

# ADJUSTMENT OF REPRODUCTIVE INVESTMENT AND OFFSPRING SEX RATIO IN WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) IN RELATION TO WINTER SEVERITY

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Both density-dependent factors and environmental stochasticity can impact the dynamics of free-ranging populations. The pathways through which these factors influence population dynamics can be complex and may be immediate or lagged, and cumulative effects of environmental factors have been reported. We examined the effects of the severity (snow depth and persistence and winter rainfall) of the current and previous winters on the probability that female adult and yearling white-tailed deer (*Odocoileus virginianus*) would produce a fetus, and that adult females would produce a male fetus. We used logistic regression and Akaike's information criterion to select the best models from a set of 11 a priori candidate models. The severity of the winter 1 year before gestation negatively impacted the probability that both adults and yearlings would produce a fetus. There was no evidence that the probability of yearlings or adults producing a fetus was affected by winter conditions while gestating. Further, there was no evidence that the severity of the winter during which a yearling was gestated affected its probability of producing a fetus as a yearling. As the severity of the winter of gestation increased, the probability of producing a male decreased, consistent with both the Trivers–Willard sex ratio adjustment hypothesis and the extrinsic modification hypothesis. We suggest that both the decreased probability of reproduction after severe winters and the variation in fetal sex ratio may ultimately increase lifetime fitness if they lead to the production of the fittest offspring given the available maternal resources.

Key words: environmental stress, extrinsic modification, life history, maternal condition, sex ratio variation, Trivers and Willard hypothesis, winter weather

In variable environments, reproductively mature females must weigh the fitness benefits of allocating resources to current reproduction against the resulting possible costs to future reproductive success. When maternal resources for producing offspring are limited, individuals may delay reproduction until sufficient resources are available to rear healthy offspring (Beckerman et al. 2002, 2003; Lindström and Kokko 2002). Alternatively, if the fitness returns of producing one sex are more variable than the other, females may selectively produce offspring of the sex that provides the highest fitness return given the resources available for investment (Trivers and Willard 1973). Maternal resources can be affected by environmental stochasticity and variation in population density.

The resulting effects include immediate and delayed impacts on fecundity, survival, or both, which can have important effects (Beckerman et al. 2002; Forchhammer et al. 2001; Gaillard et al. 2003; Lindström and Kokko 2002; Post and Stenseth 1999).

We characterized the effects of winter weather severity on fetus production by white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada. Nova Scotia is near the northern extent of the range of white-tailed deer and snow depth, snow persistence, and winter rainfall are the primary factors that affect body condition in this region during winter (Garroway and Broders 2005). Adult mortality due to overwinter malnutrition is minimal (Patterson et al. 2002; Whitlaw et al. 1998) and changes in population size are likely related to variation in juvenile recruitment and mortality due to hunting (Patterson and Power 2002). Fetuses are gestated over winter when forage availability does not meet overall daily energy requirements, causing females that enter winter pregnant and in poor body condition to have a reduced probability of survival (Mautz

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1978; Moen 1976) and an increased likelihood of aborting the fetus or producing a small fawn (Verme 1965).

The effects of weather on fetus production and the adjustment of offspring sex ratios have both been controversial. For example, it is unclear whether winter weather affects the density of white-tailed deer immediately (Messier 1991, 1995) or cumulatively over multiple winters (McRoberts et al. 1995; Mech et al. 1987; Patterson and Power 2002). Mech et al. (1987) and McRoberts et al. (1995) suggested that in Minnesota, the sum of the average monthly snow depth had a cumulative negative impact on fawn:doe ratios that became apparent after 3 years. Similarly, Patterson and Power (2002) suggested that population density of white-tailed deer in Nova Scotia responded to cumulative snowfall from the previous 2 years. However, if body condition (the putative mechanism impacting reproduction) is considered a continuous process one would predict that the immediate winter would have the largest effect on condition, with subsequent winters having smaller and smaller effects (Messier 1995). Accordingly, in our previous analysis of this population, we found that the body condition of individuals was most influenced by the current winter conditions, with no evidence for cumulative effects of consecutive winters (Garroway and Broders 2005). This led us to speculate that a possible explanation for previous studies finding cumulative multiyear effects of severe winters might be the detection of delayed effects within the construction of multiyear variables (i.e., a severe winter from an early year within the variable carries an inordinate weight relative to successive winters).

