Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success

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Male contests for access to receptive females are thought to have selected for the larger male body size and conspicuous weaponry frequently observed in mammalian species. However, when females copulate with multiple males within an oestrus, male reproductive success is a function of both pre- and post-copulatory strategies. The relative importance of these overt and covert forms of sexual competition has rarely been assessed in wild populations. The Soay sheep mating system is characterized by male contests for mating opportunities and high female promiscuity. We find that greater horn length, body size and good condition each independently influence a male's ability to monopolize receptive females. For males with large horns at least, this behavioural success translates into greater siring success. Consistent with sperm-competition theory, we also find that larger testes are independently associated with both higher copulation rates and increased siring success. This advantage of larger testes emerges, and strengthens, as the number of oestrous females increases, as dominant males can no longer control access to them all. Our results thus provide direct quantitative evidence that male reproductive success in wild populations of mammals is dependent upon the relative magnitude of both overt contest competition and covert sperm competition.

Keywords: horn; copulation frequency; operational sex ratio; sperm competition; raffle mechanism; sexual selection

1. INTRODUCTION

Male contests for access to receptive females are common in mammals and are widely believed to be the evolutionary mechanism driving the larger male body size and conspicuous weaponry typically observed in mammalian taxa (e.g. Geist 1966a; Clutton-Brock 1982; Andersson 1994; Lincoln 1994). However, female mammals commonly mate with two or more males (Møller & Birkhead 1989). Consequently, male reproductive success has been acknowledged to be a function of both pre- and post-copulatory strategies (Ginsberg & Huck 1989; Eberhard 1996; Gomendio *et al.* 1998), with competition between males continuing post-copulation in the form of sperm competition: 'the competition between the ejaculates of two or more males for fertilization of a given set of ova' (Parker 1970, 1998).

At its simplest, sperm competition is thought to function as a raffle, with paternity share being proportional to the number of sperm inseminated by each competitor (Parker 1982). As a result, behavioural and physiological adaptations are hypothesized to have evolved that enable males to increase the number of their sperm in female ovi-

ducts, relative to competitors, at the point of ovulation (Ginsberg & Huck 1989; Gomendio *et al.* 1998). Prominent behavioural strategies associated with sperm competition are mate-guarding of receptive females, which can be regarded as an extension of pre-copulatory contest competition, and high copulation frequencies (Møller & Birkhead 1989). Both traits enable males to influence the outcome of the sperm-competition lottery, by excluding or numerically 'swamping' the ejaculates of rival males.

This raffle mechanism is also thought to have led to the evolution of larger testes (Short 1979; Ginsberg & Huck 1989; Gomendio *et al.* 1998), thus allowing greater production, storage and, ultimately, ejaculation of sperm (Raadsma & Edey 1984; Møller 1989). There is abundant evidence that the occurrence of sperm competition is associated with large testes across mammal species (e.g. Harvey & Harcourt 1984; Kenagy & Trombulak 1986; Ginsberg & Rubenstein 1990; Heske & Ostfeld 1990; Stockley & Purvis 1993) and that the number of sperm inseminated relative to that of rival males is of importance in determining siring success under controlled conditions (e.g. Beatty 1960; Lanier *et al.* 1979; Dewsbury 1984; Ginsberg & Huck 1989; Ågren 1990; but see Stockley (1997) for a study of a natural population of common shrews, *Sorex araneus*). The collective weight of these findings strongly indicates that sperm competition selects for large testes. However, there is currently a lack of studies demonstrating that testes size is influential in determining paternity success *within* natural populations, where suc-

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cess in overt pre-copulatory contests could exert an overwhelming influence on males' ability to reproduce. Thus, there is a need to demonstrate that when females mate promiscuously, males with larger testes have a reproductive advantage.

