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Seasonal adjustment of sex ratio and offspring masculinity by female deer mice is inconsistent with the local resource competition hypothesis

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ABSTRACT

Background: Natural selection is expected to favour the dispersing sex when one sex has a greater tendency to disperse and resources are limited, i.e. during periods of high population density. This is termed the local resource competition hypothesis. Among deer mice, *Peromyscus maniculatus*, males are more likely to disperse than females. The masculinity of male deer mice can also affect the probability of their dispersal. 'Masculinity' is a continuous variable compounded from a suite of traits associated with being male (i.e. hormones, behaviours, morphology, life history).

Hypothesis: Female deer mice will produce male-biased sex ratios and more masculinized offspring when population density (and thus local resource competition) is high.

Methods: We investigated cohort sex ratio and population density in *P. maniculatus* during the breeding season of 16 consecutive years. Population density was the surrogate for local resource competition and was measured once every two weeks. We measured masculinity as ano-genital distance (AGD), which is a common measurement of masculinity in mammals and a correlate of testosterone levels, in 6-day-old wild *P. maniculatus* offspring during the breeding season (May through August) of 2011 and investigated whether masculinity was correlated with population density in a manner consistent with local resource competition.

Results: Sex ratio did not correlate as predicted with local resource competition; females produced more female-biased litters when density was high. However, maternal adjustments to masculinity did correlate with litter sex ratio, suggesting that sex ratio and masculinity might covary in response to some selection pressure other than local population density.

Keywords: ano-genital distance, sex ratio manipulation, masculinity, *Peromyscus*, population density, Rodentia.

INTRODUCTION

Fisher (1930) stated that parents are expected to allocate resources equally towards sons and daughters, yet biased sex ratios are common in wild animal populations (summarized in Grant and Chamley, 2010; Hayes *et al.*, 2010; Navara, 2010). This contradiction has been investigated in detail in

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several study systems and a variety of current sex ratio theories have made different predictions (summarized in Sikes, 2007). For example, sex ratio should vary with maternal body condition (Trivers and Willard, 1973), philopatry and mating system [local resource competition (Clark, 1978; Silk, 1983)], offspring body condition and sexual maturation rate [first cohort advantage (Wright *et al.*, 1995)], or environmentally induced changes to maternal condition [extrinsic modification (Post *et al.*, 1999; Forchhammer, 2002)]. Sex ratios may vary with the costs of producing high-quality male versus female offspring (Clutton-Brock and Iason, 1986), but the ultimate goal is to produce as many reproductively successful offspring as possible (Trivers and Willard, 1973; Armitage, 1987; Silk and Brown, 2008; Monclùs and Blumstein, 2012).

One of the most commonly tested hypotheses about adaptive sex ratio manipulation is local resource competition. This hypothesis applies to species that experience variation in population density and exhibit sex-specific dispersal (Clark, 1978; Silk, 1983; Sikes, 2007). In periods of high population density, natural selection is predicted to favour the production of the dispersing sex in order to decrease competition for local resources within the natal territory (Clark, 1978). For example, in woodland deer mice (*Peromyscus maniculatus*), which exhibit male-biased dispersal (Fairbairn, 1977), the local resource competition hypothesis would predict that more males ought to be produced during periods of high population density. This concept has been both supported and rejected in a variety of taxa but has received varying levels of support in the commonly used model organism, *Peromyscus* (Goundie and Vessey, 1986; Havelka and Millar, 1997). Havelka and Millar (1997) demonstrate a male-to-female bias in *Peromyscus* sex ratio across one breeding season and attribute this shift to changes in temperature and precipitation but neglect to test other seasonal variables such as population density. Outright support or rejection of this concept would provide a valuable contribution to the limited sex ratio literature on this genus.

