

Soay rams target reproductive activity towards promiscuous females' optimal insemination period

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Female promiscuity is thought to have resulted in the evolution of male behaviours that confer advantages in the sperm competition that ensues. In mammalian species, males can gain a post-copulatory advantage in this sperm 'raffle' by inseminating females at the optimal time relative to ovulation, leading to the prediction that males should preferentially associate and copulate with females at these times. To the best of our knowledge, we provide the first high-resolution test of this prediction using feral Soay sheep, which have a mating system characterized by male competition for access to highly promiscuous females. We find that competitive males time their mate guarding (and hence copulations) to occur close to the optimal insemination period (OIP), when females are also increasingly likely to 'cooperate' with copulation attempts. Subordinate males practice an alternative mating tactic, where they break the integrity of the consort pair and force copulations on females. The timing of these forced copulations is also targeted towards the OIP. We thus provide quantitative evidence that female promiscuity has resulted in the evolution of reproductive strategies in which males 'load' the sperm raffle by targeting their mating activity towards female OIPs, when the probability of sperm-competition success is at its greatest.

Keywords: sperm competition; promiscuity; mate guarding; alternative mating tactic; Soay sheep

1. INTRODUCTION

Sperm competition, at its simplest, is assumed to operate as a 'raffle' (Parker 1982). However, it is commonly a 'loaded raffle' in which males can gain an advantage through, for example, post-copulatory female choice (Eberhard 1996), differences in the fertilizing capacities of ejaculates (Lanier *et al.* 1979) or sperm-precedence patterns (Parker 1970). While post-copulatory female choice and inherent fertility may be beyond male influence, males can have some control over the timing or order of their inseminations to improve their chances of siring offspring. It is the last male to copulate that usually sires most offspring in insects (Parker 1970; Simmons & Siva-Jothy 1998) and birds (Birkhead & Møller 1992). In mammals, however, sperm-precedence patterns are determined by the timing of insemination relative to ovulation (Ginsberg & Huck 1989). This is thought to be because mammalian sperm require up to several hours within the female reproductive tract to 'capacitate' (become biochemically active; Austin 1952) before being able to fertilize ova. Sperm within ejaculates vary in capacitation time and are short-lived once capacitated (Harrison 1996). Thus, a male that inseminates a female allowing time for peak capacitation of the ejaculate at the point of ovulation (i.e. within the 'optimal insemination period' (OIP)) will have a greater chance of siring than will males copulating either earlier or later in oestrus (Ginsberg & Huck (1989), but see Hunter (1995) for an alternative explanation for the greater sperm-competition success of optimally timed inseminations).

The significance of the OIP as a post-copulatory determinant of siring success in mammals has been widely

demonstrated in laboratory and agricultural studies. These studies show that males achieve greatly enhanced sperm-competition success by copulating only a few hours closer to the OIP than their competitors (e.g. rabbits, Miller *et al.* 1969; swine, Dziuk 1970; sheep, Jewell *et al.* 1986; hamsters, Huck *et al.* 1989; see also reviews by Ginsberg & Huck 1989; Gomendio & Roldan 1993; Dziuk 1996). However, evidence supporting the prediction that males will therefore compete for copulations with females at, or around, their OIP is scarce, and is limited to studies that examine male behaviour across the days of oestrus (e.g. Grubb 1974; Bercovitch 1986; Hogg 1988) or anecdotal evidence reported incidentally (e.g. Farentinos 1972; Packer & Pusey 1983; Milton 1985; Boinski 1987; but see Lisk *et al.* (1989) for an account of golden hamsters, *Mesocricetus auratus*, under semi-natural conditions). Thus, the potential influence of female OIPs on male reproductive behaviour remains largely unexplored.

