

Assessing the effects of resource availability and parity on reproduction in female Cape ground squirrels: resources do not matter

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Abstract

The reproductive output of iteroparous females is influenced by parity and resource availability. To gain a better understanding of the reproductive decisions made when animals are faced with potential trade-offs between current and future reproduction; we investigated the relationship of parity and resources availability on reproductive intervals and success by comparing the performance of primiparous and multiparous female Cape ground squirrels *Xerus inauris* from two study sites that differed in resource availability. Our study included the correlation of reproductive behavioral data with fecal hormonal information to establish a normative endocrine profile for pregnancy and lactation. Parity had a major influence on juvenile emergence with multiparous females having more juveniles emerge successfully. Resource availability did not influence reproductive output, either because of an interaction among multiple resource components including quantity, predictability and length of time those resources were available or because other factors (such as predation or parasitism) have a greater impact on reproductive success.

Introduction

The timing and success of an animal's reproductive attempts reflects a complex interaction among many environmental and physiological factors (Wallen & Schneider, 2000). An examination of the relationship among these factors can provide insights into the reproductive decisions made when animals are faced with potential trade-offs between current and future reproduction. Two factors that often play a prominent role in this interaction are resource availability (Wingfield & Kenagy, 1991; Shanley & Haim, 2004) and parity, an indication of an animal's previous experience with bearing viable offspring (Clutton-Brock, 1984; Wang & Novak, 1994).

Resource availability, in terms of food and water, may be the most critical environmental factor for successful reproduction (Bronson, 2000). Low resource levels often increase nutritional stress and lower body condition that subsequently affects reproduction (Lee, Majluf & Gordon, 1991). As female body mass is a good indicator of body condition (Wauters & Dhondt, 1989), a significant decrease in body mass may ultimately result in extending the duration of reproduction as well as reducing reproductive success. Lighter females often have longer lactation periods and longer inter-estrous intervals (Bronson & Marsteller, 1985; Lee *et al.*, 1991), although gestation is unaffected by resource level due to the dominant role genetics plays in determining its length (Racey, 1981). Lower-condition

females often have more failed reproductive attempts (Duquette & Millar, 1995) as well as smaller litter sizes (Murie & Dobson, 1987; Risch, Michener & Dobson, 2007) and/or lighter juveniles (Wauters, Bijmens & Dhondt, 1993).

A second factor influencing reproductive success in mammals is parity, which is the number of times a female has given birth (Wang & Novak, 1994). In many iteroparous vertebrates, a female's reproductive success typically increases early in life and levels off as she ages (Sydesman *et al.*, 1991; Ericsson *et al.*, 2001). This increase early in life may be due to body condition, maternal experience and/or maternal restraint. Compared with their multiparous counterparts, primiparous females have lower body condition, lack maternal experience and/or maintain the ability to restrain reproduction in the hopes of greater future reproductive success (Wang & Novak, 1994; Dobson & Michener, 1995). Constraint hypotheses suggest that reproductive output is lower in first-time mothers either due to poorer body condition or the lack of skills and efficiency necessary for successfully rearing offspring. The restraint hypothesis suggests that first-time mothers conserve their input into current reproduction in anticipation of more successful future reproduction (Forslund & Pärt, 1995). The body condition constraint hypothesis predicts that the reproductive output of primiparous females will be the same as multiparous relative to their body mass. Conversely, both maternal experience constraint and

restraint hypotheses predict primiparous females to have lower reproductive output compared with multiparous females of the same mass (Broussard, Dobson & Murie, 2008).

Data on the effects of parity and resource availability on free-living rodents are surprisingly limited. As the activities of small mammals, particularly rodents, are typically secretive, collecting the necessary data to establish reproductive profiles is often difficult. The recent advances in the use of fecal steroid analysis allow for confirmation of reproductive activity through the non-invasive collection and analysis of a free-living animal's fecal matter. Hormonal data, combined with behavioral and morphological data, can accurately reflect the reproductive status of individuals (Whitten, Brockman & Stavisky, 1998).