Evidence for facultative sex ratio adjustment in mammals also has been variable (Festa-Bianchet 1996), although a recent meta-analysis suggests that there may be consistent support for the hypothesis of Trivers and Willard (1973) among ungulates (Sheldon and West 2004). This hypothesis states that when the fitness of one sex is more variable, the cost of rearing that sex is higher, and the maternal resources available for investment in offspring vary, it should be adaptive for females to produce more offspring of the sex that yields the highest fitness returns given maternal resources (Trivers and Willard 1973). In sexually dimorphic species such as white-tailed deer, males grow faster and for a longer period than females, making males the more energetically expensive sex to produce (Jarman 1983). Reproductive success of males is also more variable and more dependent on body size (Jarman 1983), such that smaller, poorer-quality males may rarely sire offspring, whereas larger, higher-quality males may sire many. In contrast, lower variability in reproductive success among females should reduce the difference in reproductive output between high- and low-quality females relative to the difference between high- and low-quality males (Trivers and Willard 1973). Therefore, females with limited resources for reproduction should produce daughters, whereas strong, healthy females should produce sons. For white-tailed deer, arguments have been made for both male- and female-biased sex ratio adjustment by females in good condition (Burke and Birch 1995; Degayner and Jordan 1987; Verme 1983).

Here, we explore patterns of reproductive success and offspring sex ratio variation in white-tailed deer to determine the effects of environmental stochasticity and maternal condition on offspring production. Specifically, we examine the effects of the severity of the current and previous winters on the probability of yearlings producing a fetus, of adults producing a fetus, and of adult females producing a male fetus. Our analyses yield new and intriguing insights into the factors affecting offspring production and, hence, the demography of white-tailed deer populations at the northern end of this species' range.

## MATERIALS AND METHODS

Our study animals were primarily road-killed individuals that were sampled and georeferenced by Nova Scotia Department of Natural Resources staff within 3 days of death. Deer were aged as fawns (< 1 year), yearlings (1.5 years), or adults (> 2 years) by examining tooth wear and development (Severinghaus 1949). Some authors have suggested that road-killed deer do not represent a random sample because more malnourished animals may be particularly likely to travel on snow-cleared roads to reduce energy expenditure (O'Gara and Harris 1988). However, other researchers have demonstrated that the composition of road-killed samples is determined primarily by traffic flow, population density, and sex- and season-specific behaviors (Allen and McCullough 1976; Groot Bruinderink and Hazebroek 1996; McCaffery 1973; Mysterud 2004). Visual assessment of femur marrow fat for animals in our data set revealed a full range of body conditions (40% of samples had visually assessed femur marrow fat values greater than 85%, 28% of samples were estimated to have values between 50% and 85%, 18% of samples had values between 25% and 50%, and the remaining 14% of samples had values below 25%—Garroway and Broders 2005), suggesting this sample did not consist of a particularly malnourished subset of the population.

*Data set attributes and analyses.*—To assess the impact of current and previous winters on the probability of fetus production, we analyzed data on reproduction by yearling ( $n = 236$ ) and adult ( $n = 1,241$ ) females. We analyzed yearlings separately because they were the only reproductive animals for which we could determine age exactly and, hence, they provided insight into the effects of the winter in which an individual was gestated on the probability of producing a fetus. In a logistic regression framework using Akaike's information criterion (AIC—Burnham and Anderson 2002) as a basis for model selection, we ran a set of 11 a priori candidate models representing carefully considered alternative hypotheses to assess the effects of the current and preceding 2 winters on the probability that yearling and adult females would produce a fetus (Table 1). Individuals carrying a fetus were coded as 1, whereas individuals not carrying a fetus were coded as 0. To examine sex ratio variation, we used the same candidate model set but added a variable for the number fetuses a mother carried to account for individuals carrying multiple fetuses (FETUS: coded as 0 if there was only 1 fetus and 1 if there were 2