A generally unrelated body of literature suggests that individual masculinity, rather than simply an individual's sex, is associated with many fitness-related attributes (Moore and Power, 1992; Lindstrom, 1999; Monclús and Blumstein, 2012). In mammals, masculinity is commonly measured as ano-genital distance (AGD) – the distance from genital papilla to anus (Ryan and Vandenbergh, 2002). It is positively correlated with testosterone levels (Clemens, 1974; Ryan and Vandenbergh, 2002), is often repeatable (Gandelman *et al.*, 1977; Dusek and Bartos, 2012; but see Dusek *et al.*, 2010), and on average males have a larger AGD than females (Clark and Galef, 1990; Ryan and Vandenbergh, 2002). Both the presence of siblings *in utero* and the sex of those siblings have a strong influence on the AGD of an individual (Ryan and Vandenbergh, 2002), but mothers can also influence offspring AGD through a maternal endocrine effect (Navara, 2010). Beyond the effects of sex ratio, litter size, and the sex of the individual offspring, mothers with higher levels of androgens produce offspring with longer AGDs, or in other words, offspring who are masculinized (Clemens, 1974; Moore, 1992; Moore and Power, 1992; summarized in Ryan and Vandenbergh, 2002; Rosenfeld and Roberts, 2004). Many variables influence offspring AGD, but it generally reflects offspring hormonal variation that begins *in utero* and is associated with adult behaviours such as the frequency of aggressive encounters (Monclús and Blumstein, 2012) and life-history traits such as age of reproductive maturity and fitness (Monclús and Blumstein, 2012).

Masculinity (measured as AGD) has also been associated with the probability of dispersal in several wild rodents. In Belding's ground squirrels, experimentally increased testosterone levels in juvenile females increased individual dispersal distance over control females (Nunes *et al.*, 1999). The AGD of females from male-biased litters has been found to be larger than that of females from female-biased litters [*Peromyscus californicus* (Cantoni *et al.*, 1999)], and females with larger AGD values have been shown to have higher levels of testosterone [yellow-bellied marmots (Monclùs and Blumstein, 2012)] and an increased probability of dispersal [Belding's ground squirrels (Holekamp *et al.*, 1984; Nunes *et al.*, 1999)]. It would therefore appear that both increases in testosterone and longer AGDs are associated with increased probability of dispersal across multiple families of rodents.

Integrating local resource competition and individual masculinity

In general, mothers are expected to produce offspring with attributes that increase fitness through the production of grand-offspring. The local resource competition hypothesis fundamentally suggests that mothers should produce offspring that are more likely to disperse when competition for local resources is high. This has, thus far, led to predictions of maternal adjustments to offspring sex ratio because offspring sex is often a strong predictor of dispersal probability. Maternal adjustments to other offspring phenotypes that affect the probability of dispersal in response to population density, however, would also be consistent with the local resource competition theory. Here we suggest that maternal adjustments to offspring masculinity, despite offspring sex, can also affect their probability of dispersal if more masculinized offspring are more likely to disperse. Masculinity might provide a mechanism for fine-scale maternal adjustments to fitness-related traits in offspring (e.g. dispersal probability) that differ between sons and daughters. In these cases, we would predict that maternal adjustments of sex ratio should parallel maternal adjustments of AGD. For example, if male-biased sex ratio adjustment provides a fitness advantage, then we would expect that mothers who produce offspring with a lengthened AGD would also gain a fitness advantage. This integration of sex ratio adjustment and masculinity (in both sons and daughters) would be expected to occur whenever offspring sex and masculinity affect fitness through a common underlying mechanism such as dispersal.

Woodland deer mice

Woodland deer mice (*Peromyscus maniculatus*) have litter sizes that range from four to eight offspring. Females typically mate during a post-partum oestrus and demonstrate multiple male mating within litters (Birdsall and Nash, 1973). *Peromyscus* exhibit male-biased dispersal (Fairbairn, 1977) and often experience extreme fluctuations in sex ratio (Kaufman and Kaufman, 1982) and population density (Falls *et al.*, 2007), so local resource competition could provide a reasonable explanation for adjustments to offspring sex ratio. According to the local resource competition hypothesis, *Peromyscus* ought to produce male-biased litters when population density is high (i.e. high local resource competition).

