TEMPORAL VARIATION IN SEX ALLOCATION OF WHITE-TAILED DEER

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ABSTRACT

For several decades the Trivers-Willard hypothesis has been at the forefront of debates concerning differential investment of females into offspring sex. The main consistency in these debates has been the focus on how female condition influences offspring sex: very few studies have deviated from this line of investigation. We hypothesized that factors other than female condition may influence offspring sex and investigated how conception date influences offspring sex using white-tailed deer (*Odocoileus virginianus* Zimmerman) as a model. We found that during the first half of the breeding season (prior to 22 Jan) more males were conceived, while more females were conceived during the second half of the breeding season (after 22 Jan). We suggest that time available for development of offspring during their first year is an important factor in determining offspring sex. Offspring born early during the conception period have more time available for development relative to their late-born counterparts, and thus have greater potential for large body size and dominance later in life, important factors in the reproductive success of males. As a result, females conceiving early will maximize fitness by producing male offspring who will have more opportunity for growth prior to their first winter. Females conceiving later should invest in daughters because daughters have less variability in lifetime fitness and greater probability of achieving some measurable reproductive success; late-born sons will be at a competitive disadvantage when breeding. We hypothesize that in species where competition for mates is high and lifetime reproductive success of the sex competing for mates varies considerably, that females who conceive early will maximize fitness by investing in the sex that competes for access to mates.

INTRODUCTION

Since Trivers and Willard (1973) published their hypothesis concerning individual variation in investment of sons and daughters, considerable attention has been directed towards understanding what factors drive this differential investment in ungulates. If a female has the ability to choose a reproductive strategy that maximizes future fitness, the framework for such a strategy must balance risk and reward, where both risk and reward are measured in production of grandchildren. Trivers and Willard (1973) suggested that females in poor condition should invest in daughters because female offspring require less parental investment, and female offspring raised by poor mothers will reproduce whereas male offspring likely will not. This hypothesis has been found to hold true for a variety of ungulate species (Clutton-Brock et al., 1984; Rutberg, 1986; Kojola and Eloranta, 1989; Kucera, 1991), yet in some studies (Verme, 1983; Skogland, 1986; Hewison and Gaillard, 1996) the opposite has been found: females in good condition produce more daughters than sons. The local resource competition hypothesis (Clark, 1978; Silk, 1983) suggests that these alternative findings are due to competition for resources rather than maternal condition. Females in good condition should invest more heavily in the sex that does not disperse (females), while those in poor condition should invest more heavily in the dispersing sex (males) to reduce future competition.

These opposing theories have led to some confusion regarding the mechanism underlying variation in secondary sex ratios of ungulates. We will show that until now, a powerful yet simple hypothesis for influencing secondary sex ratios has been mostly overlooked as an alternative or complementary factor in influencing offspring sex. Date of conception has the potential to explain considerable variation that can be found in patterns of offspring sex ratios in ungulates. Trivers and Willard (1973) based their hypothesis on the assumption that mothers in better condition should invest more in costly sons because these mothers would have increased resources available to produce successful sons (Hewison and Gaillard, 1999). Sons are more costly to produce than daughters because of greater rates of growth (Clutton-Brock et al., 1982; Wilkinson and van Aarde, 2001), and greater milk consumption (Clutton-Brock et al., 1982). Total resources available to a neonate during its first year, however, also depend on when it is born: individuals born early have more time available to accumulate resources before winter than individuals born later. Males born earlier may demonstrate greater body size (Green and Rothstein, 1993), antler development (Schmidt et al., 2001), and dominance (Green and Rothstein, 1993) throughout life than their later-born counterparts, ultimately leading to greater reproductive success (Clutton-Brock et al., 1979; Gibson and Guinness, 1980). In general, males conceived late in the breeding season may be at a competitive disadvantage, suggesting that females that conceive later should produce daughters. Our theory concerning the effects of conception date on offspring sex ratios differs from Trivers and Willard (1973) in that offspring sex is influenced by time available for development, rather than an individual female's ability to provide resources to her offspring.

In this study, we investigated the relationship between date of conception and offspring sex ratio in white-tailed deer (*Odocoileus virginianus* Zimmerman). Saalfeld et al. (2009) reported that female white-tailed deer in Michigan differentially invested in sons early in the breeding season, and produced more females as the breeding season progressed. We similarly hypothesized that there would be a greater proportion of male than female offspring born early during the breeding season, and there would be an increase in the proportion of female offspring born as the breeding season progressed in Alabama. White-tailed deer are a unique model to examine factors influencing secondary sex ratios of offspring; they have reproductive characteristics that meet assumptions of the Trivers-Willard model (Trivers and Willard, 1973; Hewison and Gaillard, 1999) and theoretically should display fetal sex ratios where females in good condition invest more heavily in sons. However, the preponderance of data with white-tailed deer suggest that females in good condition produce more daughters than sons (Verme, 1983; 1985), which lends credence to the local resource competition hypothesis.