fetuses). The sampling unit for this analysis was the fetus ( $n = 794$ ), with male fetuses coded as 1 and female fetuses coded as 0. Significance of the top-ranked models was tested using permutation tests to determine whether model effects were different from that expected by chance (dependent variable was permuted 1,000 times). Model variables were considered to have significant effects if parameter estimates were greater than or less than 95% of permuted values ( $P < 0.05$  or  $P > 0.95$ ; 1-tailed test).

*Weather variables.*—Our previous analyses of these data demonstrated a strong relationship between body condition (quantified by visually assessed femur marrow fat) and snow depth and persistence, and winter rainfall. As a result, we included explanatory variables for these 2 weather factors in the model set for analyses of the effects of the current as well as the previous 1 and 2 winters (Garroway and Broders 2005). Current-year snow depth and persistence and rainfall variables (SNOWDEPTH and RAINFALL) were calculated as the sum of weekly averages of each variable during the winter of death, with data collection continuing until the week of death. Variables for the winters 1 and 2 years before death were calculated as the sum of weekly averages of each variable over the entire preceding 1 and 2 winters, respectively (1 winter previous variables: SNOWDEPTH1YA and RAINFALL1YA; 2 winters previous: SNOWDEPTH2YA and RAINFALL2YA). Weather data were recorded at 13 weather stations across Nova Scotia (Meteorological Service of Canada—Atlantic Region, Environment Canada Halifax Province, Nova Scotia) between 1 November and 15 May (earliest snow accumulation to latest snowmelt). Deer were assigned to the weather station located nearest to site of death using ArcGIS (Environmental Systems Research Institute Inc. 2003). The average distance between a sampling locality and the nearest weather station was  $33 \text{ km} \pm 19 \text{ SD}$  ( $n = 1,477$  deer).

Hosmer and Lemeshow goodness of fit tests for the global model (model including all variables) were used to assess the appropriateness of variables for inclusion into the candidate model set (Burnham and Anderson 2002; Hosmer and Lemeshow 2000). Hosmer and Lemeshow goodness of fit tests are specific to logistic regression analyses and test whether model predictions of the dependent variable are different from observed values. For  $P > 0.05$ , the model fit is good (Hosmer and Lemeshow 2000) and the variables warrant further consideration (Burnham and Anderson 2002). In contrast, for  $P < 0.05$ , the model fit is poor and inclusion of the variables should be reassessed (Burnham and Anderson 2002).

*Decision criteria.*—We calculated the difference between the AIC for each model and the AIC for the best approximating model ( $\Delta i$ ). For each model with  $\Delta i < 2$  (i.e., the model set with an approximately 0.95 probability of containing the top model—Burnham and Anderson 2002; Richards 2005), we present the normalized model Akaike weights ( $w_i$ ; probability that the  $i$ th model is the best model explaining the data given the model set). For the variables contained within the best model set, we present parameter estimates ( $\beta \pm SE$ ) and odds ratios (antilogarithm of  $\beta$ ) with associated 95% confidence intervals (95% CIs—Hosmer and Lemeshow 2000). Models

**TABLE 1.**—Terms in the a priori candidate model set for logistic regression analyses of the influence of the current and previous 1 and 2 winters on the probability of adult and yearling female white-tailed deer (*Odocoileus virginianus*) producing a fetus and of adult females producing a male fetus (with the addition of the variable FETUS to each model).