Of the prior reproductive studies involving free-living ground squirrels, most have involved hibernating species with short annual breeding seasons while little work has been conducted with year-round breeders. Cape ground squirrels *Xerus inauris* are group-living, non-hibernating rodents endemic to the open plains of southern Africa (Herzig-Straschil, 1978). They typically inhabit areas with varying degrees of aridity and resource availability (Skurski & Waterman, 2005). Female social groups are made up of one to three breeding adult females and related offspring and live separately from males (Waterman, 1995). Adults breed year round and while individual females can successfully produce up to four litters a year, they frequently fail to raise offspring to weaning (Waterman, 1996). Pregnant females isolate themselves from their social group at parturition and remain isolated until offspring emerge or until a litter is lost during lactation. Females become sexually mature at *c.* 7–9 months of age although maturity may be delayed as a result of reproducing in groups (Waterman, 2002).

The aim of this investigation was to examine the influences of parity and resource level on the reproductive intervals and success in the cooperative breeding female Cape ground squirrel using behavioral and fecal progesterone data to monitor reproductive status. We predicted that females inhabiting areas with higher resource levels would have shorter lactation and inter-estrous intervals, larger litter sizes, heavier juveniles and more successful juvenile emergences. We predicted that females with greater breeding experience would have greater reproductive output than primiparous females in support of the maternal experience constraint and the restraint hypotheses. Accordingly, multiparous females would have shorter lactation and inter-estrous intervals as well as larger litters, heavier juveniles and more successful juvenile emergences. Regardless of resource level or parity, litter size in Cape ground squirrels is constrained with females rarely having more than two offspring (Herzig-Straschil, 1979). Consequently, we did not predict a trade-off in litter size and juvenile body weight. Owing to the importance of supporting reproductive behavioral data with information on fecal hormone concentrations, we also aimed to establish a normative endocrine profile during pregnancy and lactation for free-ranging Cape ground squirrels.

Materials and methods

Resource availability and study sites

Fieldwork was conducted at two sites that differ in quantity and variability of rainfall and consequently, resource availability. The correlation between rainfall and resource availability is especially high in arid and semi-arid environments (Neal, 1984; Happold & Happold, 1992). Our low resource site was on a 3500 ha farm 185 km south-east of Windhoek, Namibia (23°25'S, 18°00'E) in the Kalahari bushveld region (Waterman, 1995). Our high resource site was at the S.A. Lombard Nature Reserve, South Africa (27°35'S, 25°35'E), a 3660 ha reserve consisting of Cymbopogon-Themeda veld and Kalahari grassland on a flood plain (van Zyl, 1965). The South African site receives an average annual rainfall of 502 mm (range: 241–965; years 1952–2004) compared with 220 mm (range: 60–506; years 1979–2004) at the Namibian site. Because rainfall at our low resource site is highly variable, we combined the data from the present study with data from a previous study (Waterman, 1996) conducted at the same site (1989–1991) in order to obtain a more accurate estimation of our reproductive parameters. Rainfall during these years varied from 161 mm (1989–1990) to 251 mm (1990–1991). All methodologies were identical apart from the collection of fecal progesterone data (only collected in the present study). Precipitation at both sites is confined mainly to November–April (Herzig-Straschil, 1979; Waterman, 1996). Data were collected from May to November 2004 in South Africa and in Namibia from July to October 2004.

The South African site received average rainfall during both 2002–2003 and 2003–2004 rainy seasons (474, 510 mm, respectively). The Namibian study site experienced a drought year during the 2002–2003 rainy season (66 mm of rain) while the 2003–2004 rainy season was average (209 mm). Annual total rainfall in Namibia was much more variable and unpredictable than the South African site with coefficients of variation of 45.7 (1980–2006) and 28.1% (1980–2006), respectively. During the growing season when temperatures are warm enough for plant growth (September–April), the Namibian site received rainfall 4.46 ± 0.29 months out of 8 months (range: 1–7) with a coefficient of variation of 33.1% (1980–2006), while the South African site received rainfall 6.73 ± 0.13 months out of the 8-month growing season (range: 6–8) with a coefficient of variation of 9.91% (1980–2006).