The free-living Soay sheep (*Ovis aries*) on St Kilda, Scotland, UK, provide an ideal opportunity to examine male behaviour and morphology with respect to pre- and post-copulatory reproductive strategies. Soay males compete fiercely to gain access to females, and males of larger horn and body size have previously been shown to have an advantage in these contests (Preston 2001; Preston *et al.* 2001). Soay males also guard receptive females, copulating with them at approximately half-hourly intervals (Grubb 1974). Despite these episodes of mate-guarding, Soay ewes are highly promiscuous, copulating with up to 10 different consort males within a single day of their 2 day oestrus (Preston 2001). Sperm competition is therefore intense in this species, as further demonstrated by paternity analyses, which reveal that 74% of twins are sired by different males (Pemberton *et al.* 1999). Consistent with sperm-competition theory, Soay males have testes that are approximately four times heavier than would be predicted for their body mass (Stevenson 1994; Preston 2001), indicating that males are likely to have high sperm-production rates, large sperm reservoirs and large numbers of sperm in their ejaculates (Raadsma & Edey 1984; Møller 1989).

To determine the relative importance of pre- and post-copulatory strategies for male reproductive success in feral Soay sheep, we use life-history data and observations of behavioural and paternity success to address the following questions: (i) what determines a male's ability to gain and subsequently monopolize access to females? (ii) is male morphology important in determining the frequency of copulations during consortship? and (iii) which male attributes are ultimately favoured in this promiscuous system, and, specifically, do the putative benefits of large testes translate into actual increased reproductive success?

2. METHODS

(a) *Study site and population*

An unmanaged population of Soay sheep has been resident on the St Kilda archipelago (57°49′ N, 08°34′ W) for over a millennium. Hirta is the largest island in the group (638 ha), and has a population that fluctuates between 600 and 2000 sheep as a result of periodic population crashes (Coulson *et al.* 1999). This investigation focuses on a relatively discrete population of animals ranging within the Village Bay study area (175 ha) to the southeast of Hirta, which fluctuates between 200 and 600 individuals in size, and has a female-biased population sex ratio (males : females) that varies between 0.27 and 0.7. Since 1985, around 95% of lambs born within the study area have been eartagged, and are thus of known age. Adults (2 years or over) comprise 39% to 66% of the study area population, and the adult sex ratio varies between 0.1 and 0.41. A detailed description of the study area and population can be found elsewhere (see Jewell *et al.* 1974).

(b) *Morphometric data*

Morphometric variables used in these analyses were collected in the Augusts of 1995 to 1999, when a large proportion (range

of 49–67%) of the study area population were measured within a two-week period in each year. Hind-leg lengths were measured from the tubercalcis of the fibular tarsal bone to the distal end of the metatarsus and are taken here to be an index of skeletal or body size. Horn length was measured from the base, along the outer curvature of the spiral, to the tip. Testicular circumference was taken at the widest point of the scrotum, and is a reliable proxy for testes mass in domestic sheep (Knight 1977). August measurements of testicular circumference are highly correlated with measurements of the same males during the rut ($r = 0.84$, d.f. = 12, $p < 0.001$).

(c) *Behavioural observations*

A team of observers carried out behavioural watches during daylight hours, beginning in the pre-rutting period in mid-October, and continuing to the end of the rut in mid-December. All data were collected from 1995 to 1999, and come from 47 individually identifiable males that were watched repeatedly throughout the rut. Where possible, focal animals were watched a minimum of three times in each week, balancing watches on individuals throughout each week. The behaviour of focal animals was recorded for 1 h on any given occasion, producing 13.6 ± 5.21 (mean ± s.d.) hours of behavioural data per male each year. Two hour watches were occasionally performed on individuals that had been difficult to locate ($n_{watches} = 34$), and watches were terminated early when the focal animal was lost from view ($n_{watches} = 119$). Consortships were defined as a close spatial relationship between a male and female (typically within 5 m), with frequent courtship and attempted defence of the ewe by the ram. The study area was continually monitored for consorts throughout each day, providing an indicator of the numbers of females in oestrus. Mounts were defined as copulation attempts if the male's forelegs made contact with the female's rump.

(d) *Conceptions, births and paternities*

Daily censuses of the study area were made for lambing females in March and April, so providing an accurate measure of the number of females lambing on a given day, and thus the number of females conceiving 151 days earlier during the rut (there is a close mirroring of conception and lambing dates (Jewell *et al.* 1974)). Soon after birth, lambs were captured and tissue-sampled for genetic analysis. Paternity was assigned at the 80% confidence level using microsatellite DNA genotypes of lambs, known mothers and possible sires, with the paternity inference software CERVUS 1.0 (Marshall *et al.* 1998). For further details of this approach see Pemberton *et al.* (1999).

