enough for them to sexually mature. Thirteen years of live-trapping data indicate that only 3.6% of all females recruited into the trappable population bred as young-of-the-year (YY). Exclusion of those YY females who were born too late in the season to have bred and those who may have bred outside the trappable population indicated that only 14% of YY females with the opportunity to breed did so. Most females who bred as YY conceived within days of emerging from their natal nest. Breeding by YY females was associated with longer breeding seasons, which were lengthened through later cessation rather than earlier initiation of breeding, increased nestling growth rates and female-biased litters. The results of this study support the conclusion that nestling growth rates are important for YY breeding in these populations. Further, it appears that nestling growth varies annually, as well as among litters within breeding years, but not among individuals within breeding litters.

**Keywords:** age at first reproduction, delayed maturation, individual quality, nestling growth, *Peromyscus maniculatus*, sex ratio.

**Résumé :** Les femelles de la souris sylvestre (*Peromyscus maniculatus*) de la vallée du Kananaskis, en Alberta, se reproduisent rarement durant l'été où elles sont nées, malgré le fait que la saison de reproduction soit suffisamment longue pour leur permettre d'atteindre la maturité sexuelle. Les données de 13 années de captures indiquent que seulement 3,6 % des femelles susceptibles d'être capturées se sont reproduites en tant que jeunes de l'année (JA). Si on exclue les femelles JA nées trop tard en saison pour se reproduire, ainsi que celles qui pourraient s'être reproduites à l'extérieur de la population piégée, on constate que seulement 14 % des femelles JA aptes à se reproduire l'ont fait. La plupart des femelles s'étant reproduites en tant que JA ont conçu dans les premiers jours suivant leur sortie du nid où elles sont nées. La reproduction des femelles JA est associée aux saisons de reproduction plus longues, caractérisées par une fin tardive plutôt que par un démarrage hâtif de la reproduction, ainsi qu'à des taux de croissance plus rapides et des portées comportant davantage de femelles. Les résultats de la présente étude confirment que les taux de croissance des nouveau-nés sont importants en ce qui a trait à la reproduction des jeunes de l'année dans ces populations. De plus, il en ressort que la croissance des jeunes varie annuellement, ainsi qu'entre les portées à l'intérieur des différentes années, mais pas entre les jeunes à l'intérieur des portées.

**Mots-clés :** âge à la première reproduction, maturité retardée, qualité individuelle, croissance des nouveaux-nés, *Peromyscus maniculatus*, rapport des sexes.

## Introduction

Age at first reproduction is a critical life history trait because of its potential influence on population growth (Cole, 1954; Lewontin, 1965; Reiter & Le Boeuf, 1991) and individual fitness within populations (Bell, 1980; Stearns, 1992). Among species of mammals, age at first reproduction depends on body size, with larger mammals reproducing for the first time later than smaller mammals (Wootton, 1987). Within deer mice (*Peromyscus maniculatus*), however, age at first reproduction is determined primarily by the length of the breeding season. In southern populations, females born early in the season regularly breed during the summer of their birth (Howard, 1949; Sullivan, 1977; Gashwiler, 1979; Millar, Wille & Iverson, 1979; Gyug & Millar, 1981), whereas in northern populations where breeding is restricted to as few as five weeks, there is not enough time for females to successfully raise offspring in the summer of their birth, so sexual maturation is delayed until the following

spring (Gyug, 1979; May, 1979; Mihok, 1979; Gilbert & Krebs, 1981; Gyug & Millar, 1981; Krebs & Wingate, 1985).

Within the Kananaskis Valley, Alberta, few female deer mice breed as young-of-the-year (YY) despite having a breeding season which appears to be long enough for them to do so (Millar & Innes, 1983; 1985; Teferi & Millar, 1993; Millar, 1994). Delayed sexual maturation as an adaptive reproductive strategy is expected when the benefits of early maturation are outweighed by an associated increase in mortality or decrease in future fecundity (Stearns, 1992). Limited data suggest, however, that neither overwinter survival nor future reproductive success are negatively affected by breeding among YY female deer mice (Teferi & Millar, 1993). As a result, it appears that the delayed age at first reproduction in female deer mice in the Kananaskis Valley is the consequence of some social or ecological constraint.