We examine the promiscuous mating system of feral Soay sheep (*Ovis aries*) on St Kilda, Scotland, UK. The Soay sheep mating season is characterized by overt male contests for access to receptive females during their two-day oestrus, combined with periods of mate guarding (consorts) of variable duration (Grubb 1974). Males that are able to gain and monopolize access to oestrous females are of larger body size and have larger horns, which is likely to be the result of the importance of these attributes in intrasexual combat (Coltman *et al.* 1999; Preston 2001; Preston *et al.* 2001, 2003). Smaller males hold consorts infrequently, and instead practice an alternative mating tactic resembling 'coursing' behaviour in subordinate big-horn rams (*Ovis canadensis*) (Hogg 1984; Stevenson *et al.* 2003). Subordinate males, often lambs, satellite consort pairs, attempting to break the integrity of the consort. Once this is achieved, the female flees and subordinate rams attempt forced copulations while pursuing the female in a high-speed chase.

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Soay females will often experience rapid mate switching, having been recorded copulating with up to 10 different consort males within a single day of their oestrus (Preston 2001). Female acceptance of multiple mates, combined with the apparent success of forced copulations by subordinate rams (Pemberton *et al.* 1999), makes sperm competition a pervasive feature of this mating system. Soay sheep are thus an ideal model species for examining male behavioural strategies with respect to female OIPs. In this study, we use 4 years of behavioural data to test two predictions: (i) that males of higher competitive ability will preferentially associate with females at or around their OIP; and (ii) that subordinate males practising alternative mating tactics will target their forced copulation attempts at periods closer to female OIPs.

2. MATERIAL AND METHODS

(a) *Study site and population*

Feral Soay sheep are a primitive breed, which have resided within the St Kilda archipelago (57°49' N, 08°34' W) for over a millennium. A fluctuating number of between 600 and 2000 individuals range freely over the open terrain of Hirta (638 ha), the largest island in the group, and our study focuses on the relatively discrete population that inhabits the Village Bay area (175 ha) to the southeast of the island. Periodic population crashes result in a study population that oscillates between 200 and 600 individuals in size, and higher male mortality in these crashes leads to female-biased sex ratios (males : females) of between 0.27 and 0.7. Since 1985, *ca.* 95% of newborn lambs in the study area have been ear-tagged and are thus individually identifiable and of known age. Adults (2 years or over) comprise 39–66% of the study population, and adult sex ratios vary between 0.1 and 0.41. A detailed description of the study site and population can be found elsewhere (see Jewell *et al.* 1974).

(b) *Morphometric data and competitive ability*

Male horn and hind-leg lengths were measured between August and November of each year. Hind-leg lengths were measured from the tuberculis of the fibular tarsal bone to the distal end of the metatarsus, and are taken to be a linear indicator of skeletal or body size. Horn lengths were measured from the base, along the outer curvature of the spiral, to the tip. An index of 'competitive ability' was used in analyses to estimate a male's ability to compete successfully for access to receptive females. Competitive ability is predicted from male horn and hind-leg lengths measured in millimetres using the logistic regression equation $\text{logit}(y) = -13.78 + 0.00653x + 0.0494z$, where x is the horn length and z is the hind-leg length. This equation is parameterized by a generalized linear mixed model (GLMM) that investigated the phenotypic determinants of a male's ability to compete for access to, and copulations with, receptive females (Preston 2001; see also Preston *et al.* (2001) for use of this approach). Competitive ability increases with larger horn and body sizes, so we use 'large' and 'competitive' interchangeably. Competitive ability also reflects dominance standing, and correctly predicted the outcome of 71% of 54 dyadic dominance interactions between adults recorded in 1997–1999 (Preston 2001).