Parity

Females were placed into one of two categories: primiparous and multiparous. We could determine the day of first estrus of females through a combination of behavioral, hormonal and trapping data. Behaviors specific to the day of estrus (e.g. increased male activity including sniffing, chasing and copulating with estrous female) provided a direct indication of the age of sexual maturity. In addition, characteristics of a female's vulva can be used to estimate the day of estrus, as the vulva swells greatly a few days before and on the day of

estrus (Waterman, 1996) and can contain sperm plugs following estrus (B. A. Pettitt, unpubl. data). Primiparous females had undeveloped nipples (light colored and small) at the beginning of the study and their first estrus was observed during the study followed by an escalation in fecal progesterone (indicative of pregnancy) and isolation from their social group (indicative of parturition). Females that lost their litters during pregnancy were not considered primiparous, while females that lost their litters during lactation were considered primiparous. Females were considered multiparous if the nipples were dark and elongated, indicating that they had previously lactated (Waterman, 1996).

Reproductive intervals

Behavioral and/or trapping data on squirrels were collected daily. Length of gestation was calculated from the day of estrus (as established using behavioral, hormonal and trapping data) until the day of isolation (parturition). Length of lactation was calculated from the day of isolation to juvenile emergence. Inter-estrous intervals were determined only for females that successfully reared young. Females were assumed to have lost litters during lactation if they returned from isolation prematurely (before lactation could have been completed) and without offspring. We calculated inter-estrous intervals from the day of estrus to the day of the subsequent estrus.

Reproductive success

We measured reproductive success in terms of juvenile emergence (either successful if at least one juvenile emerged or unsuccessful), litter size and mean juvenile body mass. Pregnancies were considered successful if juveniles emerged and rejoined the social group with their mothers. Pregnancies were considered unsuccessful if the female rejoined the social group prematurely and with no offspring. We obtained all juvenile body mass data within 2 weeks of emergence. As maternal body mass often influences reproductive success variables, we also measured the body mass of all females within 1 week of estrus.

Assessing reproductive status

We used three measures to assess the reproductive status of females: morphological, behavioral and fecal steroid hormone data.

First, we attempted to trap individuals every 3 days to document morphological changes of a female's vulva and nipples and to collect hormone samples. Swollen and open vulvas indicated sexual receptivity and a recent estrus while elongated and swollen nipples indicated lactation. Squirrels were trapped using the procedures outlined in Waterman (1995).

Second, we collected behavioral data indicative of changes in reproductive status. We observed 14 female social groups (eight at South African site for 142 days; six at Namibian site for 94 days) to assess reproductive status and behaviors. We collected behavioral data using all

occurrences, focal (during estrus) and scan sampling (Altmann, 1974). Our observations were made from trees, hides and vehicles using 10 × 50 binoculars. We marked individuals for permanent identification using PIT tags (AVID, Norco, CA, USA) and freeze-marking (Quick Freeze; Rood & Nellis, 1980) and for identification at a distance, we dye-marked squirrels (Rodol D, Lowenstein & Sons Inc. New York, NY, USA; Melchior & Iwen, 1965). We recorded all interactions with males, female proceptive behavior (spatial cohesion between female and male) and mating behaviors (copulation attempts, aboveground copulations, female and male entering/exiting burrow simultaneously). Estrous periods were documented when behaviors were consistent with reproductive activity (Waterman, 1998).

Lastly, we used fecal steroid hormones as an indicator of changes in reproductive status. Like all mammals, Cape ground squirrels excrete metabolized reproductive hormones in their feces that can be extracted and analyzed to determine an individual's reproductive activity. We collected feces from all 14 social groups. Most Cape ground squirrels readily defecate immediately after being trapped (Pettitt, Wheaton & Waterman, 2007). We collected fecal samples in the morning (6:00–10:00 AM) to avoid heat stress during mid-day. Samples were collected within 30 min of trapping, frozen immediately and returned to the United States on dry ice for fecal steroid analysis.