Several hypotheses concerning the observed rarity of YY breeding in the Kananaskis Valley have been tested but no clear explanation has been found (Lusk & Millar, 1989; Teferi & Millar, 1993; Woolfenden & Millar, 1997; MacDonald, 1997). Lusk & Millar (1989) found evidence

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for social inhibition of YY reproduction in a one-year manipulative study, but this was later refuted (Teferi & Millar, 1993). In their examination of characteristics of breeding individuals and populations over seven years, Teferi & Millar (1993) suggested that individual quality, measured as nestling growth, may be more important than social factors. High nestling growth rates have been associated with YY breeding (Lusk & Millar, 1989; Teferi & Millar, 1993), but these increased growth rates may be an unrelated consequence of the experimental manipulations (*e.g.*, decreased density, food addition).

Here we examine seven years of data on unmanipulated populations analyzed by Teferi & Millar (1993), with an additional six years of data on the same populations. The objectives of this study were to: *i*) quantify the extent of breeding by YY, *ii*) re-examine the importance of individual quality in YY breeding, and *iii*) examine several new characteristics of years and litters in which breeding by YY occurred to determine why so many female deer mice do not breed during the summer of their birth.

### Material and methods

Two populations of *P. maniculatus borealis* were monitored through mark-recapture live-trapping in the Kananaskis Valley, Alberta (51° N, 115° W) during the breeding seasons (May to August) of 1985 through 1997. Two trapping grids, consisting of an array of trapping stations approximately 20 m apart, were initially 4.4 ha and 6.0 ha in size (1985-1986) but were later split into four grids 1.3, 1.7, 2.2, and 1.7 ha in size (1987-1997). The timing of breeding on these trapping areas, however, suggested that the four grids were acting as two distinct populations only, and so data for the two pairs of grids were combined. As a result, data are presented for two grids per year. All trapping grids were established in rocky creek beds which represent prime deer mouse habitat (Millar, Innes & Loewen, 1985). One Longworth live-trap, baited with a mixture of sunflower seeds and oats, and supplied with cotton bedding, was set at each trapping station. Each grid was trapped approximately two nights per week from May to August, in all years, and traps were locked open between trapping nights.

Individual mice were identified by unique Monel #1 ear tags affixed to each mouse at the time of first capture. At capture, each individual mouse was identified and its sex, weight, reproductive status, and location were recorded. Age was determined by pelage characteristics (grey = YY, brown = overwintered). Weight was measured to the nearest 0.5 g using a Pesola spring balance. Reproductive status was assessed for males as testes scrotal (large and descended) or nonscrotal, and for females as nonperforate, perforate, pregnant (swollen abdomen), lactating (large and prominent nipples), or pregnant and lactating.

Parturition was evident by changes in female weight and reproductive status. Parturition dates were estimated as the median date between a female's last capture as pregnant and first capture as lactating. All overwintered (OW) females were coated with fluorescent powder at each capture and powder trails were followed to identify nest locations (Lemen & Freeman, 1985; Sharpe & Millar, 1990).

Additional traps were set near a female's nest and at the trapping station where she was most frequently captured starting at 21 days after parturition so that her offspring would be captured upon first emergence from the natal nest. Emerged young were assigned to dams based on the date and location of first capture, and by the presence of fluorescent powder (Millar, Derrickson & Sharpe, 1992). The use of fluorescent powder to assess mother-offspring relationships has been validated for *P. californicus* using DNA fingerprinting (Ribble, 1992). Juveniles which could not be assigned to a resident dam were considered to be immigrants. Trappability of both OW and YY mice are high in these populations (Lusk & Millar, 1989; Sharpe & Millar, 1991; Woolfenden & Millar, 1997) and estimates of age at first capture for YY (mean = 32.2 days, SD = 9.5,  $n = 873$ ) indicate that we were able to capture offspring soon after emergence from the natal nest.

Environmental conditions were considered to be suitable for the raising of offspring until the final parturition of the season. The length of the breeding season was therefore measured as the length of time from first to last parturition of the season for each population. The last conception of the season was assumed to be the date of last parturition minus 24 days gestation (Millar, 1989). Females were considered to have been born early enough to have bred as YY if they entered the trappable population prior to the last conception of the breeding season. YY females were assumed to have bred if they were identified as pregnant or lactating. On average, breeding YY females were first reported as pregnant 11.3 (range: 0-24) days prior to parturition.