(c) *Behavioural observations*

A team of observers carried out focal watches on adult females during their 2 days of oestrus. Watches were performed during

daylight hours, beginning at the onset of the rut in November and continuing to the end of the rut in mid-December from 1996 to 1999. Females entering oestrus were identified by continual consort searches of the study area throughout each day; a consort was defined as a close spatial relationship between a male and a female (typically within 5 m), with frequent male courtship and defence of receptive females. Females were watched if they had not previously been seen in consort, and were thus likely to be at the onset of oestrus. We watched 55 females on their first day of oestrus, and observations continued for 32 of these through their second day of oestrus. The identities of consorting males, the times of consort initiation and termination, and the occurrence and timing of copulation attempts and chases involving the focal ewe were recorded. For consorts that had formed before the onset of focal watching, or continued after the watch had terminated, consort initiation or termination was estimated as the beginning or end of the watch, respectively. Copulation attempts were defined as mounts in which the male's forelegs made contact with the female's rump. From 1998, copulation attempts were categorized by their success or failure: a successful copulation was recorded when the ram's forelegs and chest made contact with the female's back and vigorous thrusting was observed; all other copulation attempts were deemed to have failed. Focal watches were terminated when females resisted all copulation attempts, and received only transient interest from males.

(d) *Data analysis*

Data were analysed using mixed-effects models in GENSTAT 5 (release 3.22), which control for the repeated measures of behaviour by fitting the identity of individuals as a random effect (GENSTAT 5 Committee 1993). Binary dependent variables were used to examine variance in the occurrence and success of consort males' copulation attempts and the occurrence of subordinates' forced copulation attempts. In these cases, GLMMs were implemented, and dependent variables were linearized using a logit-link function. A pool of explanatory variables was assessed in analyses aimed at determining the proximate mechanisms of variation in the competitive abilities of the males consorting with females, and female receptivity (see §§ 3a,b); in each analysis the minimal model was arrived at by a process of stepwise deletion (McCullagh & Nelder 1983), with significance being taken as $p < 0.05$. The exclusion probabilities reported were obtained by adding the previously deleted explanatory term to the minimal model. Year was tested as a categorical explanatory term in all models, but was excluded ($p > 0.12$).

Unless otherwise stated, our analyses were restricted to consorts involving adult males. For the analysis of alternative mating tactics, only chases that resulted from active harassment by subordinates were included; chases resulting from unwanted courtship by the consorting male were excluded. Sample sizes vary across the analyses, as life-history data were not available for all consort males.

Behavioural oestrus was defined as beginning at the first point at which a female did not try to evade the copulation attempts of a male. It is possible that females may have accepted copulations before the onset of focal watching in some cases; however, we do not believe that this would lead to any systematic bias in our analyses. We estimated the OIP to be 12 h after the onset of behavioural oestrus, as this is the midpoint of the 9–15 h OIP that has been demonstrated in a study of domestic sheep (Jewell *et al.* 1986), which is also consistent with the conclusions of earlier investigations (Slee 1964; Dziuk 1970). The minimum and

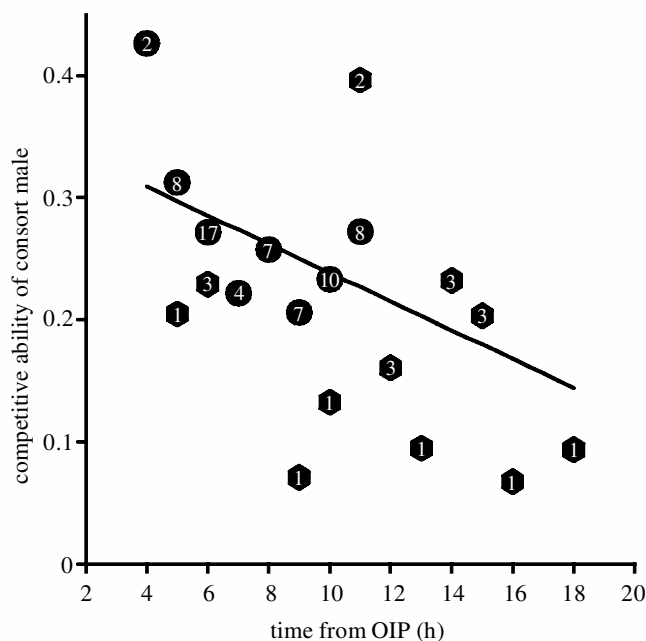


Figure 1. The competitive ability of guarding Soay rams as a function of time from the OIP. The fitted line is predicted from a linear mixed-effects model (see § 3a), regression equation: $y = 0.3549 - 0.0117x$. For illustrative purposes, the data are divided into consorts occurring on pre- (circles) and post- (hexagons) OIP days, and the mean competitive ability of consort males for each hour is plotted; the embedded numbers indicate the total number of observations grouped.