Progesterone concentrations were obtained via enzyme immunoassay analysis (EIA) of fecal samples from adult breeding. The progesterone EIA was previously validated for Cape ground squirrel fecal samples indicating that the EIA measures progesterone concentrations accurately (Pettitt *et al.*, 2007). All samples (average of 28.2 ± 3.2 samples per female), controls and standards were assayed in duplicate. The sensitivity of the P4 assay was 11.3 ± 4.6 pg well⁻¹. Inter-assay coefficient of variation was 7.8 (20% binding) and 13.6% (60% binding) ($n = 42$ plates). Intra-assay coefficient of variation was 6.5 and 4.2% for low and high pools, respectively ($n = 42$ plates).

All research protocols involving live squirrels were performed in a humane manner, followed American Society of Mammalogists guidelines and had received prior approval from the University of Central Florida's Institutional Animal Care and Use Committee.

Data analysis

When data were found to be normal (Shapiro–Wilk test), we used parametric tests; otherwise we used non-parametric tests (Zar, 1996). The effects of parity and resource level on length of gestation, lactation, inter-estrous interval and juvenile mass at emergence were tested using either a two-way ANOVA using resource level and parity as fixed factors or a non-parametric Kruskal–Wallis test for variables with smaller sample sizes ($n = 2$). We controlled for litter size and maternal body mass by performing two-way ANCOVAs with litter size and maternal mass at estrus as covariates. Results from both the ANOVA and ANCOVA tests for all variables gave the same results. The effects of parity and

resource level on litter size and successful juvenile emergence were tested with χ^2 -tests and associated interaction effects were tested with three-way model selection log-linear tests. All analyses were performed in SPSS 11.5 software (SPSS Inc., Chicago, IL, USA). Unless otherwise indicated, means \pm 1 SE are reported. Level of significance was set at 0.05 for each analysis. Steroid concentrations of fecal extracts are reported as nanograms per gram of wet feces.

Results

We collected data on 30 female Cape ground squirrels at the Namibian study site and 25 females at the South African site. The 30 females in Namibia consisted of seven primiparous and 23 multiparous individuals. The 25 females in South Africa consisted of 10 primiparous and 15 multiparous females.

Progesterone concentrations and profiles

Pregnant females had significantly higher fecal progesterone concentrations than non-pregnant female Cape ground squirrels ($F_{1,12} = 87.0$, $P = 0.001$; one-way ANOVA). Pregnant females had a progesterone concentration of $2196.5 \pm 251.5 \text{ ng g}^{-1}$ ($n = 6$), while non-pregnant females averaged $39.0 \pm 10.7 \text{ ng g}^{-1}$ ($n = 7$).

All successful pregnancies showed a significant increase above baseline in progesterone concentrations following the day of the estrus ($t = -3.46$, d.f. = 3, $P = 0.04$; paired t -test) and concentrations continued to rise until the day of parturition when progesterone dropped significantly (comparing the pre-parturition peak with the day of parturition, $t = 2.569$, d.f. = 5, $P = 0.05$; Fig. 1). In 88% (7/8) of pregnancies that resulted in successfully emerged offspring, females showed a second peak of fecal progesterone during lactation. Following lactation, concentrations of progesterone dropped markedly and remained consistently low showing no signs of cyclic ovarian activity until the subsequent estrus.

Resource effects on reproductive intervals

The length of gestation and inter-estrous intervals did not differ between squirrels from the two resource levels.

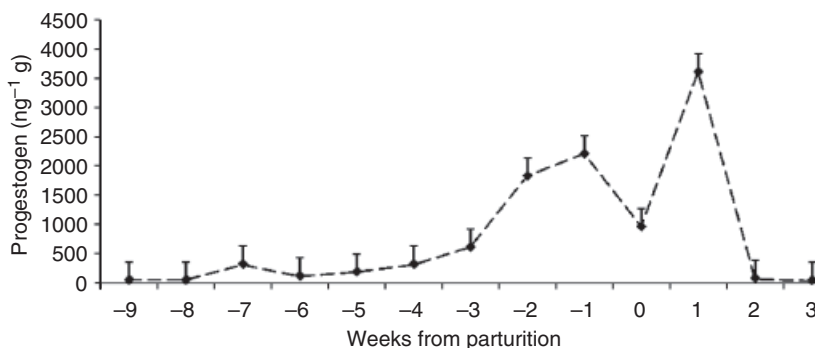


Figure 1 Mean fecal progesterone concentrations for pregnant female Cape ground squirrel *Xerus inauris* ($n = 9$).

