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Ejaculate investment in a promiscuous rodent, *Peromyscus maniculatus*: effects of population density and social role

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ABSTRACT

Questions: How does average male investment in ejaculates vary with changing population density (and thus with the risk of sperm competition) in a promiscuous species? Do individual male investment strategies vary with population density?

Data studied: Total testicular mass, somatic mass and annual population density for wild-caught male deer mice, *Peromyscus maniculatus*, collected by snap-trapping over a 23-year period in Algonquin Provincial Park, Ontario, Canada.

Search methods: We analysed the relation between mean testicular mass and mouse population densities across years. To investigate individual investment patterns, we compared the relation between total testicular mass and somatic mass among males for years differing in population density.

Conclusions: Average investment in the testes was positively correlated with annual population density. An individual's investment in testes depended on both the abundance of rival males and on relative body size, a trait associated with social rank.

Keywords: ejaculate investment, mating system, *Peromyscus maniculatus*, population density, sexual selection, sperm competition, testicular mass.

INTRODUCTION

Sperm competition is the post-copulatory competition between the ejaculates of rival males for the fertilization of a female's ova (Parker, 1970). This widespread phenomenon has influenced the evolution of a broad diversity of sexual behaviours, as well as anatomical and physiological traits (for reviews, see Smith, 1984; Birkhead and Møller, 1992, 1998). Sperm competition theory (Parker, 1990, 1998) predicts that when females mate with more than one male, and their ejaculates overlap temporally in the female's reproductive tract, selection will favour those male traits that improve the ability to secure paternity. Many interspecific comparative studies (e.g. Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986; Briskie, 1993; Hosken, 1997; Byrne *et al.*, 2002) have found that relative testis size is frequently positively correlated with the potential for sperm

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competition, supporting the hypothesis that there is an adaptive basis for variation in ejaculate investment.

In many species, the opportunity for promiscuity (and thus sperm competition) is closely related to the distribution of sexually mature individuals, which in turn is influenced by the dispersion of resources in the environment (Emlen and Oring, 1977; Davies and Lundberg, 1984; Ostfeld, 1990). Thus, spatial or temporal variation in ecological conditions may shape the probability [or 'risk' (Parker, 1998)] that a population's males experience sperm competition (Birkhead and Møller, 1992), and affect their reproductive tactics. For instance, a high local density of breeding adults can increase the opportunity for promiscuity due to a greater likelihood of interactions between the sexes (Emlen and Oring, 1977; Reynolds, 1996). This prediction has been supported by field studies that have found that the frequency of polyandry or extra-pair copulations and fertilizations is positively related to the local population density (Davies and Lundberg, 1984; Westneat and Sherman, 1997). As a result, the risk of sperm competition experienced by males may vary temporally, and selection should favour the evolution of males who can respond to cues in the social environment and adopt reproductive tactics that maximize fitness (Gage and Barnard, 1996).

Most attempts to investigate male responses to variation in the risk of sperm competition have been laboratory-based, and have involved experimentally placing males into social situations that differ in the probability of sperm competition (e.g. Gage and Baker, 1991; Gage and Barnard, 1996; Wedell and Cook, 1999; Hosken and Ward, 2001). Few studies have examined male responses to varying social situations in free-living populations, where individuals experience natural levels of variation in the risk of sperm competition (but see Ribble and Millar, 1992; Stockley and Purvis, 1993; Pitcher and Stutchbury, 1998).

The deer mouse, *Peromyscus maniculatus* (Rodentia; Muridae), is a good model species in which to study whether the response of males to changing socio-sexual conditions is adaptive with respect to the risk of sperm competition. Deer mice have a polygynous or promiscuous mating system (Wolff, 1989; Ribble and Millar, 1996) and lack many of the characteristic traits of monogamy [e.g. sexual monomorphism, small litter size, slow maturation, extensive paternal behaviour (Dewsbury, 1981a)]. Moreover, several ecological and social factors probably alter the actual intensity of their promiscuity (Wolff, 1989).