To date, there is limited information on masculinity in *Peromyscus* and the association between AGD, masculinity, and dispersal has yet to be investigated, but masculinity has previously been found to be positively associated with dispersal distance in other rodents (Holekamp *et al.*, 1984; Cantoni *et al.*, 1999; Nunes *et al.*, 1999; Monclùs and Blumstein, 2012). We thus predicted that deer mice would produce more male-biased litters, and/or more masculinized offspring, when population density was high and more daughters, and/or more feminized offspring, when population density was low.

METHODS

Data collection

Long-term small mammal study

We investigated fluctuations in cohort sex ratio and population density of *Peromyscus maniculatus* across 16 years to determine whether females adjusted sex ratio in a manner consistent with the local resource competition hypothesis. These data were collected each year between 1996 and 2011 from seventeen 100-m transects placed in eight different forest habitats including coniferous, mixed forest, and pure hardwood stands in Algonquin Provincial Park, Ontario, Canada (for detailed methods, see Falls *et al.*, 2007). Transects were live-trapped for three consecutive nights every two weeks between May and August of each year (see Fryxell *et al.*, 1998; Falls *et al.*, 2007).

Population density was calculated as the number of captures (adult, sub-adult, and juvenile combined) per 100 trap-nights. Within this study area, *Peromyscus* population densities have been shown to respond to wide regional variation in food availability across a 43-year time period (Fryxell *et al.*, 1998; Falls *et al.*, 2007), so we assumed that these data from a range of habitats in Algonquin Park would reasonably characterize the seasonal change in population density where our mice were captured. Population density and cohort sex ratio, measured as the proportion of young-of-the-year individuals at first capture that were male, were calculated for each year. Young-of-the-year were considered to be individuals who weighed less than 16 g and had either grey or mottled grey and brown pelage (Schug *et al.*, 1991). All animals were sexed based on their genitals.

Measuring masculinity

As part of a separate study (see Stewart and McAdam, 2014), we measured the ano-genital distance (AGD) of 175 offspring from 31 litters that were born in captivity between May and August 2011 at the Algonquin Wildlife Research Station in Algonquin Provincial Park, Ontario, Canada. Wild pregnant deer mice were live-trapped in the field and brought into captivity prior to parturition, hence these females did not breed during their post partum oestrus. Parturition dates of each litter were known from observing mothers on a daily basis. After birth, offspring were visually sexed, weighed to the nearest 0.01g, and both body length and ano-genital distance were taken at post-natal day six using digital calipers (precision 1 mm).

Weight and body length have been found to covary both isometrically (Graham and Gandelman, 1986; Drickamer, 1996; Ryan and Vandenbergh, 2002; Hotchkiss and Vandenbergh, 2005) and allometrically (summarized in Dusek *et al.*, 2010) with AGD in Rodentia. When AGD is divided by either of these parameters, it is termed the ano-genital distance index [AGDI (Dusek *et al.*, 2010)]. However, we did not use AGDI as a measure of masculinity because body size and AGD did not vary isometrically in our data. Instead, we used AGD and corrected for body size by including it as a covariate in our models.

Seasonal changes in population density for 2011 were calculated in the same way as for the long-term small mammal study (see also Fryxell *et al.*, 1998; Falls *et al.*, 2007). Population density was measured as captures per 100 trap-nights (equivalent to two weeks of trapping on each line) using data from the 2011 long-term small mammal survey within Algonquin Park. Time period within our statistical models refers to these two-week periods.

All laboratory procedures received approval from the University of Guelph Animal Care Committee (AUP# 08R063) and Ontario Parks.

Statistical analysis

Long-term small mammal study

Two methods were used to evaluate the correlation between cohort sex ratio and population density: (1) a Pearson's correlation involving data from all 16 years, and (2) a de-trending analysis to account for temporal trends across years (see Kantelhardt *et al.*, 2002). Both cohort sex ratio and population density were de-trended using the residuals of models (one for each of sex ratio and density) that included year and year^2 as continuous fixed effects. This approach removed long-term directional trends in density and sex ratio that might be caused by other directionally changing variables, such that sex ratio and population density were now measured relative to recent years, which likely provides a better measure of local resource competition than absolute density.