Model statement
Weather subset
SNOWDEPTH
RAINFALL
SNOWDEPTH, RAINFALL
SNOWDEPTH1YA
SNOWDEPTH2YA
RAINFALL1YA
RAINFALL2YA
SNOWDEPTH1YA, RAINFALL1YA
SNOWDEPTH2YA, RAINFALL2YA
SNOWDEPTH, RAINFALL
SNOWDEPTH, SNOWDEPTH1YA, SNOWDEPTH2YA

from this set were considered important if permutation tests indicated that effects were significantly different from the average of the random permutations and based upon the breadth and position of the 95% CI around the odds ratio of variables. All analyses were conducted in S-PLUS 7 (Insightful Corp., Seattle, Washington).

## RESULTS

Winter weather varied considerably during the course of this study. The average ( $\pm SD$ ) yearly value for snow depth and persistence was  $279 \pm 229 \text{ cm}$  (range 15–1,175 cm). The average yearly value for rainfall was  $83 \pm 22 \text{ mm}$  (range 32–142 mm). Of the 1,241 adult females analyzed, 535 carried twins and 251 carried singletons. The remaining 455 adult females did not carry a fetus. Of the 236 yearlings analyzed, 87 carried twins and 86 carried singletons. The remaining 63 yearlings did not carry a fetus. For the sex ratio analyses, fetuses from 149 adult females carrying singletons (85 male and 64 female fetuses) and 322 adult females carrying twins (88 female:female twins, 174 male:female twins, and 60 male:male twins) were analyzed.

*Probability of fetus production.*—Hosmer and Lemeshow goodness of fit tests indicated that the global model fit the data and that the 6 initial variables warranted further consideration with an AIC model selection strategy ( $P = 0.35$ ). Three models for predicting the probability that a yearling would produce a fetus had  $\Delta i < 2$  (Table 2). Of these, the univariate model RAINFALL1YA ( $\beta_0$ :  $2.4370 \pm 0.7680 \text{ SE}$ ,  $\beta_{\text{RAINFALL1YA}}$ :  $-0.0151 \pm 0.0070 \text{ SE}$ ) had a 55% probability of being the best model ( $P = 0.028$ ; Table 2). There was some evidence for effects of RAINFALL2YA and SNOWDEPTH1YA in the model selection although 95% CIs of parameter estimates overlapped zero, indicating that the effects of these variables were likely minimal. The odds that a yearling female would produce a fetus after exposure to 90 mm of winter rainfall (arbitrarily chosen to represent above-average exposure to winter rainfall) in the previous year relative to no exposure to

**TABLE 2.**—Difference between the top-ranked and the *i*th model ( $\Delta_i$ ) for logistic regression models within 2 Akaike information criterion points of the top-ranked model. Normalized Akaike weights ( $Nw_i$ ) and the sum of normalized Akaike weights ( $\Sigma Nw_i$ ) also are shown. Models are listed in order of decreasing fit to the data.

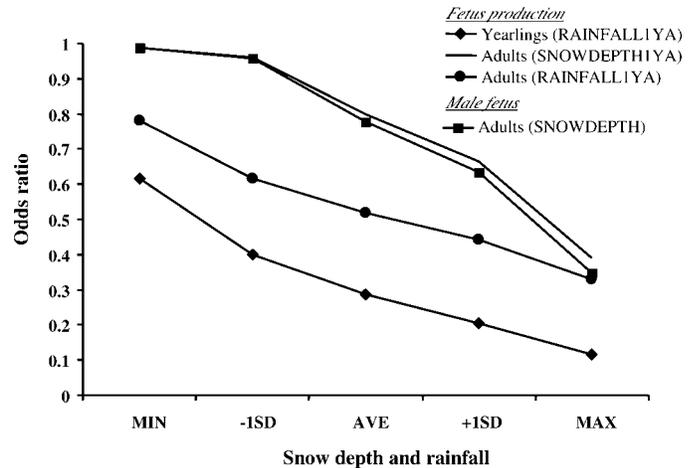
Model	$\Delta_i$	$Nw_i$	$\Sigma Nw_i$
<b>Yearlings</b>			
RAINFALL1YA	0.000	0.551	0.551
RAINFALL2YA	1.743	0.230	0.781
SNOWDEPTH1YA, RAINFALL1YA	1.847	0.219	1.000
<b>Adults</b>			
SNOWDEPTH1YA, RAINFALL1YA	0.000	1.000	1.000
<b>Fetal sex ratio</b>			
SNOWDEPTH, FETUS	0.000	0.560	0.560
SNOWDEPTH, RAINFALL, FETUS	1.828	0.224	0.784
SNOWDEPTH, SNOWDEPTH1YA, FETUS	1.909	0.216	1.000