maximum times from the OIP for each mate-guarding period were used as explanatory terms when testing for an association between male competitive ability and the proximity to the OIP. For males holding consorts on the first day of oestrus (when females have yet to reach their OIP), the time of consort termination was taken as the minimum time from the OIP. On the second day of oestrus, at which point the OIP has passed, the time of consort initiation is taken as the minimum time from the OIP. For the maximum time from the OIP, the situation is reversed.

3. RESULTS

(a) Male competitive ability

The competitive abilities (as determined by horn and body sizes) of the different rams that were observed defending females varied widely during the period of oestrus. We tested a number of measures of progression through oestrus to examine which proximate factor best explained this variation. Our analysis revealed a strong and significant negative relationship between the competitive abilities of consorting males and the closest times to the OIP that males defended females (linear mixed-effects model examining the competitive abilities of consorting males versus the closest times to OIP: $n_{\text{consorts}} = 83$, $n_{\text{females}} = 44$, effect = 0.0117, s.e. = 0.004 02, Wald statistic (χ^2) = 8.48, d.f. = 1, $p = 0.004$, random effect (RE) = female identity; only males that attempted to copulate with consort females are included in the analysis; figure 1). Thus, larger rams held consorts with females at times closer to the OIP. The number of consort mate switches, day of oestrus (first or second day), time from oestrus

onset and time of day were also examined as possible factors influencing the size of males consorting with the focal ewe, but none was significant after controlling for the temporal proximity of consorts to the female's OIP ($p > 0.3$). This does not appear to be solely a consequence of competitive males being able to maintain consorts until the OIP, as larger males also tended to form consorts with females at times closer to the OIP, and to terminate them earlier once past the OIP (linear mixed-effects model examining the competitive abilities of consorting males versus the furthest times from OIP: $n_{\text{consorts}} = 83$, $n_{\text{females}} = 44$, effect = -0.008 28, s.e. = 0.004 34, Wald statistic $\chi^2 = 3.64$, d.f. = 1, $p = 0.054$, RE = female identity; only males that attempted to copulate are included). Although we present analyses of the times at which rams guarded females relative to the OIP, analyses of insemination times yield comparable results and levels of significance to those presented here (unpublished analysis).

(b) Female receptivity

Although competition between males appears to be of major importance in determining when in a female's oestrus males form consorts, females are able to reduce male success once in consort by resisting their attempts to copulate. Opportunistic observations of female responses to copulation attempts recorded in 1998 ($n_{\text{attempts}} = 130$) revealed that, out of 34% of copulation attempts that were clearly unsuccessful, an estimated 62% failed as a result of the female moving off as the ram mounted. Females also position themselves uphill from males, or beside boulders, resulting in further failed copulation attempts (B. T. Preston, personal observation). Female resistance to copulation attempts appeared to decrease with increasing proximity to the OIP, so augmenting the advantage to males mate guarding at, or near, the OIP (GLMM examining the relationship between the success of copulation attempts and proximity to the OIP: $n_{\text{attempts}} = 434$, $n_{\text{females}} = 30$, $n_{\text{males}} = 35$, effect = -3.708, s.e. = 1.641, Wald statistic $\chi^2 = 5.11$, d.f. = 1, $p = 0.024$, RE = female and male identity; figure 2). Day of oestrus is not associated with the success of copulation attempts when controlling for proximity to the OIP ($p > 0.2$). While males may have aborted some copulation attempts without female influence, time from the OIP also provided greater explanatory power than any correlated male attribute investigated (for competitive ability, horn length, body size and age all $p > 0.2$). Thus, the major source of variation in the success of copulation attempts appears to have been their timing relative to the OIP, rather than potential female choice for, or male competence resulting from, competitiveness, body size, horn size or experience.