To determine whether this population of *Peromyscus* demonstrated frequency-dependent shifts in sex ratio, we used a Pearson's correlation to test for a negative relationship between adult sex ratio and cohort sex ratio. This would support Fisher's theory of sex ratio adjustment in response to frequency-dependent selection, whereby the production of more daughters is favoured when the population is male-biased.

Measuring masculinity

To test predicted changes in secondary sex ratio and offspring masculinity in response to local resource competition during 2011, Pearson's correlations were used to determine if there were associations between population density and either litter sex ratio or masculinity. We measured maternal adjustments to masculinity by first correcting AGD for variation due to offspring sex, body size, and litter sex ratio. In this mixed-effect model of AGD (log-transformed), we included body length (log-transformed), the proportion of male siblings in the litter, and the offspring's sex as predictors. Litter identity was included as a random effect because multiple offspring from the same litter were not independent. The residuals of this model, therefore, measured how masculinized an individual mouse was compared with what we would predict based on its body size, sex, and the sex ratio of its littermates. As a result, any direct effects of the offspring's sex or of the intra-uterine effects of the sex ratio of the litter it was born into on its AGD are accounted for in this model. Residuals of this model (hereafter referred to as 'corrected AGD'), therefore, represent any additional maternal adjustments to masculinization beyond indirect effects on masculinization that occur through maternal adjustments to offspring sex ratio (i.e. these residuals are independent of sex ratio). We used Pearson's correlations to determine whether population density was correlated with either sex ratio or raw AGD values. We then used our corrected AGD values as our response in a second mixed-effect model that included population density as a continuous fixed effect in order to determine the effect that population density had on corrected AGD. Time period was included as a random effect in this model to account for the fact that several offspring were born within each time period in which density was measured.

All statistical analyses were performed in R v.2.13.2 (R Development Core Team, 2011) and mixed effect models used the nlme package (Pinhero *et al.*, 2011). All data were tested for normality and all model assumptions were met.

RESULTS

Long-term variation in density and sex ratio

Across the 16 years of study, annual cohort sex ratio varied from 45% to 83% male (mean = 60%, S.D. = 11%, $n = 16$). Over this same period, annual population density ranged from 2.2 captures per 100 trap-nights to 19.2 captures per 100 trap-nights (mean = 7.7, S.D. = 4.9, $n = 16$). There was no overall correlation between cohort sex ratio and population density across years ($r = -0.36$, $n = 16$, $P = 0.17$). However, after de-trending the cohort sex ratio and population density data, there was a significant negative correlation between cohort sex ratio and overall population density ($r = -0.51$, $n = 16$, $P = 0.04$; Fig. 1), indicating that more female-biased litters were produced when density was high. This was opposite to the predictions of the local resource competition hypothesis.

A positive correlation between adult sex ratio and cohort sex ratio across years ($r = 0.60$, $n = 16$, $P = 0.02$) demonstrated that more sons were produced when the adult sex ratio was male-biased. This was opposite to the expected adjustments of sex ratio in response to adult sex ratio according to Fisher's idea of frequency-dependent selection.

Effects of density on sex ratio and masculinity in 2011

Between 12 May and 28 August 2011, 175 *P. maniculatus* offspring were born in captivity to 31 wild-captured mothers. The sex ratio of each litter varied between 0% and 80% male (mean = 46%, S.D. = 24%, $n = 31$). Mean population density changed dramatically within