ANCOVA results for the effects of resources on gestation, lactation and inter-estrous interval were non-significant ($P > 0.05$). Gestation length for females in Namibia were no different from those in South Africa (47.00 ± 1.53 days, $n = 11$ and 50.85 ± 1.30 days, $n = 13$, respectively; ANOVA, $F_{1,23} = 0.24$, $P = 0.63$). The inter-estrous interval of successful Namibian females averaged 130.50 ± 8.95 days ($n = 8$) and those of successful South African females averaged 139.00 ± 9.00 days [$n = 2$; $H(1) = 0.61$, $P = 0.43$; Kruskal–Wallis]. Lactation data were only available for South African squirrels, which averaged 47.50 ± 2.17 days ($n = 10$).

Resource effects on reproductive success

Juvenile body mass, successful juvenile emergence and litter size did not differ between sites. Namibian juveniles weighed 241.21 ± 18.10 g ($n = 14$) at emergence compared with 190.00 ± 23.25 g ($n = 8$; $F_{1,21} = 0.17$, $P = 0.69$) in South Africa. Neither emergence success [Namibia 16/31, 51.6%, South African squirrels 11/24, 45.8%; $\chi^2(1) = 0.18$, $P = 0.67$] or litter size [Namibia: 1.53 ± 0.17 offspring, $n = 16$; South Africa: 1.45 ± 0.21 offspring, $n = 11$; $\chi^2(2) = 0.77$, $P = 0.68$] differed.

Parity effects on reproductive intervals

The ANCOVA results for the effects of parity on gestation, lactation and inter-estrous interval were non-significant ($P > 0.05$). Gestation averaged 49.08 ± 1.05 days ($n = 24$) and did not differ between multiparous (50.14 ± 1.29 days, $n = 14$) and primiparous (47.60 ± 1.72 days, $n = 10$) females ($F_{1,23} = 2.25$, $P = 0.15$). Likewise, lactation did not differ between multiparous (47.25 ± 2.60 , $n = 8$) and primiparous (48.50 ± 4.50 , $n = 2$) individuals [$H(1) = 0.02$, $P = 0.90$], nor did inter-estrous interval [multiparous females interval = 134.63 ± 8.34 days, $n = 8$; primiparous females interval = 122.50 ± 17.00 days, $n = 2$; $H(1) = 0.27$, $P = 0.60$].

Parity effects on reproductive success

Multiparous females had more successful juvenile emergences than primiparous females [$\chi^2(1) = 4.88$, $P = 0.03$; Fig. 2]. However, litter size did not differ between

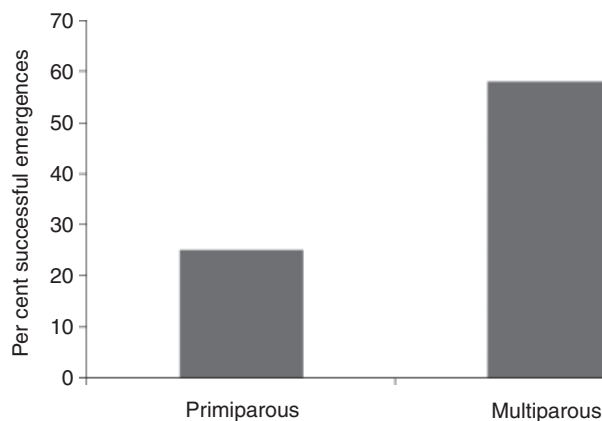


Figure 2 Per cent of successful juvenile emergences for primiparous ($n=16$) and multiparous ($n=38$) female Cape ground squirrels *Xerus inauris*.

multiparous (1.50 ± 0.14 offspring, $n = 22$) and primiparous females [1.50 ± 0.29 offspring, $n = 4$; $\chi^2(2) = 0.74$, $P = 0.69$] and mean juvenile body mass did not differ between litters born to primiparous females (229.00 ± 41.89 g, $n = 3$) versus litters born to multiparous females [221.84 ± 16.42 g, $n = 19$, $H(1) = 0.04$, $P = 0.85$]. Additionally, parity and resource level did not significantly interact with respect to successful juvenile emergences [$\chi^2(1) = 1.58$, $P = 0.21$; three-way model selection log-linear analysis].