The length of the breeding season and the occurrence of YY breeding differed among years, and between the two monitored populations within years. As a result, grid\*year combinations were used as the broadest unit of study rather than simply years. In one grid\*year, no mice of any age bred. The remaining 25 grid\*years were classified as breeding or nonbreeding depending on whether any YY females bred. Within breeding grid\*years, litters that contained at least one female and that were born early enough to have bred were classified as either breeding (at least one YY female from the litter bred) or nonbreeding (no YY females from the litter bred). Life history variables thought to be important to YY breeding were compared between breeding and nonbreeding groups within both of these levels of analysis (grid\*years, litters) as well as between breeding YY females and their nonbreeding littermates (individual level of analysis).

### STATISTICAL ANALYSES

Continuous variables (breeding season length, parturition date, litter size) were compared between breeding and nonbreeding groups using *t*-tests, while the sex ratio of offspring was analysed using  $\chi^2$  tests. Four separate ANCOVAs were used to compare the juvenile weights at first capture (g), corrected for estimated age at first capture (days), between breeding and nonbreeding groups. Age at first capture was a significant covariate for all comparisons (ANCOVA; grid\*years  $F_{1,22} = 6.3, p = 0.02$ ; litters  $F_{1,59} = 20.8, p < 0.0001$ ; individuals male *versus* female  $F_{1,51} = 15.0, p = 0.0003$ ; individuals female *versus* female  $F_{1,36} = 17.8,$

$p < 0.0002$ ). Assuming a constant birth weight, this corrected weight was also a measure of growth between birth and first capture and will be referred to hereafter as nestling growth rate. Seventy-three of 935 juveniles had very large ( $> 0.7$  g/day) or very small ( $< 0.2$  g/day) nestling growth rates, and were considered to have been improperly matched with dams. They were therefore classified as immigrants. In order to avoid potential problems associated with pseudoreplication (Hurlbert, 1984), nestling growth rates were averaged for all individuals within each grid\*year or litter.

All analyses were performed using the STATISTICA (StatSoft Inc., 1994) software package. The length of the breeding season data were log transformed in one case to ensure homogeneity of variance (Zar, 1996). All dates are presented as Julian dates. Values are presented as means  $\pm$  SE unless otherwise stated.

## Results

### HOW MANY FEMALES BREED AS YY?

In the 13 years of the study, 22 of the 606 (3.6%) females recruited into the populations bred during the summer of their birth. The average length of the breeding season in the 25 grid\*years of this study was 76.8 days (standard deviation = 24.5 days; range 36 to 140 days). Twenty-two of the 25 grid\*years had at least one female emerge into the trappable population prior to the last conception of the season, indicating that YY breeding could have occurred in almost all grid\*years. Of the 250 YY females recruited into the trappable population within the time period suitable for breeding, only 8.8% bred. Our ability to identify pregnant YY females from a single capture was limited. Some YY females were prematurely identified as pregnant, while others were not identified as pregnant until the time of parturition. It is therefore possible that some YY females bred, but did not remain in the trappable population long enough to have been assessed as such. Of the 141 mice born early enough to have bred and which remained on the grid for at least 30 days (maximum length of time needed to detect pregnancy given conception within six days of emergence), 20 bred (14.2%). Of the 118 mice born early enough to breed and which remained on the grid until the final parturition of the season, 17 bred (14.4%).

Sixteen of the 22 breeding YY females had known birthdates. Of these 16 females, 10 conceived within three days of entering the trappable population. The remaining six mice conceived  $29.2 \pm 17.9$  (standard deviation) days after entering the trappable population and were from one season (1986).

### GRID\*YEARS

There were 17 grid\*years in which no breeding by YY females occurred and 8 grid\*years in which YY breeding did occur. Breeding grid\*years had significantly longer breeding seasons ( $96.8 \pm 10.1$  days) than nonbreeding grid\*years ( $67.5 \pm 3.9$  days;  $t_{23} = 3.32$ ,  $p = 0.003$ ). This difference was the result of a significantly later cessation of breeding, but not a significantly earlier initiation of breeding in years when YY bred in the summer of their birth (Figure 1). It is possible that the extended breeding season was simply