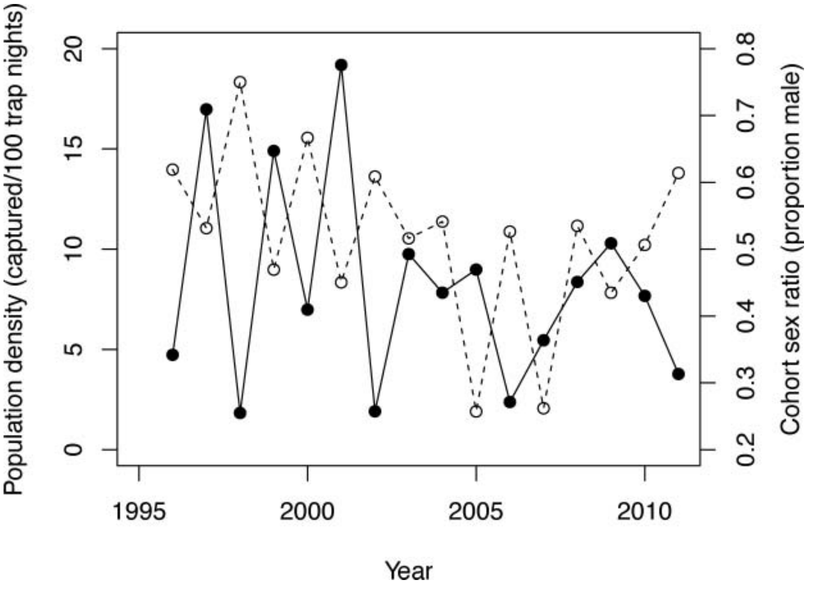

Fig. 1. Both population density and annual cohort sex ratio varied across 16 years in *Peromyscus*, where sex ratio was on average male-biased across this time period. After de-trending, cohort sex ratio and population density are negatively correlated, which is opposite to our predictions based on the local resource competition hypothesis.

this breeding season, where population density rose, across eight time periods, from 5 captures per 100 trap-nights in May to 44 captures per 100 trap-nights in August.

Our corrected AGD measurement accounted for the effects of sex ($\beta = 0.38 \pm 0.02$, $t_{139} = 15.42$, $P < 0.001$), sex ratio of littermates ($\beta = -0.15 \pm 0.09$, $t_{29} = -1.78$, $P = 0.08$), and body size ($\beta = 0.006 \pm 0.004$, $t_{139} = 1.44$, $P = 0.15$) as well as among-litter variance (variance = 0.023). Contrary to the predicted positive correlation between population density and the percentage of males within a litter, population density was negatively correlated with secondary sex ratio ($r = -0.31$, $n = 31$, $P < 0.0001$), with raw AGD measurements ($r = -0.36$, $n = 174$, $P < 0.0001$), and with our corrected AGD measurement (corrected for body size, sex, and sex ratio; $n = 8$, slope = −0.0016, $P = 0.06$; Fig. 2), which were opposite to our predictions associated with local resource competition.

DISCUSSION

Sex ratio adjustments in response to environmental variations, such as temperature, precipitation, and habitat scale, have been investigated in *Peromyscus* (Goundie and Vessey, 1986; Havelka and Millar, 1997) whereas variations in masculinity in this genus are to date relatively unknown. Through studying both sex ratio and masculinity within the same population of *Peromyscus*, both within one year and in relation to a reliable and well-researched long-term study, we found that mothers adjusted secondary sex ratio and masculinity in response to a change in population density, but these adjustments were in the opposite direction of the predictions of the local resource competition hypothesis. There was a negative correlation between cohort sex ratio and population density in both the long-term data and within the