Adult female body mass at estrus

We did not have data on maternal body mass at estrus for primiparous females in Namibia, so our analysis of resource availability effects includes only multiparous females from each site. Likewise, our analysis of parity effects includes only South African females. Namibian females had a similar adult female body mass at estrus (576.43 ± 15.88 g, $n = 7$) compared with South African females (589.75 ± 14.19 g, $n = 20$; $F_{1,26} = 0.26$, $P = 0.61$; one-way ANOVA). Body mass at estrus was higher in multiparous (633.00 ± 19.68 g, $n = 10$) than in primiparous females (546.50 ± 6.83 g, $n = 10$; $F_{1,19} = 17.24$, $P = 0.001$; one-way ANOVA); however, adult body mass at estrus had no effect on successful juvenile emergence after controlling for parity and resource availability ($n = 27$, $F_{19,27} = 1.26$, $P = 0.42$; ANCOVA).

Discussion

This investigation established a normative progesterone profile for pregnant and lactating females and examined the influence of parity and resource availability on the reproduction of the cooperatively breeding Cape ground squirrel. Resource availability did not appear to influence reproductive output. Parity only influenced juvenile emergence with multiparous females having more juveniles emerge successfully.

Normative progesterone profile

Monitoring reproductive behaviors and corresponding changes in steroid hormone concentrations are essential to accurately assess the reproductive status of individuals (Schwarzenberger *et al.*, 1997). During a typical pregnancy, progesterone concentrations rise until an abrupt decline immediately preceding parturition then progesterone levels remaining low throughout lactation (Bronson, 1989; Belding's ground squirrels *Spermophilus beldingi*, Nunes *et al.*, 2000; grey squirrels *Sciurus carolinensis*, Tait, Pope & Johnson, 1981).

While Cape ground squirrels showed similar patterns involving a gradual rise during gestation, progesterone concentrations increased again during lactation. This bimodal pattern (one peak during pregnancy and one peak during lactation) occurs in other sciurid species including black-tailed prairie dogs *Cynomys ludovicianus* (Foreman & Garris, 1984), woodchucks *Marmota monax* (Concannon, Baldwin & Tennant, 1984), California ground squirrels *Spermophilus beecheyi* (Holekamp, Nunes & Talamantes, 1988) and yellow-bellied marmots *Marmota flaviventris* (Armitage & Wynne-Edwards, 2002). This hormonal rise may prevent a second ovulation (and consequently a late-season pregnancy) from occurring in obligate annual breeders and hibernators (Armitage & Wynne-Edwards, 2002).

Although Cape ground squirrels are non-hibernators and year-round breeders, these squirrels are found in extremely arid environments that could result in higher energetic stress during reproduction, especially lactation (Degen, 1997). Consequently, they could benefit by preventing subsequent ovarian activity too soon after parturition and thus maintain adequate energy reserves during lactation. Adequate energy reserves are critical for successful reproduction in Cape ground squirrels as breeding ceases during times of drought (Waterman & Fenton, 2000). Because female Cape ground squirrels have fairly good survivorship (Waterman, 1996), they may readily inhibit their reproductive systems during stressful events as lactation (short term) or drought (long term) until the odds of successfully reproducing are more favorable. This could influence the trade-offs they make between current and future reproductive investment.

Effects of resource levels on reproduction

We predicted our higher resource site would have shorter reproductive intervals (i.e. shorter lactation and inter-estrous intervals) as well as greater reproductive success (i.e. greater successful juvenile emergence, larger litter size and/or heavier juveniles). These patterns have been seen in a number of ground squirrel species in which lower maternal body condition, associated with low resource availability, is correlated with smaller juveniles, smaller litter sizes and less successful reproductive attempts (Dark, Stern & Zucker, 1989; Michener, 1989; King, Festa-Bianchet & Hatfield, 1991; Rieger, 1996). Our study found, however, no difference in any of these reproductive factors that supports the null hypothesis that resource availability does not influence reproductive output.

