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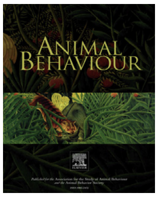

Size-dependent ejaculation strategies and reproductive success in the yellow dung fly, *Scathophaga stercoraria*

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Theory predicts that sperm competition will favour the production of larger ejaculates. However, because the benefits of greater reproductive investment are balanced by the costs of spermatogenesis, expenditure should depend on male physiology, mating rate and the relationship between additional investment and fertilization gains. In the yellow dung fly, *Scathophaga stercoraria*, males adopt size-dependent alternative mating tactics that are associated with discrete ecological resources (foraging and oviposition substrates), although males switch between these environments throughout their lives. By copulating on foraging substrate (fruit or flowers), males can bypass intense mate competition that occurs at oviposition sites (cow dung), but as a consequence, must occupy a disfavoured mating role (i.e. face a greater risk that their ejaculate will be displaced from storage prior to fertilization). Small males often mate on foraging substrate, whereas large males mate in this environment only during feeding bouts. Optimal ejaculate expenditure should therefore depend on male size and their current mating role. By measuring copula duration (i.e. ejaculate expenditure) of natural matings and assigning paternity to resulting offspring, we confirmed that copulations on dung sire approximately three times as many offspring as those on foraging substrate. Furthermore, large males reduced copula duration on fruit, as predicted, since this strategy enables greater investment into high-payoff matings on dung. Conversely, small males copulated for shorter durations on dung than on foraging substrate, perhaps to minimize the risk of being displaced from copula by a rival. These patterns of ejaculate expenditure translated into greater offspring production for large males on dung and for small males on fruit. We discuss the possible proximate factors driving these size- and context-dependent patterns of ejaculate allocation by yellow dung fly males. Together, our findings shed light on the allocation strategies and reproductive consequences of alternative mating tactics.

Postcopulatory sexual selection arises due to the co-occurrence of unrelated sperm within the female reproductive tract and is common in insects due to widespread polyandry and long-term sperm storage (Birkhead & Møller, 1993; Eberhard, 1996; Neubaum & Wolfner, 1999; Parker, 1970a; Simmons, 2001; Thornhill & Alcock, 1983). Theory predicts that such selection should drive the evolution of larger ejaculates that more effectively dilute or displace sperm from previous matings (Parker, 1982, 1990, 1993; Parker & Begon, 1993; Parker, Immler, Pitnick, & Birkhead, 2010), and numerous comparative and experimental studies have supported this expectation across taxa (Gage, 1994; Harcourt, Harvey, Larson, & Short, 1981; Hosken & Ward, 2001; Immler et al., 2011; Manier et al., 2010; Pitnick, Miller, Reagan, & Holland, 2001; Stockley, Gage, Parker, & Møller, 1997). Increasing investment in spermatogenesis, however, comes with energetic costs that require males to extend foraging and development time (Ferkau & Fischer, 2006; Pitnick, Markow, & Spicer, 1995; Pitnick & Miller, 2000), decrease mating rate (Dewsbury, 1982) and/or divert resources from other critical physiological processes (e.g. growth, immunity) to compensate (Parker & Pizzari, 2010; Scharf, Peter, & Martin, 2013; Simmons, 2011). Selection should therefore favour life-history strategies that efficiently allocate resources and maximize lifetime reproductive success across naturally variable environmental conditions (e.g. risk of sperm competition, pathogen abundance, food availability).

Species in which males adopt status-dependent alternative mating tactics present a unique opportunity to study how different life-history demands shape resource allocation strategies.

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Dominant males generally compete with one another and defend females, which in turn favours the production of exaggerated weaponry or body size (Oliveira, Taborsky, & Brockmann, 2008; Shuster & Wade, 2003). In contrast, subordinate males bypass precopulatory mate competition and, as a consequence, are forced into disfavoured mating roles with reduced fertilization success per mating. For example, in sneak–guard mating systems, guard males only face sperm competition when sneak males successfully infiltrate their territories, whereas sneak males encounter sperm competition from guards in essentially all matings. This tactic-specific variation in pre- and postcopulatory sexual selection intensity has driven divergent selection on male phenotype and resulted in male dimorphism (or trimorphism) in some species, where each phenotype is specifically associated with a mating tactic (e.g. small, weaponless males sneak and large males with weaponry guard; intermediate phenotypes are rare or absent) (e.g. Eberhard & Gutierrez, 1991; Kelly, 2005; Simmons, Emlen, & Tomkins, 2007). Under these conditions, subordinate males generally divert resources from growth or the development of secondary sexual traits and instead disproportionately invest in testis size, which allows the production of larger, more competitive ejaculates that help compensate for their mating roles (Gage, Stockley, & Parker, 1995; Simmons & Emlen, 2006; Simmons, Tomkins, & Hunt, 1999). This pattern of resource allocation is observed even when subordinate male mating rates are low (Neff, Fu, & Gross, 2003). In contrast, little is known about resource allocation strategies in species where male behavioural tactics or the associated mating roles facultatively change throughout an individual's life (e.g. in response to male physiological condition or fluctuations in the local intensity of male–male competition), as is expected when male body size (or status) exhibits continuous variation (Taborsky, 1994, 1998; Waltz & Wolf, 1984). In this scenario, males may instead alter reproductive investment in a context-dependent manner based on their current mating role or physiological state (Bonduriansky, 2001; Lüpold, Manier, Ala-Honkola, Belote, & Pitnick, 2011; Nicholls, Burke, & Birkhead, 2001; Wedell & Cook, 1999; Wedell, Gage, & Parker, 2002). However, allocation strategies and their reproductive consequences in such mating systems remain poorly understood.