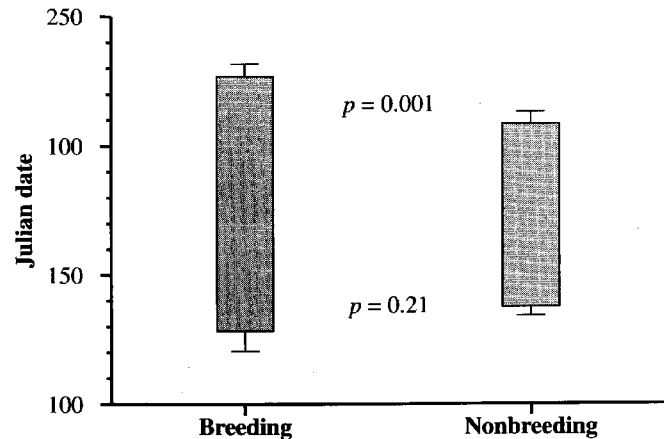


FIGURE 1. First and last parturition dates for grid\*years in which at least one YY, female, deer mouse bred, and for grid\*years in which no YY breeding occurred. The shaded area represents the deer mouse breeding season. The bottom of the boxes represent the mean (-SE) first parturition date ( $t_{23} = 1.29$ ,  $p > 0.20$ ). The top of the boxes represent the mean (+ SE) last parturition dates ( $t_{23} = 3.65$ ,  $p = 0.001$ ).

due to the addition of YY parturitions at the end of the season. In three grid\*years, the final parturition of the season was for a YY breeder. If these breeding seasons are restricted to consider only OW breeders, the difference between breeding and nonbreeding grid\*years in both the length of the breeding season, and the end of breeding remain significant (log transformed breeding season length  $t_{23} = 1.95$ ,  $p = 0.032$ ; end of breeding  $t_{23} = 1.93$ ,  $p = 0.03$ ). In addition, the number of YY females born early enough to have bred increased with the length of the breeding season ( $r = 0.84$ ,  $p < 0.0001$ ,  $n = 25$ ). If breeding is random among individual YY females, we would expect grid\*years with more potential YY breeders to have a higher probability of containing at least one YY breeder. Breeding grid\*years still tended to have longer breeding seasons than nonbreeding grid\*years as a result of a later cessation of breeding, when controlled for the number of potential YY breeders within a grid\*year (covariate =  $\log_{10}$  [number of potential YY breeders + 1]), although these differences were no longer significant (ANCOVA; breeding season length  $F_{1, 22} = 1.89$ ,  $p = 0.18$ ; start of breeding  $F_{1, 22} = 0.01$ ,  $p = 0.93$ ; cessation of breeding  $F_{1, 22} = 3.47$ ,  $p = 0.08$ ).

Breeding grid\*years had higher nestling growth rates than nonbreeding grid\*years (Table I), but there was no difference in the sex ratio of offspring produced (breeding 231F : 220M; nonbreeding 226F : 196M;  $\chi^2_1 = 0.48$ ,  $p > 0.4$ ).

### LITTERS

Within breeding grid\*years, 62 litters had at least one female which emerged prior to the last conception of the season indicating that females in these litters were born early enough to have bred in the summer of their birth. Of these 62 litters, 13 contained at least one YY female who bred.

Litters with at least one breeding female (breeding litters) did not differ in parturition date, or litter size from nonbreeding litters (Table II), but breeding litters did have higher nestling growth rates than their nonbreeding counterparts (Table I). Breeding litters were also female biased (breeding 75% female; nonbreeding 52% female; Table II). However,

TABLE I. Hierarchical analysis of weight at first capture (g) corrected for estimated age at first capture (days) between grid\*years, litters, and individuals with or without breeding by YY female deer mice in the Kananaskis Valley, Alberta

Level of analysis	Weight at first capture - Breeding (g)	Weight at first capture - Nonbreeding(g)	Breeding versus nonbreeding
Grid*year	11.36 ± 0.38 (8) <sup>a</sup>	9.96 ± 0.30 (17) <sup>a</sup>	$F_{1,22} = 6.87, p = 0.016$
Litter	12.86 ± 0.56 (13) <sup>b</sup>	11.18 ± 0.30 (49) <sup>b</sup>	$F_{1,59} = 5.32, p = 0.025$
Individual	13.03 ± 0.68 (16) <sup>c</sup>	12.74 ± 0.58 (23) <sup>c</sup>	$F_{1,36} = 1.91, p = 0.176$

Data are presented as means ± SE, corrected for estimated age at first capture.