MATERIALS AND METHODS

The data was analyzed on secondary sex ratios of female white-tailed deer ($n = 472$) collected during 1995-2002 by the Alabama Division of Wildlife and Freshwater Fisheries as part of their spring-summer reproductive surveys. Using firearms, the Division annually collected 100-200 female deer from management areas throughout the state of Alabama. Following collection, they examined fetuses and determined age (days) and sex according to Hamilton et al. (1985). Date of conception was determined by backdating from the date of collection. Collections took place during May and June, as the peak of breeding for Alabama deer normally occurs during January (Causey, 1990) with births in late summer (late July – early September). We subdivided fetuses for which we had determined age into 6 groups (prior to 7 Jan, 7 Jan – 15 Jan, 16 Jan – 21 Jan, 22 Jan – 27 Jan, 28 Jan – 5 Feb, and after 5 Feb) of comparable sample size ($n = 187$ to $n = 234$) based upon conception date. These 6 periods were selected only to make sample sizes within each period as close to equal as possible. We tested whether sex ratios differed from equality and compared sex ratios between sampling periods using a Pearson chi-square (Wilson and Hardy, 2002).

RESULTS

Table 1. Sex ratio of fetuses collected from female white-tailed deer during six periods of conception during the breeding season in Alabama, USA, during 1995-2002.

Conception period					
#	Start	End	# of males	# of females	% males
	------	6 Jan.	129	105	55.12
2	7 Jan.	15 Jan.	123	105	53.95
3	16 Jan.	21 Jan.	120	97	55.30
4	22 Jan.	27 Jan.	103	113	47.69
5	28 Jan.	5 Feb.	95	110	46.34
6	6 Feb.	------	100	87	53.48

Mean date of conception was 21 January ($n = 778$; SE = 0.594), and mean number of fetuses per gravid doe was 1.749 ($n = 780$; SE = 0.019). We detected a sex ratio for the entire study that was slightly skewed towards males (52.1%), but this did not differ from equality ($X^2 = 1.0913$; $P = 0.296$). Sex ratios for the six conception periods did not differ from equality ($P > 0.25$; Table 1), but we did detect differences in proportions of males when comparing periods. When comparing the sex ratio of the first 3 periods against that of the last 3 periods, we found that a greater proportion of males (54.79%; $X^2 = 4.28$; $P = 0.039$) were conceived during the first half of the breeding season than during the second half (49.01% males).

DISCUSSION

Our data support our original hypothesis that conception date influences sex ratio of offspring in white-tailed deer: females differentially invest (e.g., tend to produce males or females) in male and female offspring at different times during the breeding season based partly upon projected time available for postnatal development. More male deer were conceived in the first half of the breeding season, and more females were conceived later in the breeding season. Although this pattern has been documented in a few mammals, specifically elk (Kohlmann, 1999), red deer (Clutton-Brock et al., 1982) (*Cervus elaphus* Linnaeus), and some seal species (Coulson and Hickling, 1961; Stirling, 1971), only one study (Saalfeld et al. 2009) has noted the significance of this pattern relative to the theoretical framework of Trivers and Willard's (Trivers and Willard, 1973) hypothesis. Saalfeld et al. (2009) documented a pattern similar to what was found in this study, where females invested more heavily in male offspring early in the breeding, and increased investment in females later in the breeding season. White-tailed deer are a temperate species that experience poor food availability during winter throughout their range and a marked decline in growth after 14 weeks of age, followed by little or no growth during winter (Ullrey et al., 1967). As a result, females who conceive early during the breeding season maximize opportunity for growth of their offspring. Because body size of juvenile male deer at the end of the first year is associated positively with lifetime reproductive success (Suttie, 1983), females that conceive early will maximize fitness by producing sons. However, environmental constraints (e.g., poor food availability, cold temperatures, etc.) set a limit on how early successful birthing, and hence breeding, can begin. After the peak of the breeding season (22 Jan), females maximize fitness by producing daughters. In polygynous species, variation in fitness of daughters is less variable than that of sons: most females will reproduce as they do not compete for access to mates as do males (Clutton-Brock et al., 1982). As a result, females maximize fitness in late conceptions by producing daughters that are almost assured of successful reproduction, rather than males that may not be reproductively competitive because of inferiorities in dominance, body mass, and antler development.