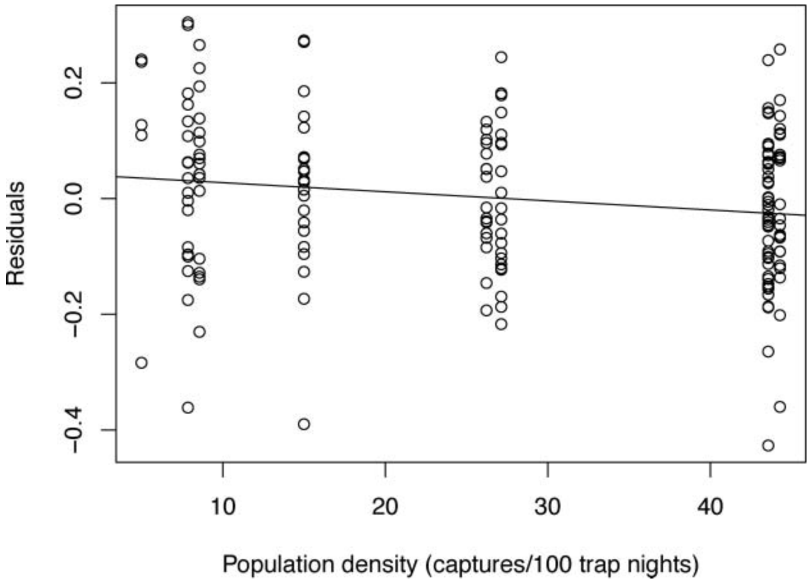

Fig. 2. Corrected ano-genital distance (AGD) in *Peromyscus* did not increase in response to increasing population density across eight time periods, as predicted by the local resource competition hypothesis. Plotted AGD values have been corrected for the effects of sex, litter sex ratio, body length, and among-litter variance.

breeding season of 2011, as well as a negative correlation between litter sex ratio and population density and corrected AGD and population density within the breeding season of 2011. In other words, non-dispersing individuals (females and feminized individuals) were produced during high population density, which is opposite to our predictions based on local resource competition and should result in the production of philopatric offspring that increase competition with mothers for resources. This trend does not support the local resource competition hypothesis for sex ratio adjustment within this *Peromyscus* system when local resource competition is measured in terms of population density. It remains possible, however, that females adjust offspring sex ratio in response to other resources such as mates or food resources that are not reflected in measures of population density.

While we did not find support for the local resource competition hypothesis for sex ratio manipulation, we did find evidence that maternal adjustments to offspring AGD and litter sex ratio in response to population density were both in the same direction. This finding supports our general concept of integrating sex ratio and masculinity because it demonstrates that mothers adjusted these offspring attributes in parallel and that they might be substitutable, at least to some degree. For example, if a sex ratio shift towards a more male-biased sex ratio provides a fitness advantage to the mother, then a shift towards more masculine offspring could also do the same. Masculinity might, therefore, provide an additional metric with which to test adaptive hypotheses that have previously been interpreted only with respect to sex ratio. Thus although we reject local resource competition as an explanation for variation in both sex ratio and masculinity, it remains possible that female deer mice were adjusting both sex ratio and masculinity in response to population density because of the fitness benefits of producing daughters and more feminized offspring when population density was high.

There are several possible reasons why the sex ratio of litters and masculinity of offspring were opposite to what we had predicted based on the local resource competition hypothesis. First, it is possible that local population density experienced by mothers differed from the regional population density that we measured. *Peromyscus* density fluctuates regionally in this system (Fryxell *et al.*, 1998), so we assumed that our density estimates would reasonably reflect local population density where mothers were trapped. However, it seems very unlikely that these differences would contradict the general pattern of seasonal population density increase that we documented in 2011, which is typical of most small mammal populations (Krebs, 1996). Nevertheless, further studies that explicitly examine the effects of local population density experienced by individual females are needed. Second, many studies confound population density and resources (Dantzer *et al.*, 2013), and represent a general inability to measure actual resource competition in most ecological systems. Third, perhaps an alternate form of resource competition is overriding the influence of regional population density on female reproductive decisions and behaviour. An example of this would be a locally clumped distribution of food abundance. If food is scarce, but clumped close to the natal site, we would expect mothers to produce offspring with limited dispersal tendencies despite increases in competition between mother and offspring. Havelka and Millar (1997) suggest a similar concept – that microhabitat is an important predictor of female reproductive success in *Peromyscus*. Expanding our 2011 data collection to include other microhabitat factors such as local density, food abundance, or mate availability over a period of several years would allow us to test these alternative hypotheses.