(c) Mate-guarding durations and copulation probability

The longest consorts experienced by females on pre-OIP days (the first day of oestrus) were twice the length of those occurring post-OIP (second day of oestrus) (paired t -test on female's longest consort durations (regardless of consort male's age) pre- and post-OIP: $t_{(31)} = 5.37$, $p < 0.001$; figure 3). The shorter duration of consorts on post-OIP days was not solely the result of females leaving oestrus, or failing to attract males, as 72% of these females formed consorts with additional males

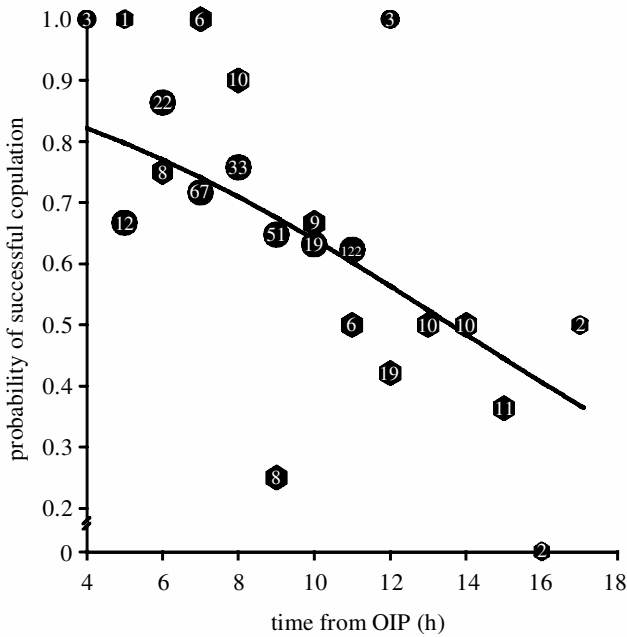


Figure 2. The probability that Soay rams would successfully copulate in relation to their proximity to the OIP. The fitted line is predicted from a GLMM (see § 3b), logistic regression equation: $\text{logit}(y) = 2.205 - 0.1545x$. For illustrative purposes, the data are divided into copulation attempts occurring on pre- (circles) and post- (hexagons) OIP days, and are grouped by hour. Embedded values indicate the number of observations grouped and small symbols are plotted where there are fewer than five observations.

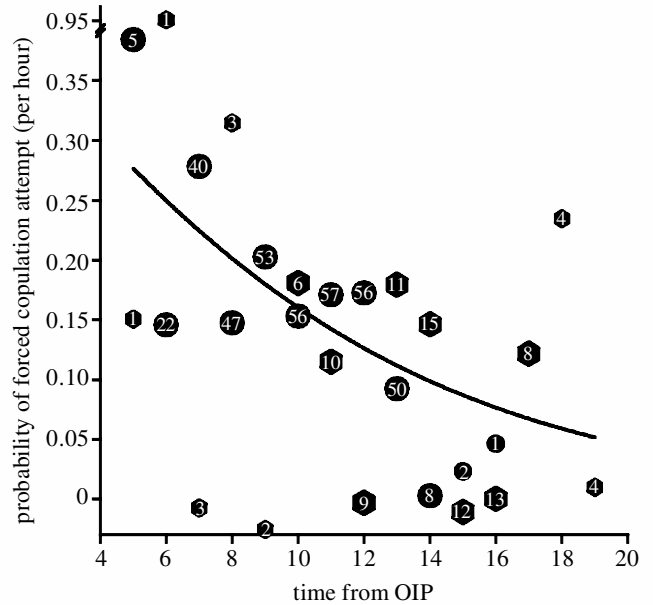


Figure 4. The probability of observing subordinate Soay rams attempting to force copulations on females as a function of time from the OIP. The fitted line is predicted from a GLMM (see § 3d), logistic regression equation: $\text{logit}(y) = -0.266 - 0.139x$. Data are controlled for the duration of each hour for which females are guarded; valid data points can thus report probabilities of < 0 or > 1 . For illustrative purposes, the data are divided into pre- (circles) and post- (hexagons) OIP days, and are grouped by hour. Embedded values indicate the number of observations grouped and small symbols are plotted where there are fewer than five observations.