(e) *Analysis*

All analyses were restricted to adult males that had morphometric data available for the year under consideration. Juvenile males (less than 2 years of age) practise an alternative mating tactic (Stevenson *et al.* 2003), and will be considered elsewhere. Behavioural and paternity data presented in tables were analysed using generalized linear mixed models (GLMMs) in GENSTAT 5 (release 3.22). These control for the repeated measures of behaviour and paternity by fitting male identity as a random effect (GENSTAT 5 Committee 1993). A pool of explanatory variates was assessed in each model: age, weight, horn length, basal horn circumference, hind-leg length, testicular circumference, consort duration (time spent in consort within the focal watch) or watch duration for behavioural analyses and numbers of females in oestrus (or conceiving); year was tested as a factor.

Table 1. GLMMs of male consort success and copulation rates. The aim of the analyses was to determine the phenotypic characteristics of males that influenced their consort success ($n_{watches} = 617$, $n_{males} = 34$, constant $= -9.850$) and estimated copulation rates ($n_{consorts} = 192$, $n_{males} = 30$, constant $= -7.717$).

(The response variables are binary, indicating whether the focal male was observed in consort, or attempting a copulation whilst in consort, during focal watches. Watches occurring between the time the first female was recorded in oestrus and the end of the rut five weeks later are included. Dependent variables are linearized with the use of a logit link function. All other phenotypic characteristics (see § 2) were excluded from models with $p > 0.08$.)

term	d.f.	effect	s.e.	Wald statistic (χ^2)	p-value
consort success					
number of oestrous females[a]	1	1.665	0.157	111.91	<0.001
male horn length	1	0.006 21	0.002 12	8.62	0.003
male weight	1	0.0941	0.0289	10.59	0.001
estimated copulation rates					
consort duration	1	0.000 622	0.000 131	22.55	<0.001
male testicular circumference	1	0.0228	0.008 62	6.96	0.008

[a] Log transformed.

All two-way interactions were also tested. The minimal model was determined via stepwise deletion (McCullagh & Nelder 1983), and significance was taken to be $p < 0.05$. All data presented in the figures are controlled for terms remaining in the relevant minimal model; valid data points can thus report probabilities of below zero or greater than unity. Sample sizes vary according to the analysis, as life-history data were not available for all individuals. Routine measurement of adult testes size was not initiated until 1995, and thus paternities predating this time are not included in the analysis of siring success. Specific details of analyses are contained within table or figure legends as appropriate.

3. RESULTS

(a) *Male phenotype and consort success*

Horn length appears to be an important determinant of males' 'consort success' (the probability that they will be observed defending oestrous females during focal watches), because rams with larger horns were observed guarding ewes more frequently (table 1; figure 1*a*). However, male weight also appears to be important in this respect, as heavier males were also more likely to be observed in consort (table 1), after controlling for horn length.

Male consort success is likely to be a function of their ability to find a receptive female, where body condition is expected to be important, and their ability to defend that female from rival males, which is likely to be influenced by both body size and condition. To investigate further, we partitioned weight into skeletal size and condition components (see figure 1 legend for methods). We then refitted our minimal model, exchanging weight for skeletal size and condition as explanatory variables. The results reveal that the importance of body weight is the result of the independent effects of both skeletal size and body condition (figure 1*b,c*). As well as being more likely to be seen in consort, across the rut as a whole, large-horned and heavy males spent a greater proportion of their time defending oestrous ewes (multiple regression, the dependent variable was the time spent in consort across the rut expressed as a proportion of total focal watching time for each male: for horn length, effect $= 0.000 704$, s.e. $= 0.000 232$, $\chi^2 = 9.22$, d.f. $= 1$, $p = 0.002$; for weight, effect $= 0.0109$, s.e. $= 0.003 23$, $\chi^2 = 11.29$, d.f. $= 1$, $p = 0.001$; $n = 34$, the response is $\log(x + 1)$ transformed, and the analysis controls for significant differences between years).