In deer mice, the activity patterns of mature males are closely tied to those of mature females (Metzgar, 1979), and males will maintain home ranges, at least in part, to obtain access to females in reproductive condition (Wolff, 1985; Ostfeld, 1990). The ability to access these females will often depend on the local population density, which normally varies from 1 to 25 individuals per hectare (Banfield, 1974). At high densities, socially dominant males are able to monopolize the home ranges of several females (Mihok, 1979; Wolff and Cicirello, 1990), simultaneously displacing subordinate males [who become transient, and have limited exposure to mature females (Mihok, 1979)]. When population densities are low, neighbouring females no longer occupy contiguous home ranges (Wolff, 1985), and males generally interact with fewer females (Mihok, 1979). Thus, in free-living populations of deer mice, the density of breeding individuals has the potential to dramatically influence the amount of intrasexual competition, and thus the risk of sperm competition, that is faced by males.

Studies of wild deer mouse populations have also provided indirect evidence that the local risk of sperm competition can be quite variable. Genetic parentage analyses have shown that between 10% and 43% of litters are sired by multiple males (Birdsall and Nash, 1973; Merrit and Wu, 1975; Ribble and Millar, 1996), and estimates of testis size also vary dramatically between populations (Kenagy and Trombulak, 1986; Ribble and Millar, 1992). Unfortunately, none of these studies report breeding population densities, so it is impossible to determine whether differences in the risk of sperm competition associated with population density contributed to any of this variation.

Evolutionarily stable strategy (ESS) modelling of sperm competition was used by Parker (1990) to predict how a male's investment in his ejaculate should facultatively change in response to the overall risk of sperm competition. In this model, males should increase their expenditure on sperm in direct proportion to the risk of sperm competition to prevent loss of paternity to rival males. We tested this prediction using data collected from adult males in a free-living population of *P. maniculatus* whose breeding season population density fluctuated almost five-fold over a 23-year period (Fig. 1), and thus has potentially experienced much variation in sperm competition risk.

METHODS

Study area and field methods

We used data obtained from a *P. maniculatus* population located in the vicinity of Lake Sasajewun, Algonquin Provincial Park, Ontario, Canada (48°30′N, 78°40′W) that was studied as part of a larger investigation of population dynamics in small mammals (Fryxell *et al.*, 1998). During May–September from 1965 to 1987, deer mice were collected during bi-monthly trapping sessions that usually spanned three to four consecutive nights. Trapping took place along trap-lines that consisted of 20–40 stations located at 10-m intervals in stands of hardwood forest dominated by sugar maple, *Acer saccharum*. At each station, either one or two snap-traps (Woodstream Museum Special or Victor Four-Ways traps) were deployed. Traps were baited with a mixture of rolled oats and peanut butter, and set before sunset. The following morning, traps were checked and dead mice were taken to the laboratory for measurement. Male mice were weighed to the nearest 0.1 g, dissected, and the length and width of the left testis measured to the nearest millimetre.

As snap-traps collected both mature and immature mice, it was necessary to differentiate between them, as only the former are relevant for this study of sperm competition. Sexually mature mice typically have testes more than 7 mm long (Jameson, 1953; Gram *et al.*, 1982), so we analysed data only from males that met this criterion. To ensure that we studied only males in full breeding condition, we restricted our analyses to mice collected on days of the year 165 through 215, corresponding to the peak breeding period of May and early June in this (J.B. Falls, personal communication) and other (Beer and MacLeod, 1966; Sadleir, 1974) deer mouse populations. Additionally, we used data only from years where at least 10 sexually mature males had been captured during the peak breeding period, to ensure that the calculated mean values would be reasonably accurate. In total, 124 mice from nine different years were used in the analyses (Fig. 1).

Estimates of ejaculate investment

Using the testis length (cm) and width (cm) of mature males, we employed Møller's (1991) corrected formula to calculate the combined mass (g) of both testes as $[2 \times 1.083\ \mathrm{g}^{-3} \times 1.33\pi \times$ (radius of testis width)$^2 \times$ radius of testis length], and used this measure (hereafter called 'testicular mass') as an index of energetic investment in ejaculates. It is generally accepted that sperm production capacity is correlated with the size of the testes, since the number of