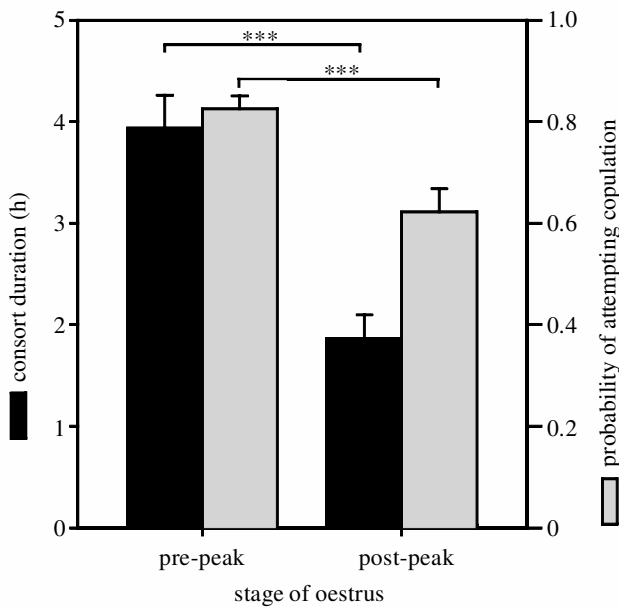


Figure 3. Pre- and post-OIP observations of focal Soay female's longest consort duration (black bars indicate mean \pm s.e.). The probability that the consorting ram attempted to copulate with the focal female (grey bars indicate probability \pm s.e.). Lines over the bars indicate statistical comparisons. *** $p < 0.001$.

after their longest consort had ended, and 91% went on to receive additional copulation attempts. While inseminations may still have some chance of fertilizing ova post-

OIP, continued guarding seems likely to have a minimal impact on males' reproductive success compared with the effect of finding a female who is yet to reach the OIP. However, males entering consort post-OIP were also less likely to attempt copulations (GLMM examining the probability of a copulation attempt pre- and post-OIP: $n_{\text{consorts}} = 244$, $n_{\text{females}} = 54$, Wald statistic $\chi^2 = 11.19$, d.f. = 1, $p < 0.001$, RE = female identity; figure 3). The probability that a male attempted a copulation was unaffected by the proximity to the OIP when controlling for day of oestrus ($p > 0.2$).

(d) *Alternative mating tactics*

Examination of the timings of chases initiated by subordinates suggests that males that were unable to gain exclusive access to females during the OIP were able to detect when these periods occurred, and timed their activity accordingly. Attempts to force copulations on ewes were increasingly likely at times around the OIP (GLMM of the likelihood of a chase in any given hour with time from OIP as an explanatory variable: $n_{\text{hours}} = 499$, $n_{\text{females}} = 54$, effect = -0.139 , s.e. = 0.0484 , Wald statistic $\chi^2 = 8.27$, d.f. = 1, $p = 0.003$, RE = female identity, controlling for the proportion of each hour for which females were guarded; figure 4). It could be argued that subordinates' attempts to gain coercive copulations increase in frequency around the OIP because these are the periods when they are least able to gain access to females. However, this seems unlikely to be the case, since males are never saturated with receptive females; the

median operational sex ratio (sexually mature males : receptive females) recorded here was 32.5 (range of four to 236), thus many males were always available to attempt forced copulations.