(b) *Male phenotype and copulation rate*

Whilst consort success is likely to be a good indicator of a male's ability to gain access to and subsequently guard oestrus females, consorts do not always result in copulations (22% of males did not attempt a copulation during the entirety of their consort; B. T. Preston, I. R. Stevenson and K. Wilson, unpublished data from focal observations on oestrous females). Testicular size appears to be the key determinant of copulation rate within consorts. After controlling for consort length, males with larger testes were more likely to be observed attempting copulations (table 1; figure 2). No other physical attribute of males included in our analysis contributed to the observed variation in copulation rate.

(c) *Male phenotype and paternity success*

The role of horns in determining access to receptive females was echoed by a strong positive correlation with paternity success (table 2; figure 3*a*). Testicular size, which was not (independently) associated with a male's probability of gaining access to females (table 1), was positively associated with paternity success (figure 3*b*), becoming progressively more important as the number of females conceiving increased (table 2, testicular circumference : number of conceiving females interaction; figure 3*c*). Previous analysis of male siring success in this population, which did not include testicular circumference as an explanatory variate, had indicated that male body size was a significant predictor of siring success in Soay sheep (Preston *et al.* 2001). In the current analysis, body size did not explain a significant amount of variation ($p = 0.14$). Thus, to remove the possibility that covariation between testes size and body size has confounded this analysis, we refitted our model, replacing testicular circumference with 'residual testicular circumference' (using residual values from a linear regression of testicular circumference on hind-leg length) and hind-leg length. The
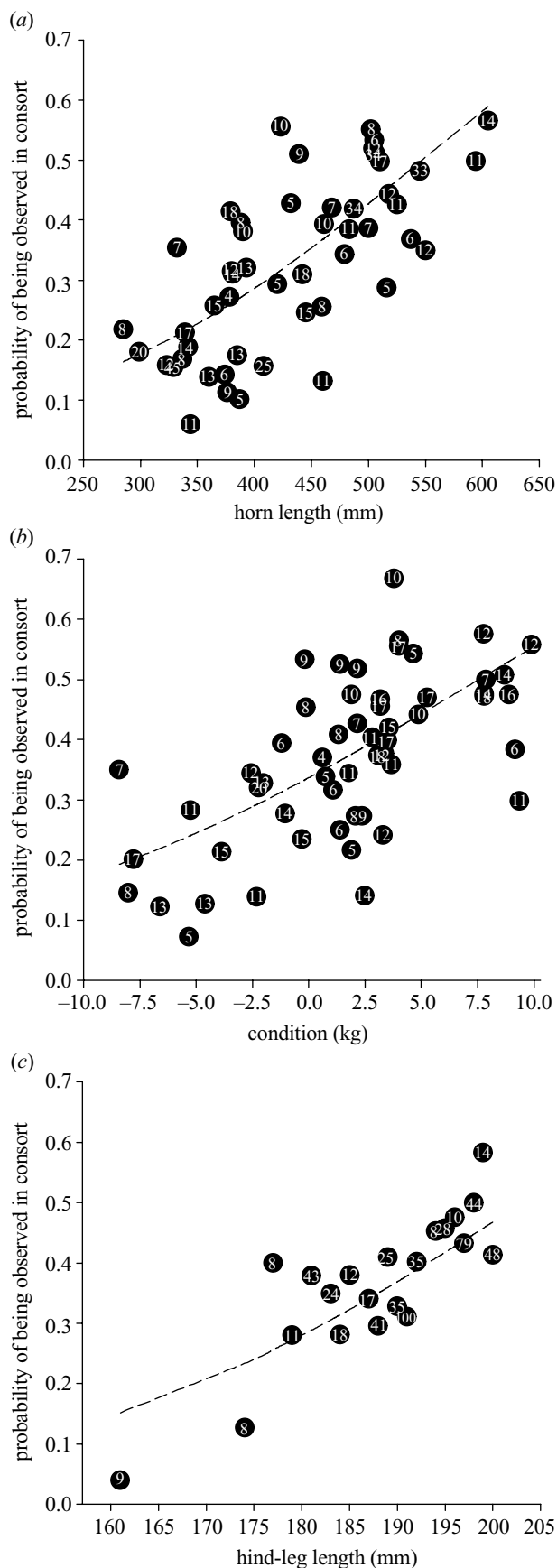
(a)