winter rainfall was 0.26 (95% CI: 0.07–0.89), indicating that individuals were 3.84 times (inverse odds ratio) less likely to produce a fetus after exposure to more severe than average versus no winter rainfall during the preceding year (Table 3). The odds of a yearling producing a fetus steadily decreased over the full range of winter rainfall values analyzed for this variable (Fig. 1). None of the top models (Table 2) contained a variable related to the winter conditions during the year that a yearling gestated a fetus.

For predicting the probability that an adult female would carry a fetus, all models except for the top model had  $\Delta_i > 2$  and so only the top model was interpreted ( $P = 0.030$ ; Table 2). This model contained the variables RAINFALL1YA and SNOWDEPTH1YA ( $\beta_0$ :  $0.3125 \pm 0.2825 SE$ ,  $\beta_{\text{RAINFALL1YA}}$ :  $-0.0078 \pm 0.0030 SE$ ,  $\beta_{\text{SNOWDEPTH1YA}}$ :  $-0.0008 \pm 0.0003 SE$ ). The odds that an adult female would produce a fetus after exposure to 90 mm versus 0 mm of winter rainfall during the preceding year was 0.50 (95% CI: 0.29–0.84), which indicates that females were 2.02 times less likely to carry a fetus after exposures to more severe than average versus no winter rainfall (Table 3). The odds that a female would carry a fetus after exposure to 500 cm versus 0 cm of snow (arbitrarily chosen to

**TABLE 3.**—Parameter estimates ( $\beta \pm SE$ ) and odds ratios ( $\pm 95\%$  CI) for variables from the top-ranked models from logistic regression analyses of determinants of yearling and adult female reproduction and fetal sex ratio variation. Odds ratios for snow depth represent exposure to 500 cm versus 0 cm of snow and odds ratios for rainfall represent exposure to 90 mm versus 0 mm of rain.

Model terms	$\beta$ (SE)	Odds ratio (95% CI)
<b>Yearlings</b>		
RAINFALL1YA	-0.0151 (0.0079)	0.26 (0.07–0.98)
<b>Adults</b>		
SNOWDEPTH1YA	-0.0008 (0.0003)	0.67 (0.50–0.90)
RAINFALL1YA	-0.0078 (0.0030)	0.50 (0.38–0.65)
<b>Fetal sex ratio</b>		
SNOWDEPTH	-0.0009 (0.0004)	0.64 (0.43–0.94)



**FIG. 1.**—Changes in the logistic regression odds (antilogarithm of parameter estimates multiplied by a given value for that variable) of female white-tailed deer yearlings and adults producing a fetus and adult females producing a male fetus after exposure to the minimum (MIN), the average  $-1 SD$  ( $+1SD$ ), the average (AVE), the average  $+1 SD$ , and the maximum (MAX) values analyzed for significant winter weather variables. As odds ratios decrease below 1 the odds of producing a fetus become increasingly less likely.

represent above-average exposure to snow depth) during the preceding winter was 0.67 (95% CI: 0.50–0.90), indicating that adult females were 1.50 times less likely to carry a fetus after exposure to more severe than average versus no winter snowfall (Table 3). Again for these variables, the odds of an adult female producing a fetus steadily decreased over the full range of values analyzed for these variables (Fig. 1). There was no evidence that winter conditions during the year in which an adult female gestated a fetus affected the probability of producing a fetus in that year.