4. DISCUSSION

The reproductive behaviour of Soay males appears to be heavily influenced by the occurrence of the OIP within a female's oestrus. Larger more competitive males monopolized access to females at times closer to the OIP when their sperm-competition success was likely to be enhanced. The post-copulatory advantage gained by mating during the OIP could explain why large adult males (above average skeletal size) were 2.8 times more likely to be assigned a paternity in the first two weeks of the rut than smaller adults, when they were only 1.5 times more likely to be observed copulating (Preston *et al.* 2001). It may also explain why the siring success of larger males towards the end of the rut, when they had depleted their sperm reserves, was similar to that of smaller males, despite larger males having up to 1000-fold fewer sperm in their ejaculates (Preston *et al.* 2001). Mating during the OIP can, in part, overcome inherent differences in the fertilizing abilities of males' ejaculates (Dziuk 1996), and it seems likely that this will be the case with transient differences caused by depleted sperm reserves.

The influence of the OIP on male reproductive success was not confined to putative post-copulatory mechanisms, as females became increasingly receptive to copulation attempts at times around the OIP. A consequence of this variation in receptivity is that large males that monopolize the OIP will tend to encounter lower female resistance to copulations than smaller consort males attempting to copulate earlier or later in the period of oestrus. Since female behaviour would thus seem likely to result in differential siring successes of male phenotypes, it appears to be a form of 'indirect female choice' (Wiley & Poston 1996), which may be a feature of other mammalian mating systems. For example, subordinate golden hamsters gain access to oestrous females that had been guarded by dominant males at the point when their receptivity is declining (Lisk *et al.* 1989), and a similar situation may occur in tassel-eared squirrels, *Sciurus aberti ferreus* (Farentinos 1972). This enhanced female receptivity to males that defend them during the OIP could be easily mistaken for direct female mate choice in other species, as a correlation between female willingness to engage in copulations and male phenotype may be indicative of either paternity-biasing mechanism (Wiley & Poston 1996).

The attempts of subordinate males to force copulations on females during high-speed chases also appear to have been targeted towards the OIP. This seems likely to be a primary mechanism by which lambs achieve what may be considerable siring success, sometimes gaining in excess of 30% of the paternities assigned in any given year (Pemberton *et al.* 1999).

Our results show that consort males are reluctant to copulate with females after the OIP, when their ejaculate would have insufficient time to reach peak capacitation before ovulation occurs (Jewell *et al.* 1986; Ginsberg & Huck 1989). Although this finding may be influenced by

a lack of female receptivity, this is minimized by analysing all attempts at copulation by consort males, whether apparently successful or not. This reluctance to copulate with post-OIP females is consistent with findings in thirteen-lined ground squirrels, where males rejected oestrous females that had mated with competitors if they could, on average, achieve greater siring success by searching for another receptive female (Schwagmeyer & Parker 1990).

Differential mating responses of males with stage of female oestrus have been reported in several other mammalian taxa. Under semi-natural conditions, dominant male golden hamsters guarded females from competitors from the onset of oestrus, but delayed their own copulations until 3 or 4 h later, when putative sperm-competition success was at its highest (Lisk *et al.* 1989). Adult male savannah baboons (*Papio cynocephalus*) appear to compete more intensely for females on the two most likely days of conception (Bercovitch 1988), though an earlier study indicated that dominant males were no more likely to copulate with females on these days than were subordinates (Bercovitch 1986). Male lions (*Panthera leo*) may cease copulating the day before terminating consorts with females, even though females remain receptive to copulations from other males following the termination of the consort (Packer & Pusey 1983). These diverse taxa, in which male mating behaviour varies with stage of female oestrus, point towards a potential generality of our findings in mammalian species.

In conclusion, the behaviour of both Soay males and Soay females appears to be heavily influenced by the occurrence of an OIP in the oestrus of females, when the probability of sperm-competition success is at its greatest. Males appear to compete most intensely for access to females around the OIP, and a heightened female receptivity to copulation attempts at these times seems likely to produce further reproductive benefits for successful competitors. Studies on several other mammalian species have noted an increased intensity of male activity within females' oestrus, suggesting that the occurrence of OIPs may be of widespread importance in mammalian taxa. Thus, a relatively fine-scale determination of female OIPs is likely to prove valuable in the discovery and interpretation of both male and female reproductive strategies, and should be carefully considered in studies of mammalian reproductive behaviour.

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