Resource predictability can influence life-history strategies with animals in highly unpredictable environments investing more in current reproduction even if this lowers their capacity for future reproduction (Hirshfield & Tinkle, 1975; Stearns, 1992). For species inhabiting areas with stable resource levels, maintaining a balance between current and future reproduction should be more desired (Stearns, 1992). Our study saw similar levels of reproductive output (i.e. juvenile body mass and successful juvenile emergence) at both sites. However, during times of drought at the low resources site, females cease to breed (Waterman & Fenton, 2000). The cessation of breeding during drought followed by higher reproductive output than predicted in the less predictable and lower resource site suggests that squirrels at this site could be putting greater effort than predicted toward current reproduction.

The temporal nature of resource availability may play a much larger role in reproduction than the actual amount of resources (Waterman, 1996; Hayssen, 2008). Squirrels inhabiting areas with shorter periods of resource availability are limited in their energetic resources and are more likely to constrain their reproduction. While female Cape ground squirrels at our South African site see twice the rainfall as the Namibian females, the amount of time that resources are available is approximately the same (i.e. January–April). Thus, the fact that we found no difference in reproductive output between our two study sites may be a consequence of the two sites having abundant resources for a similar length of time.

Our data suggest that something other than resources could be constraining reproduction in Cape ground squirrels. Larger group sizes have a negative impact on the survival of juveniles (Waterman, 2002), and the larger group sizes in South Africa may have a negative effect on reproductive success of adult females. Parasites and predators are another large constraint on successful female reproduction in female Cape ground squirrels (Waterman, 2002; Hille-gass, 2007). Parasitized females have lower resting metabolic rates, lower body fat, spend more time foraging and grooming, and have significantly fewer offspring than parasite free females (Hille-gass, 2007; Scantlebury *et al.*, 2007).

Effects of parity on reproduction

The increase in reproductive success typically seen early in the life of many iteroparous vertebrates (Clutton-Brock, 1984) was also seen in female Cape ground squirrels. Multiparous females had more successful juvenile emergences than primiparous females. Because female body mass had no effect on successful juvenile emergence after controlling for parity and resource availability, we do not accept the body condition constraint hypothesis as an explanation for the difference in reproductive output. Broussard *et al.* (2008) tested similar predictions in Columbian ground squirrels *Spermophilus columbianus* and found that experienced females had greater reproductive success, concluding that constraint in terms of previous weaning experience provided the best explanation. In their study, future survival and

subsequent reproductive success was not influenced by prior reproductive investments (Broussard *et al.*, 2008). Consequently, they were able to rule out the restraint hypothesis. Our results provide evidence for both the maternal experience constraint and restraint hypotheses.

The greater reproductive success in multiparous females could be a result of more behavioral and physiological experience with previous litters and/or maternal restraint. Multiparous female rodents typically have had more opportunities to enhance their parental skills and therefore are more competent in their maternal care. Experienced females are more responsive to offspring and spend more time in parental care than primiparous (Wright & Bell, 1978; Swanson & Campbell, 1979; Wang & Novak, 1994). Physiological differences between primiparous and multiparous females include hormonal and metabolic differences (Stern & Siegel, 1978; Künkele, 2000). In addition, some primiparous females lower their energy allocation in their first reproductive attempt to avoid possible costs and save their energy for somatic growth or future reproduction (e.g. red squirrels *Tamiasciurus hudsonicus*, Descamps *et al.*, 2007). Primiparous mothers may also limit their first reproduction to achieve greater paybacks when investing in reproduction at older ages (Forslund & Pärt, 1995).

In conclusion, we found that multiparous female Cape ground squirrels were more successful at producing weaned offspring than were primiparous although the body masses or litter sizes of the offspring did not differ. Surprisingly, we did not find differences in reproductive traits when comparing a low resource site with a high resource site. This lack of difference could be a consequence of females at the low resource site investing more in current reproduction during years of adequate rainfall because of a complete cessation of reproduction during drought. An alternative possibility is that other factors, such as predation or parasite loads, could have large impacts on the reproductive success of females, regardless of resources.

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