Our proposed theory has some similarities to results that have been previously reported for opossums (*Didelphis virginiana* Kerr) and some avian species. Wright et al. (1995) found that female opossums produced a greater proportion of males in their first litter of the season and a greater proportion of females in their second litter. The first-cohort advantage hypothesis (Wright et al., 1995) suggests that male opossums born in the first litter (weaned in May) achieve greater reproductive success during their first breeding season because of greater body size than males born in second litters (weaned in August). Undoubtedly, the 3 months of additional time available for growth of first litter males should aid in physical development and allow for greater success when competing for females during their first breeding season. However, most large mammals differ in that there is only one cohort produced during each calendar year, and thus there is only one breeding period. As a result, female white-tailed deer must adjust their strategy for production of male and female offspring based upon timing of conception within a single breeding season, rather than between breeding seasons.

In some avian species, particularly raptors, seasonal shifts in sex ratios have been documented. Dijkstra et al. (1990) found that the sex ratio of European kestrel (*Falco tinnunculus* Linneaus) broods decreased as laying dates became later. Because male reproductive success is greater for those born early, early broods should be biased towards males to maximize fitness of the mother. Similar results have been reported for American kestrels (*Falco sparverius* Linneaus), where early in the breeding season, most sex-biased broods were biased towards males and the reverse was true later in the breeding season (Smallwood and Smallwood, 1998). However, data from several other raptor species have suggested that female offspring tend to predominate earlier in the breeding season and males later (Olsen and Cockburn, 1991; Zijlstra et al., 1992; Leroux and Bretagnolle, 1996). These discrepancies are explained by Daan et al. (1996), who suggested that in raptors, the influence of early birth date on male and female offspring differs by species. They state that the sex whose age at first breeding is most strongly correlated with an early birth date should predominate in early clutches.

Sex ratios near the end of the breeding season may depart from our proposed theory of

female investment. Rather than mothers continuing to invest in female offspring near the conclusion of the breeding season, our data suggest they once again produce more sons than daughters. As the breeding season comes to a close, females appear to follow a pattern similar to that predicted by the local resource competition hypothesis (Clark, 1978; Silk, 1983). Both late-born male and female offspring normally have lower probability of survival and successful reproduction than their earlier-born counterparts (Smith and Anderson, 1998; Keech et al., 2000). Therefore, at some point during the conception period it may be in the best interest of the mother to produce the dispersing sex (e.g., a son) because of fitness costs associated with producing a poor daughter that will compete for resources. Juveniles are challenged during their first 6 months of life with acquiring resources (e.g., nutrients) needed for both growth and energetic reserves for winter survival. Early-born ungulates have opportunity for growth prior to establishing energetic reserves, while late-born fawns must build energetic reserves during this period of growth. As a result, late-born offspring tend to have lower body mass during winter, which can result in reduced over-winter survival (Clutton-Brock et al., 1987; Takatsuki and Matsuura, 2000) or cause them to experience long-term deficiencies in body mass, antler development, and reproductive success (Green and Rothstein, 1993). Because both sons and daughters that are born extremely late will experience constraints on growth, survival, and reproduction, females should invest in the sex that will produce the greatest potential payoff in terms of grandchildren, but cost the least in terms of competition for resources for her, her past and future offspring, and her grandchildren. Because projected survival and expected lifetime reproductive success are below average for these late-born offspring (Clutton-Brock et al., 1987; Green and Rothstein, 1993; Takatsuki and Matsuura, 2000), it may be counterproductive to produce a poor daughter that will establish a sympatric home-range and compete for resources with the mother and other relatives. Late-born offspring, both male and female, that do breed will likely experience poor reproductive success relative to their counterparts, resulting in a low "payoff" to the mother in terms of grandchildren. As a result, it may be in the best interest of late-conceiving females to invest in male offspring that will disperse, which is similar to that proposed by the local resource competition hypothesis (Clark, 1978; Silk, 1983), and not compete for resources during times of food scarcity because costs of resource competition may outweigh benefits in terms of grandchildren when producing late-born daughters. Saalfeld et al. (2009) documented a similar pattern in white-tailed deer where investment in the dispersing gender increased during the end of the reproductive period.

The consideration of conception date as an explanatory variable in variation of offspring sex is a significant departure from the hypothesis of Trivers and Willard (1973). In species where there exists considerable difference in lifetime reproductive success between sexes, females who conceive early should invest in the sex that has the greatest variability in lifetime reproductive success. In most cases, these will be species in which one sex competes for access to mates. Normally, when mating success is highly variable within a sex, dominance, and hence body size and development of physical attributes will be important factors in determining success. Early-born individuals possess greater potential relative to late-born counterparts to maximize body size because of greater time available for development early in life. Of course, numerous factors influence lifetime fitness, including habitat quality, genetics, etc., and any projections of fitness assume that these factors are equal.

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