Only RAINFALL1YA occurred in the top model for both the adult and yearling data sets. SNOWDEPTH1YA was included in the 3rd-ranked model for the yearling data set, although the standard error of its parameter estimate overlapped zero. Thus, it is possible that only rainfall from the previous winter influenced fetus production. Alternatively, given that our sample size for yearlings was small relative to our sample size for adults, we may have been unable to detect the effects of snow depth from the previous winter in the top-ranked models for the yearling data set.

**Variation in fetal sex ratio.**—Hosmer and Lemeshow goodness of fit tests indicated that the global model fit the data and that all 7 variables warranted further consideration with an AIC model selection strategy ( $P = 0.49$ ). There were 3 models for explaining fetal sex ratio variation with  $\Delta_i < 2$  (Table 2). The top model had a 56% probability of being the best model given the model and data set ( $P = 0.010$ ; Table 2). It contained the variables SNOWDEPTH and FETUS ( $\beta_0$ :  $0.04905 \pm 0.1870 SE$ ,  $\beta_{\text{SNOWDEPTH}}$ :  $-0.0009 \pm 0.0038 SE$ ,  $\beta_{\text{FETUS}}$ :  $-0.0974 \pm 0.1841 SE$ ). The odds that a female would carry a male fetus after exposure to 500 cm versus 0 cm snow depth during the current winter were 0.62 (95% CI: 0.43–0.91;

Table 3). The odds of an adult female producing a male fetus decreased steadily over the range of snow depth values analyzed for this variable (Fig. 1). The overlap of standard errors of the parameter estimates of FETUS with zero indicate that the number of fetuses likely had little effect on the probability of producing a male. Other variables included within the set of 3 best models were RAINFALL and SNOWDEPTH1YA (Table 2). Given that 95% CIs for parameter estimates for these variables always overlapped zero and *P*-values based upon the permutation tests for these models were not significant, these factors likely had little, if any, effect on fetal sex ratio. In contrast, standard errors and parameter estimates of SNOWDEPTH were consistent among models in which this variable occurred and 95% CIs never overlapped zero, suggesting that this variable did influence the sex of offspring produced.

## DISCUSSION

The severity of the winter before gestation, but not the winter during which gestation took place, impacted the probability that both yearling and adult females would produce a fetus, with females tending to forego reproduction after winters that were more severe than average. There was no evidence that the winter during which a yearling was gestated affected the probability that it would produce a fetus as a yearling. Finally, as the winter during which gestation occurred became more severe, the probability of an adult female carrying a male fetus decreased.

One possible explanation for failed reproduction is that long, severe winters may make it difficult for individuals that lactate well into the summer to acquire sufficient energy reserves to gestate a fetus during the following winter (Clutton-Brock et al. 1989). Possible support for this hypothesis has been found in red deer (*Cervus elaphus*—Clutton-Brock et al. 1989). In this species, barren females and females that lost their calves shortly after birth (thereby avoiding the costs of lactation) almost invariably reproduced successfully in the following year, regardless of weather severity. Further, their offspring were heavier than those of females that either lost a calf late in the lactation period or successfully weaned a calf. Thus, foregoing reproduction after a severe winter may increase the probability of producing and weaning offspring in good body condition during the subsequent year.

Previous studies have documented lagged effects of winter weather conditions on reproduction by ungulates (Post and Stenseth 1998, 1999). These findings have sometimes been interpreted as support for the hypothesis that there are cumulative multiyear effects of severe winters (Post and Stenseth 1998, 1999) and such cumulative effects have been reported for white-tailed deer (Mech et al. 1987), including the population examined here (Patterson and Power 2002). The suggested mechanism by which multiyear effects occur is an inability of individuals to fully replenish energy reserves after particularly severe winters, leading to a carryover effect of poor body condition over multiple winters. In each case where cumulative effects have been reported, they only became

measurable after 2- or 3-year periods (Mech et al. 1987; Patterson and Power 2002). We found no evidence of multiyear cumulative effects of winter weather on body condition in our study population (Garroway and Broders 2005). Based upon our findings here we speculate that 1-year delayed effects of severe winters may better explain previous findings in this and perhaps other populations.