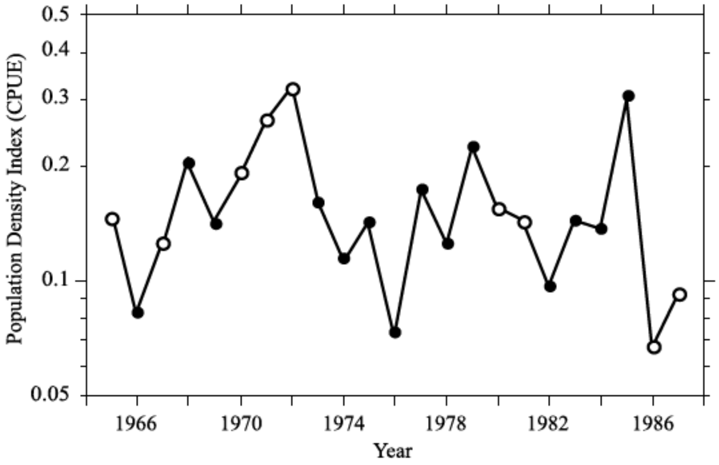

Fig. 1. Relative annual population density (catch per unit effort, CPUE) of *P. maniculatus* in the vicinity of Lake Sasajewun, Algonquin Provincial Park, Ontario, Canada during the period 1965 to 1987. Open circles indicate the years analysed in this study.

Sertoli cells, which facilitate spermatogenesis, determines the size of the mature testes (Amann, 1970; Møller, 1989; Lunstra *et al.*, 2003). We also used the regression formula of Ribble and Millar (1992), calculated from *P. maniculatus* data, to estimate testicular mass. The two estimates of testicular mass were strongly correlated ($r = 0.81$; $n = 124$, $P < 0.001$), but we used the data calculated from Møller's (1989) equation in all analyses, as it incorporates both length and width, and may thus be less subject to error.

Soma mass was calculated by subtracting testicular mass from body mass. Both testicular mass and soma mass data were log-transformed before analysis, a standard procedure for handling allometric data (Peters, 1983; Kenagy and Trombulak, 1986).

Population density estimates

To estimate local population density, mice were also live-trapped in close proximity (< 5 km) to the snap-trap lines. Using data on capture success and trapping effort during 1965–1987 from Appendix 1 of Fryxell *et al.* (1998), we calculated an index of the annual population density of deer mice in the study area as catch per unit effort (CPUE), which we log-transformed to normalize residuals (Fig. 1).

Statistical analyses

We tested our prediction that males would invest more heavily in ejaculates, as their risk of sperm competition increased, by calculating the regression of annual mean testicular mass on CPUE, both log-transformed. Annual means were used instead of individual values, since mice collected in the same year may not be independent. Time series analyses of annual means of log-transformed somatic mass, testicular mass and CPUE were implemented in JMP (SAS Institute Inc., 2002). Since none of the autocorrelation coefficients derived in these analyses were statistically significant (all $P > 0.05$), annual means were treated as statistically independent.

We calculated the slopes of reduced major axis (RMA) regressions since both the *x* and *y* variables are assumed to have natural variability (McArdle, 1988). We calculated jackknifed estimates (10,000 iterations) of slopes and their standard errors using RMA software (Bohonak, 2004). Slopes were compared using Tukey's HSD test (Zar, 1999).

RESULTS

Does population density affect average male ejaculate investment?

For sexually mature males at the peak of the breeding season, there was a significant positive correlation between mean testicular mass and mean population density (CPUE) across years ($r = 0.74$, $n = 9$, $P = 0.02$). Between low and high population densities at this site, there was a two-fold increase in ejaculate investment (Fig. 2). Since there was no significant correlation between testicular mass and somatic mass ($r = 0.14$, $n = 9$, $P = 0.70$; both variables log-transformed), we did not need to make any adjustments for size scaling in this analysis. Somatic mass was not significantly correlated with annual population density ($r = -0.22$, $n = 9$, $P = 0.55$; both variables log-transformed), suggesting that differences in mean testicular masses were not due to changes in body size associated with population density.

How does ejaculate investment by different-sized males respond to population density?