Sample sizes are in parentheses as follows:

<sup>a</sup>Number of grid\*years

<sup>b</sup>Number of litters within breeding grid\*years, with at least one female born early enough to have bred.

TABLE II. Parturition date, litter size and sex ratio of litters in which at least one YY female deer mouse bred and litters in which no females bred. All litters were born early enough to have bred and were from grid\*years in which some YY breeding did occur

Litters	<i>n</i>	Date of parturition <sup>a</sup>	Litter size <sup>b</sup>	Sex ratio <sup>c</sup>
Breeding	13	138.5 ± 6.0	4.00 ± 0.48	0.75
Nonbreeding	49	146.6 ± 3.4	4.08 ± 0.23	0.52
		$t_{60} = 1.10, p = 0.27$	$t_{60} = 0.16, p = 0.87$	$\chi^2_1 = 8.89, p = 0.003$

Data are presented as means ± SE.

<sup>a</sup>Julian date.

<sup>b</sup>Number of emerged offspring per litter.

<sup>c</sup>Proportion of females.

if breeding was random among individual females, litters containing more females would be expected to have a higher probability of having at least one YY breeder. To compensate for this, litters in which at least one YY female bred were paired with nonbreeding litters based on the number of emerged females in the litter and grid\*year. In some cases we were unable to match either the number of females in the litter or the grid\*year, so nonbreeding litters with the nearest number of females or nonbreeding litters from the other grid within the same year were used. When paired, breeding litters remained more female biased (75% female) than nonbreeding litters (53% female;  $\chi^2_1 = 5.50, p = 0.019$ ).

#### INDIVIDUALS

Females and males from breeding litters did not differ in their rates of nestling growth ( $F_{1,51} = 0.43, p = 0.52$ ). In addition, females who bred as YY had the same nestling growth rates as their nonbreeding female littermates (Table I).

### Discussion

The length of the breeding season clearly dictates age at first reproduction among populations of deer mice. Southern populations with long breeding seasons have many YY breeders, whereas OW breeding in northern populations is restricted to a short period of time, which is often insufficient to permit breeding by YY (Gyug, 1979; May, 1979; Mihok, 1979; Gilbert & Krebs, 1981; Gyug & Millar, 1981; Krebs & Wingate, 1985). However, within the Kananaskis Valley, Alberta, only 3.6% of all females recruited into the trappable populations bred as YY, despite having a breeding season which is often long enough for breeding to occur. Many females which did not breed as YY were born too late in the season or did not remain in the trappable population long enough to rule out the possibility that they bred outside the trappable population. However, time restrictions on breeding do not explain all of the constraints on age at first reproduction in this population. If

we remove these two possible reasons, a very large proportion (86%) of YY females still did not breed. The fact that females who breed as YY do not appear to suffer increased overwinter mortality or decreased future reproductive success (Teferi & Millar, 1993), suggests that many YY are unable to mature because of some social or ecological constraint.

Of the YY females that did breed, 10 of 16 conceived within three days of entering the trappable population. The six YY females which bred approximately 30 days after entering the trappable population were all from 1986, a year in which the breeding season (140 days) was nearly twice as long as the average. The conception of litters by YY females within days of entering the trappable population suggests that they are sexually mature upon emergence from their natal nest. If this is the case, the influence of any environmental factors on YY breeding, whether they relate to population density, photoperiod, food quantity, or food quality must be transmitted maternally. This has potentially important consequences for the design of experiments investigating possible constraints on age at first reproduction in these populations. The manipulation of YY females after emergence into the trappable population (Lusk & Millar, 1989; Teferi & Millar, 1993) was potentially too late to influence YY reproduction.

Since in most years breeding YY females conceived within days of emerging from the natal nest, our 30-day residency requirement is likely long enough to detect YY pregnancy in most years. However, in 1986 this requirement would not have been long enough to detect YY breeders, had they left the trappable population. Both the 30-day residence and residence until the final parturition criteria resulted in similar estimates of the proportion of YY females who bred. In fact, only 12 of the 132 mice who were resident for 30 days failed to remain on the grid until the final parturition. Defining potential YY breeders as those females who entered the trappable population prior to the last conception, and remained on the grid at least until

the final parturition of the season, ensures a conservative estimate of the number of nonbreeders regardless of when YY conception occurs, without drastically decreasing sample sizes.