STUDY SYSTEM

In the yellow dung fly, *Scathophaga stercoraria*, males express size-dependent alternative mating tactics, as well as continuous variation in body size (i.e. status), and their mating roles are known to change over time (Gress et al., 2016, 2014; Pitnick et al., 2009). For instance, 'competitor' males aggregate on fresh cow dung (i.e. the oviposition and larval substrate) where they engage in intense competition to mate with females arriving to lay their clutch of eggs (Hammer & Volsoe, 1941; Parker, 1970d). Larger body size better enables competitor males to defend their mates from 'take-overs' by rival males during protracted copulations (approximately 40 min) and the subsequent oviposition phase (Borgia, 1980, 1981; Ding & Blanckenhorn, 2002; Jann, Blanckenhorn, & Ward, 2000; Otronen, 1995; Sigurjónsdóttir & Snorrason, 1995). Because of sperm displacement and last-male sperm precedence, which have been well documented in *S. stercoraria*, successful matings on dung result in high fertilization success since copula occurs just prior to oviposition (Parker, 1970b; Simmons, Parker, & Stockley, 1999, 1996). However, competitors also mate opportunistically with nongravid females between oviposition bouts at off-pasture feeding sites (e.g. flowers or rotting fruit; Gress et al., 2014, 2016; Parker, 1970e, 1971; Pitnick et al., 2009). Using a marginal value theorem approach, Parker (1992) found that competitors should reduce ejaculate expenditure under these conditions to conserve resources for later matings on dung, where fertilization success per sperm ejaculated is expected to be higher. Such a reduction in ejaculate size (i.e. sperm number) can be achieved by simply shortening copula duration, since sperm transfer rate is constant throughout mating in *S. stercoraria* (Parker, Simmons, & Kirk, 1990).

In contrast, most small males avoid dung when male–male competition is intense. These 'patroller' males specialize in searching for females at off-pasture foraging sites where competition is low or absent (Gress et al., 2016, 2014; Pitnick et al., 2009). Parker (1992) predicted that patrollers would experience lower mating rates than competitor males based on the observation that feeding resources (and foraging females) are more dispersed in their distribution than dung pats. Based on this assumption, a second marginal value theorem model demonstrated that patrollers should respond by increasing their ejaculate expenditure per mating opportunity (i.e. longer copula duration) because additional investment into the current female would result in greater fertilization gains than leaving to search for a new mate (Parker, 1992). However, for small males, specifically, this assumption is inconsistent with recent evidence showing that these males are largely excluded from mating on dung but frequently copulate at some feedings sites, in part because females are relatively more abundant and preferentially mate with small males in this environment (Gress et al., 2014; Pitnick et al., 2009). Moreover, other recently documented differences between mating environments may further influence size- or tactic-specific copula duration, including (1) the risk of being aggressively 'taken over' by a rival during copula (Pitnick et al., 2009), (2) the status of female egg development, which influences both female attractiveness and resistance behaviour (Gress et al., 2014) and (3) physiological constraints on ejaculate production (e.g. large competitor males may only visit foraging sites when depleted of ejaculate resources, as suggested in Gress et al., 2014).

In light of these discoveries, we here quantify the relationship between male size and ejaculate expenditure in both mating environments. Additionally, using previously developed microsatellite markers, we assigned paternity to offspring produced from these matings to assess the impact of male size and mating environment on reproductive payoff.

METHODS

Size-dependent Ejaculate Expenditure and Fertilization Success Associated with Alternative Mating Roles

We collected male and female *S. stercoraria* of unknown age and mating history from off-pasture foraging sites located on the grounds of Toad Hollow Dairy Farm (Nedrow, NY, U.S.A.) throughout October and November 2013 and 2014. Foraging sites consisted of piles of apple pomace (approximately 2.5 × 1.5 × 1 m, L × W × H), which is the sugar-rich by-product of cider production and is readily available on many farms in the region given its use as livestock feed (Gress et al., 2016, 2014; Pitnick et al., 2009). The location of this substrate on the farm was approximately 20–100 m from the nearest herd of cows, depending on which pasture the cattle were grazing. Effort was made to collect males from across the full range of body sizes in approximately equal proportions. Within 60 min from the time of collection, each male was randomly paired with a female in a clear plastic vial and placed on the pomace substrate where they were allowed to copulate to completion (until genital separation occurred). After copulations ended, pairs were separated to prevent additional mating and transported back to the laboratory where males were frozen and females were housed individually in a vial with ad libitum access to sugar water and *Drosophila* (Blanckenhorn, Pemberton, Bussière,