Having established that mean testicular mass was positively correlated with CPUE, our index of annual population density, we then examined the relative investment in ejaculates

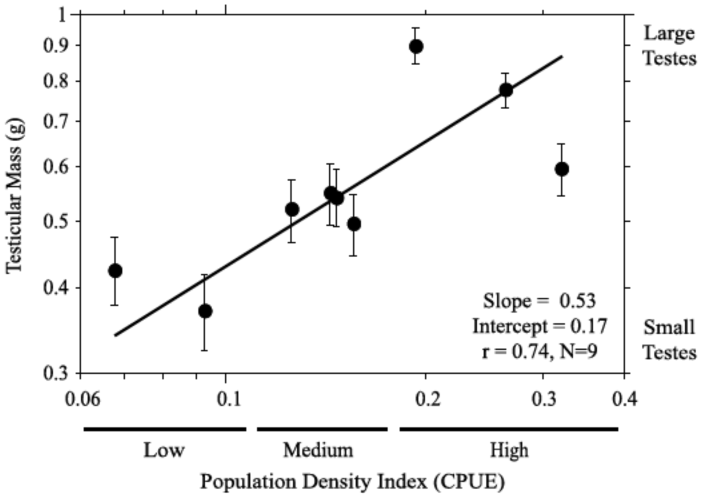

Fig. 2. Relation between mean testicular mass (± standard error) and population density (catch per unit effort, CPUE) in mature male *P. maniculatus*, both plotted on log scales. Reduced major axis regression line and statistics are shown. In subsequent analyses of testicular mass, the data were grouped according to whether they were collected in years of 'high', 'medium' or 'low' population density as indicated below the graph.

by males within years at different annual mean population densities. To do this, we categorized years as having a 'high', 'medium' or 'low' mouse population density, such that each category contained a roughly equal number of years (see Fig. 2), and then performed an analysis of covariance on testicular mass, with somatic mass and population density category as predictor variables. This analysis revealed a significant interaction between the two predictors (Table 1). Thus, the relation between testicular mass and somatic mass varied significantly between population density categories.

We then examined the relation between testicular mass and somatic mass for groups of individual adult males that were collected in years with different population densities (Fig. 3). Consistent with the results of analysis of covariance (Table 1), the regression between testicular mass and somatic mass varied with population density category. In addition, relative testicular mass, expressed as a percentage of total body mass, was significantly larger at high density (3.96%) than at low density (1.95%; *t*-test, $t_{72} = 6.4$, $P < 0.0001$; Table 2). Moreover, at high densities, there was a negative correlation between testicular mass and soma mass (Fig. 3a), while at low densities there was a strong positive correlation (Fig. 3c). Males collected at medium population densities exhibited an intermediate, positive correlation between their testicular and somatic masses (Fig. 3b). The slopes of the RMA regressions from all three population density categories were significantly different from 0 (all $|t\text{-statistics}| > 4.99$, all $P < 0.05$, randomization tests). Furthermore, the slopes of both the 'high' and 'low', but not the 'medium', population density regressions were significantly different from isometry (i.e. slope = 1), but in opposite directions.

DISCUSSION

Does population density affect average male ejaculate investment?

In the *P. maniculatus* population that we studied, the average mass of a male's testes during the peak of the breeding season was positively correlated with the local population density (Fig. 2). This is consistent with Parker's (1990) prediction that males should invest more resources in their ejaculates as the risk of sperm competition rises. Since sperm production is often a direct function of the size of the testes (e.g. Hoditscheck and Best, 1983), building larger sperm-producing organs should enhance a male's ability to transfer large numbers of sperm during copulation, and ultimately secure more paternity following post-copulatory competition between ejaculates (Parker, 1998).

In a comparative study of testis size in northern populations of *P. maniculatus*, Ribble and Millar (1992) found considerable variation in both body and testis length, some of which was attributed to differences in the length of the breeding season from site to site. They

Table 1. Results of analysis of covariance comparing the testicular mass of mature *P. maniculatus* males collected at high, medium and low population densities ($F_{5,123} = 18.8$, $P < 0.001$, $R^2 = 0.44$)

Source of variation	SS	d.f.	*F*	*P*
Somatic mass (g)	0.01	1,123	0.78	0.38
Population density category	0.60	2,123	19.0	<0.001
Somatic mass × population density category	0.18	2,123	5.7	0.004