(b)

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Figure 1. Predictors of male 'consort success'. The probability of being observed in consort as a function of (a) male horn length (controlling for terms remaining in the minimal model (see table 1)), and weight when partitioned into (b) body condition ($n = 617$, effect = 0.089 68, s.e. = 0.036 29, d.f. = 1, Wald statistic (χ^2) = 6.11, $p = 0.013$, controlling for significant effects of the number of oestrous females (log transformed), hind-leg length and horn length) and (c) hind-leg length ($n = 617$, effect = 0.040 77, s.e. = 0.018 16, d.f. = 1, Wald statistic (χ^2) = 5.04, $p = 0.025$, controlling for significant effects of the number of oestrous females (log transformed), body condition and horn length). Body condition was calculated from a regression of weight on male hind-leg measurements (data from 1985 to 1999, $n = 213$). A reciprocal model provided a good fit to the data (weight = $1/(-0.000\ 37 \times$ hind-leg length + 0.1). Condition was estimated as the residual value from the fitted model: condition = (observed weight) − (predicted weight for observed hind-leg length). Fitted lines are plotted from model predictions. For illustrative purposes, data are grouped at each 100 g deviation from average condition or millimetre of horn and hind-leg length, respectively; numbers on data points indicate the number of watches grouped.
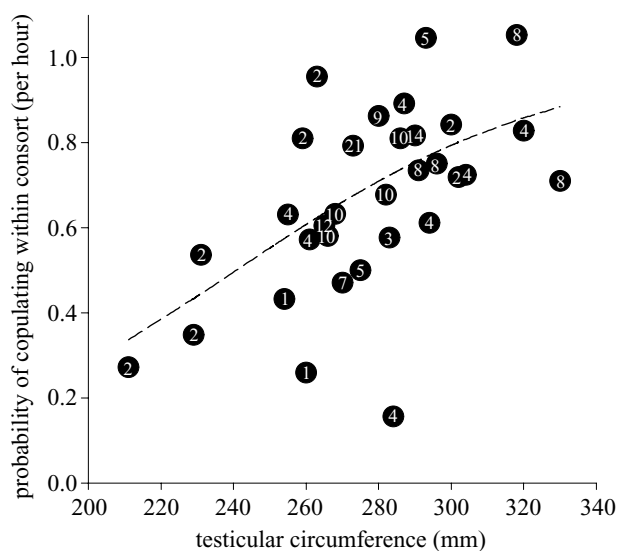

Figure 2. Testes size predicts copulation rate. The probability that a male was observed copulating during a 1 h consort as a function of testicular circumference. For illustrative purposes, data are grouped at each millimetre increase in testicular circumference; numbers on data points indicate the number of watches grouped. See table 1 for details of the analysis.

conceiving, $p = 0.01$), whereas body size is excluded (hind-leg length, $p = 0.06$).

4. DISCUSSION

(a) *The importance of horn size*

A number of authors examining intrasexual selection have acknowledged that covariation between morphometric attributes linked to reproductive success has made analyses of their relative importance difficult (e.g. Geist 1971; Clutton-Brock 1982; Andersson 1994; McElligott *et al.* 2001; Coltman *et al.* 2002). However, by taking a

results reveal that the importance of testes size is independent of body size, as residual testes size remains in our minimal model as a significant predictor of siring success (residual testicular circumference : number of females

Table 2. GLMM of male siring success. The analysis was aimed at determining the phenotypic characteristics of males that influenced their siring success ($n_{observations} = 430$, $n_{paternities} = 71$, $n_{males} = 47$, constant $= -5.646$).