High nestling growth rates were associated with breeding by YY females at the level of grid\*years and litters but not among female littermates. Because many of the females which bred as YY conceived within days of emerging from their natal nest, it is not surprising that a factor associated with maternal dependence would be important in determining whether or not YY breeding occurs. All YY breeders were first captured within the first week of pregnancy, and so it is unlikely that fetal weights contributed measurably to weights at first capture. Maternal body weights of *P. leucopus noveboracensis* do not differ from nonbreeding female body weights for the first two weeks of gestation (Millar, 1975). The examinations of weights at first capture in this study support previous findings that increased growth rates are associated with YY breeding (Lusk & Millar, 1989; Teferi & Millar, 1993), without the potentially confounding effects of experimental manipulations.

Teferi & Millar (1993) suggested that offspring quality, measured as nestling growth, may be an important factor for YY reproduction. The results of this study suggest that season and litter quality are more closely related to YY breeding than individual quality within a litter. There appear to be good years in which nestling growth rates are high and YY breeding occurs, and poor years in which nestling growth is low and no YY breeding occurs. In addition, within good quality years, breeding litters are of higher quality (higher average growth rate) than nonbreeding litters, but individual quality within a litter does not differ between YY breeders and their nonbreeding female littermates.

Breeding by YY females was associated with longer breeding seasons that do not start earlier (see also Teferi & Millar, 1993), but end later. These differences appear to be mostly due to the increased number of potential YY breeders produced during longer breeding seasons. However, when we controlled for the number of potential breeders, grid\*years with YY breeding still tended to have longer OW breeding seasons as a result of a later cessation of breeding than grid\*years when no YY breeding occurred. This association between breeding by YY females and the end of the OW breeding season is quite surprising since YY breeding occurs relatively early in the season. It is likely that YY breeding is not directly related to the end of the breeding season, but that some other unmeasured factor or factors influenced both the end of the breeding season and breeding by YY females. Supplementation of food has been shown to influence the length of the breeding season in some populations of *P. maniculatus* (Fordham, 1971; Taitt, 1981, but see Gilbert & Krebs, 1981) and age at first reproduction in *P. mexicanus* (Duquette & Millar, 1995), as well as having a modest but consistent effect on YY breeding in the populations studied here (Teferi & Millar, 1993).

Breeding YY females also came from female-biased litters. Prior intrauterine position (number of adjacent male fetuses) has been shown to influence the timing of sexual maturation in some rodent species (vom Saal, 1989). Variation in sex ratio of deer mice in these populations,

however, is thought to be due to differential survival between the sexes from birth to first capture (Havelka & Millar, 1997), suggesting that breeding YY females likely experienced the same prenatal sex ratio as their nonbreeding counterparts. Alternatively, the observed variation in sex ratio may represent an adaptive response to environmental conditions during lactation. Theory regarding adaptive variation in sex ratio suggests that mothers in good condition should bias their investment to favour the sex of offspring with the greater variation in reproductive success (Trivers & Willard, 1973). Deer mice in the Kananaskis Valley have a promiscuous mating system (Ribble & Millar, 1996), and variation in reproductive success may be greater in either sex or equal in promiscuous species (Shields, 1987). It has been shown that female deer mice who breed as YY are capable of raising almost 50% more offspring in their lifetime than those females who delay first reproduction until they are one year of age (Teferi & Millar, 1993). This increased variation in female reproductive success as a result of YY breeding may be higher than that of males. In this case, good quality mothers capable of raising daughters who can breed as YY would maximize their inclusive fitness by producing female-biased litters. Sex-specific physiological responses to environmental conditions or differential maternal investment in offspring can also be reflected in differential nestling growth, but we found no evidence of this in males and females surviving to weaning. The above hypothesis was clearly generated *post hoc*; however, the data in the current study certainly provide an impetus for its further rigorous testing.

The specific environmental factor responsible for the decreased growth rate and delayed sexual maturation of many females in these populations remains unknown. The close association between YY growth and reproduction suggests that some aspect of food availability or composition may be important, but supplementation of food (Teferi & Millar, 1993) and salt (Woolfenden & Millar, 1997), did not increase overall nestling growth or the number of females breeding as YY. Other possible dietary constraints on YY growth and reproduction, such as diet quality, require further investigation.

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