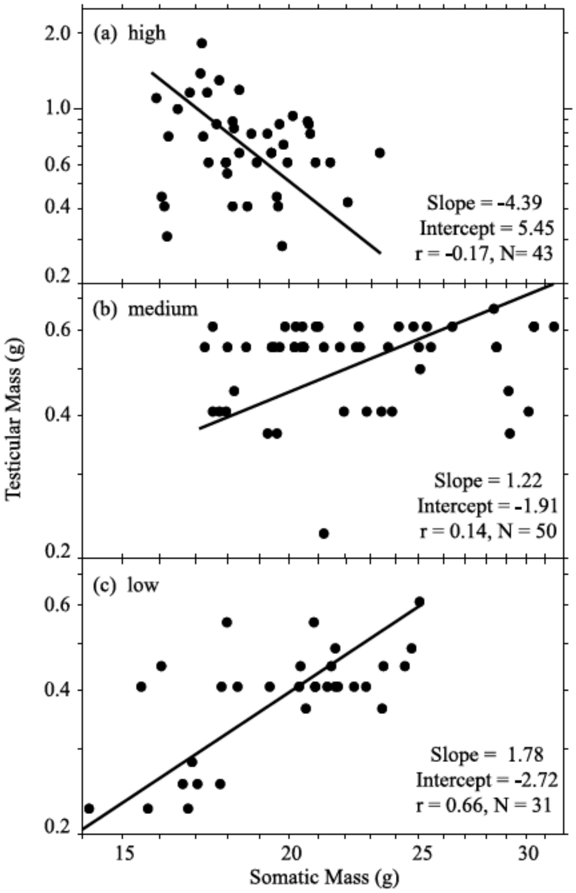

Fig. 3. Testicular mass in relation to somatic mass in mature *P. maniculatus* males collected in years with (a) high, (b) medium and (c) low population density. Reduced major axis regression lines and statistics are shown. Both testicular mass and somatic mass are plotted on log scales.

Table 2. Summary statistics (mean, standard error) for testicular mass, somatic mass and the slopes (and standard error) of reduced major axis (RMA) regressions of log testes mass on log somatic mass, for mature *P. maniculatus* males collected at three different population densities

Population density category	*n*	Testicular mass (g)	Somatic mass (g)	RMA slope
High	43	0.76, 0.03^a	18.6, 0.47^a	–4.39, 0.67^a
Medium	50	0.53, 0.03^b	22.6, 0.44^b	1.21, 0.24^b
Low	31	0.40, 0.04^c	19.9, 0.56^a	1.78, 0.20^b

Note: Values that share a letter within columns are not significantly different from each other according to Tukey's HSD test.

suggested that, in those regions with long breeding seasons, offspring born in the early spring could have enough time to mature and enter the breeding population, increasing both the local density of receptive females and the number of males competing for mates.

As a result, males would face a greater risk of sperm competition in populations located in warmer regions compared with those in colder regions (Ribble and Millar, 1992). The results of our study are consistent with this hypothesis that intraspecific variation in testicular mass is associated with differences in the likelihood of sperm competition. When population density was high (increased risk of sperm competition), males had testes that were, on average, twice as large as those of males trapped at relatively low density.

An alternative interpretation of the observed pattern of testes investment is that males are responding to some factor other than risk of sperm competition, such as food availability that covaries with population density. Thus, males might produce large testes only if there is ample food available. Although we do not have data on annual food availability, the non-significant negative relation between somatic mass and population density suggests that, if anything, mice were slightly larger in low-density years. Additionally, our interpretation has focused mainly on potential gains in sperm production associated with larger testicular mass, while there may be other testicular products, such as testosterone, whose production is also correlated with organ size (e.g. Schulte-Hostedde *et al.*, 2003; but see Joyce *et al.*, 1993, for an exception). Although we cannot address these potential covariates with the data available, the relationship between testis size, hormone levels and sperm production at different population densities presents an interesting subject for future research.

How does ejaculate investment by different-sized males respond to population density?

In this study, we make the assumption that male social dominance rank in *P. maniculatus* is positively correlated with somatic mass. Dominance ranks in male deer mice are rapidly established through antagonistic encounters, and remain stable over time (Dewsbury, 1981b). In laboratory-reared deer mice, heavier males are typically dominant over lighter males in intrasexual aggressive interactions, and dominant males are approached more frequently by females, and complete more mounts, intromissions and ejaculations with females than do subdominant males (Dewsbury, 1979). Ultimately, dominant males are able to ‘secure privileged, though not exclusive, access to females’ (Dewsbury, 1981b, p. 890). Based on these observations, it appears that somatic mass is a reasonable index of social dominance, and can be used to study whether ejaculate investment strategies of males of different social rank vary with population density.