Our study had potential methodological limitations that could explain the absence of an effect of density on sex ratio and offspring masculinity, although these cannot explain the opposite effect that we have documented here. First, our analysis of long-term patterns in sex ratio was based on tertiary sex ratios. Sex ratio theory involves maternal adjustments to either primary (at conception) or secondary (at birth) sex ratio. Using tertiary sex ratio (at recruitment) assumes: (1) that there is no differential offspring survival between birth and recruitment, and (2) that there are no differences in maternal mediation on differential survival between mothers. Litter (secondary) and cohort (tertiary) sex ratios were similar in our 2011 study across the eight time periods measured (mean litter sex ratio = 44 ± 9% male; mean cohort sex ratio was 56 ± 11% male), but it is possible that there were substantial differences between secondary and tertiary sex ratios in our long-term analysis. Second, it is possible that AGD did not adequately reflect masculinity in our mice. Ryan and Vandenbergh (2002) popularized the concept of *in utero* maternally mediated variation of offspring AGD in laboratory mice, and since then AGD measurements have been cited as a useful measurement of masculinization or feminization in rodents (Ophir and delBarco-Trillo, 2007). However, some limitations have been found associated with this measurement. AGD measurements have been found to be repeatable in adult female mice, but the oestrus cycle (Dusek and Bartos, 2012) and lactation status (Dusek *et al.*, 2010) of the mouse must be taken into consideration when measuring adults. Third, we used annual measures of density and sex ratio because the temporal resolution of these measures in the long-term dataset was limited. Annual density measures represent typical values for each year, but do not necessarily reflect the density experienced by any one mouse. In all cases, these potential limitations of our study might impair our ability to detect relationships between population density, sex ratio, and masculinity, but we see no reason why these potential problems would result in effects opposite to our initial predictions. We thus are comfortable rejecting the local resource competition hypothesis for sex ratio adjustment in this population.

Although we did not find support for the local resource competition hypothesis for sex ratio adjustment, we can discuss our findings in the context of other hypotheses for sex ratio adjustment. We demonstrated a positive correlation between adult sex ratio and cohort sex ratio across years, which is opposite to the expected adjustments of sex ratio in response to frequency-dependent selection as predicted by Fisher (1930). Our data from 2011 do fit some aspects of the first cohort advantage [FCA (Wright *et al.*, 1995; Sikes, 2007)] and Trivers-Willard [TW (Trivers and Willard, 1973)] hypotheses. Both of these hypotheses predict that males should be produced at the beginning of the breeding season in multiparous mammals, such as *Peromyscus*, because (1) the sex with the more variable fitness should be produced early in the breeding season to have the greatest opportunity for mating [FCA (Wright *et al.*, 1995; Sikes 2007)], and (2) the more costly sex should be produced during periods of high maternal condition [TW (Trivers and Willard, 1973)]. These hypotheses assume that males are costly to produce and have more variable reproductive success than females, and that mothers are in good condition at the start of the breeding season. Although *Peromyscus* males likely have more variable reproductive success than females due to frequent multiple paternity (Birdsall and Nash, 1973; Ribble and Millar, 1996), it is not known whether males are more costly to produce in this species. When assessing the Trivers-Willard hypothesis, maternal weight in this system was not correlated with litter sex ratio and maternal weight is thought to be an unreliable measure of maternal condition in *Peromyscus* (Millar *et al.*, 1992). So while our results are somewhat consistent with the first cohort advantage and Trivers-Willard hypotheses, more work must be done to adequately understand why mothers produce more female-biased litters and more feminized offspring when population density is high in this population of deer mice.

In conclusion, we found evidence that maternal adjustments of sex ratio were mirrored by maternal adjustments to offspring masculinity, but the direction of these effects was opposite to predictions based on the local resource competition hypothesis. In order to more broadly integrate maternal manipulations of offspring masculinity with other theories of sex ratio manipulation, we need a better understanding of how masculinity varies in wild systems and its associated ecological and fitness consequences. By integrating maternal manipulation of offspring masculinity with existing sex ratio manipulation hypotheses, we hope to stimulate further discussion and research on these alternative, but often complementary, ways in which mothers might adjust the attributes of their offspring to enhance fitness.

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