Both male- and female-biased sex-ratio adjustment has been reported for white-tailed deer (Burke and Birch 1995; Degayner and Jordan 1987; Verme 1981), leading to suggestions that both local resource competition (Clark 1978) and the Trivers–Willard hypothesis (Trivers and Willard 1973) contribute to observed biases in offspring sex ratios. Our findings of a small but consistent negative effect of increasing severity of the current winter on the probability of producing a male fetus may be consistent with the Trivers–Willard (1973) hypothesis. Verme (1989) reported that within all sex combinations of twins, sons were heavier at birth and as yearlings than daughters, which suggests that the cost of producing males is higher than the cost of producing females. DeYoung et al. (2006) showed that in captive white-tailed deer, the majority of offspring are sired by dominant males, demonstrating reproductive skew. This suggests that females in poor condition may benefit by producing less costly but reproductively more predictable daughters rather than undersized, energetically costly sons that are unlikely to attain social dominance and are thus unlikely to sire many offspring.

Because the probability of producing a male fetus varied with weather conditions of the current year, it is also possible that the observed sex ratio adjustment occurs independently of maternal control. Post et al. (1999) termed this the “extrinsic modification hypothesis.” According to this argument, biased sex ratios may occur when harsh environmental conditions deplete maternal resources, leading to higher fetal mortality rates associated with producing the more energetically expensive sex. The extrinsic modification hypothesis does not necessarily exclude intrinsic hypotheses such as that of Trivers and Willard (Forchhammer 2000). When environmental conditions are good, intrinsic factors may have important impacts on offspring sex ratios; as environmental conditions worsen, however, energetic stress may lead to birth sex ratio variations that are beyond maternal control (Forchhammer 2000).

The variable outcomes of sex ratio adjustment studies coupled with the lack of understanding of the physiological mechanisms controlling offspring sex have led to controversy over the existence of a relationship between maternal condition and offspring sex ratio (Festa-Bianchet 1996; Hewison and Gaillard 1999). Festa-Bianchet (1996) suggested that, given the large number and generally a posteriori nature of studies of sex ratio adjustment, a relatively high rate of occurrence of type I errors could account for a significant proportion of accounts of this phenomenon, particularly if studies that find deviations from 1:1 offspring sex ratios are more likely to be published. At the same time, a lack of understanding of the mechanisms underlying sex ratio adjustment may contribute to apparently conflicting results (Forchhammer 2000). DeYoung et al. (2004) found no evidence of Y-chromosome biased

ejaculate in white-tailed deer, suggesting that sex ratio biases are not facilitated by males. However, the time of conception has been shown to have an important impact on offspring sex in reindeer (*Rangifer tarandus*), with females that conceived during their 2nd estrous cycle of the rutting season producing more daughters than females that conceived during their 1st cycle (Holand et al. 2006). Although we cannot address the mechanism by which sex of the offspring varies in white-tailed deer, our findings, like those of Burke and Birch (1995), suggest a positive relationship between maternal condition and the probability of producing a male for white-tailed deer.

Our study presents evidence that the reproductive ecology of white-tailed deer varies, possibly adaptively, in relation to variation in winter weather. Winter weather during the year a female gestated had no effect on the probability of adults or yearlings producing a fetus, although adult females were less likely to reproduce during the year after a severe winter. We suspect that, after a severe winter, foregoing reproduction for a year may increase the likelihood of successfully reproducing in the following year (Clutton-Brock et al. 1989). Further, during severe winters, adult females may divert resources toward producing female offspring because daughters are less energetically expensive to produce and will likely contribute more to future generations than uncompetitive sons.

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