The results of our analyses on the relation between ejaculate investment and sperm competition risk (Fig. 3) are in accord with Parker’s (1990) ESS predictions for a ‘loaded raffle’ fertilization system, wherein some males (in this case, large, dominant ones) are favoured over others (i.e. small males) with respect to sperm competition. The negative correlation between testicular mass and somatic mass among individuals at high population density (Fig. 3a) indicates that smaller males invest relatively more in their ejaculates than do larger (presumably higher-ranked) males. When population densities were low, testicular mass scaled positively with somatic mass (Figs. 3b and 3c). The differences in the relation between investment in ejaculates by males of different sizes collected in years with different population densities presumably reflects how male reproductive tactics are influenced by relative access to females. In the wild, subordinate males typically have little contact with mature females at high population density (Mihok, 1979), and are predicted to invest more in ejaculates (Parker, 1990) to maximize the impact of their limited mating opportunities. Conversely, at low population density when access to females is more evenly distributed across males, dominance rank becomes less important, and subordinate males are not predicted to invest heavily in their ejaculates (Parker, 1990). When females are distantly spaced, the only way in which a male may enhance his individual reproductive success is through long, extra-territorial excursions to find other potential mates (Mihok, 1979; Wolff and Cicirello, 1990). It is notable that under low-density conditions, there was a positive allometric relationship between total testicular mass and somatic mass in our population (Fig. 3c), suggesting that larger males invested relatively more heavily in their ejaculates so that they could capitalize on these encounters with breeding females. Finally, if the sperm competition raffle had been 'fair' rather than 'loaded' (Parker, 1990), there should have been no difference in the relative ejaculate investment made by males of all sizes at different population densities. The results of our analyses do not support that hypothesis.

A previous interspecific analysis of the correlation between testis and soma sizes in mammals (Stockley and Purvis, 1993) found that small males in continuous-breeding species (i.e. those with high risk of sperm competition) had disproportionately larger testes than did seasonally breeding species (with lower risk of sperm competition), where their testicular and somatic masses were positively correlated. Our results are consistent with these findings, as we observed that the relative investment in ejaculates by males of different sizes varied with the local risk of sperm competition (Fig. 3).

Since the production of ejaculates is a non-trivial expense for *P. maniculatus* males (Dewsbury, 1982), we would expect that the costs of increased investment in the testes would be offset by the gains made in sperm competition contests. Dewsbury (1979, 1981b) observed that large (dominant) males often achieved a greater number of ejaculations with females than did small (subordinate) males. Despite this apparent difference in reproductive success, dominant males did not father a greater proportion of their mate's litters than did the subordinate males in some experiments (Table 2 in Dewsbury, 1979). Our findings suggest an explanation based in sperm competition theory: smaller males, with larger testes, are able to offset their copulatory disadvantage through a greater numerical representation of sperm in the female's reproductive tract. Based on the regression for the high population density category (Fig. 3a), a small male (17.0 g) would have had testes that were 2.4 times larger than a male that is much heavier (21.0 g). If the daily sperm production rate per gram of parenchyma for *P. maniculatus* is similar to that of *Rattus norvegicus* (see Møller, 1989), the smaller male's testes will produce 14.2×10^6 more sperm per day than those of the larger male. Under high-density social conditions, this additional sperm production capacity may allow small males to compete effectively with larger, dominant males for paternity.

Our research highlights some important issues that should be considered when undertaking future intra- and interspecific studies of sperm competition. It is common practice in interspecific studies to use a mean value of testis mass for each species (e.g. Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986). As we have shown, the ejaculate investment by *P. maniculatus* males depends on both population density and body size and cannot be readily characterized by the species' mean value. If the calculation of mean testis mass is based on solitary studies, or on those with limited sampling, this could obviously lead to inaccurate estimates, and incorrect conclusions. Similarly, intraspecific studies may misconstrue the risk of sperm competition within a population. It was only through the extended temporal scale of this study that we were able to show that risk from sperm competition is not constant from year to year. Care should be used when combining data obtained from individuals collected from different populations and times.

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