(The dependent variable is in binomial proportions, indicating whether a paternity was gained on any given day of each week in the ruts of 1995 to 1998, and is linearized with the use of a logit link function. All other phenotypic characteristics (see § 2) were excluded from the model with $p > 0.14$.)

term	d.f.	effect	s.e.	Wald statistic (χ^2)	p-value
male testicular circumference	1	−0.009	0.0128	0.50	0.480
number of conceiving females	1	−0.0908	0.0479	3.59	0.058
male horn length	1	0.007 30	0.002 22	10.86	0.001
male testicular circumference : number of conceiving females	1	0.000 406	0.000 173	5.53	0.019

multivariate-analysis approach, we have been able to tease apart the relative contributions of different physical attributes to behavioural and reproductive success. Our analyses demonstrate that horn size (irrespective of age, body size, condition and testes size) is associated with increased access to receptive females (table 1). It seems likely that this advantage results at least in part from their importance in intrasexual combat. In escalated fights, the function of horns is clear: delivering blows in vicious head-to-head clashes or to the flanks of rivals (Geist 1966a; Schaller 1977). The force of impact in these contests may be considerable and cause injury: examination of Soay skeletons has revealed that 60% of rams suffer fractures of the cervical vertebrae, presumably as a result of fighting (Clutton-Brock *et al.* 1990), and fights have been observed to result in the death of one of the combatants (B. T. Preston, personal observation). Horns also function defensively, acting as a shield, and the ridges and curvature allow males to catch and grip the blows of their rival's horns (Geist 1966a; Schaller 1977). Finally, it has also been suggested that large weaponry may intimidate rival males (Geist 1966b; Clutton-Brock 1982) or be preferred by females (Geist 1971; Clutton-Brock 1982). The behavioural advantage of large horns translates into reproductive success, with larger-horned males siring more offspring (table 2).

(b) *The importance of body size and condition*

Our finding that body size is influential in determining access to females in Soay sheep is consistent with findings in other species in which male contests appear important (e.g. Haley *et al.* 1994; McElligott *et al.* 2001) and provides further support for the idea that contests for access to females have driven the sexual size dimorphism observed in many mammalian taxa (Andersson 1994). However, before gaining access to receptive females, males must first locate them, and males spend on average 18% of their time budget across the rut travelling the island, examining ewes for signs of oestrus. Condition is likely to be important here, as males are estimated to lose *ca.* 30% of their body weight by the end of the rut (I. R. Stevenson, B. T. Preston and K. Wilson, unpublished analyses). Thus, physical exhaustion may limit the success of males in poor condition.

The exclusion of body size from our model as a predictor of siring success appears at odds with the results of a previous analysis of the phenotypic determinants of siring success in this population, where body size was found to be a significant predictor of siring success (Preston *et al.*

2001). This discrepancy is most probably the result of a reduction in sample size in the current analysis; here, only 4 years of paternity data are analysed owing to the limited availability of data on testes size, whereas previous analyses used 12 years of paternity data (Preston *et al.* 2001). The influence of body size in determining males' ability to gain and subsequently monopolize access to females (Preston *et al.* 2001; figure 1c), alongside the importance of overt contest competition in this system (as indicated by the association of male horn length with both consort and siring success), indicates that further years of study may reveal a significant effect of males' body size on their siring success, regardless of the size of their testes and horns.

(c) *The importance of synchronized oestrus*

The operational sex ratio (sexually mature males : receptive females) changes through the rut as the number of oestrous females first rises, then falls (range of 4–236; Preston 2001). Our results show that as the number of receptive females rises, the relative behavioural advantages of 'larger' males diminish (figure 4a). This is because Soay rams do not form harems, and as a consequence, larger males become 'saturated' with receptive ewes. Thus, smaller males are better able to gain access to, and copulate with, the 'surplus' females. This need not imply that sperm competition is more intense within individual females; indeed for some females the reverse may be true (Preston 2001). It simply means that overt competitive ability at high female numbers becomes a weaker predictor of a ram's success, because many males, regardless of phenotype, have the opportunity to contribute to the sperm population in female oviducts.

(d) *The importance of testes size*

Where males do not monopolize access to females, the number of sperm a male is capable of inseminating is predicted to be a strong determinant of siring success (Parker 1982). This appears to be the case in Soay sheep, as when competition for access to females became less intense males with larger testes (and hence the ability to produce, store and ejaculate more sperm) sired a greater number of lambs (figure 3c). At low female numbers, and thus high levels of overt competition, smaller males simply cannot gain access to females and thus cannot sire offspring, no matter how large their testes. Thus, there is a switch in the relative importance of pre- and post-copulatory mechanisms of male reproductive success as the number of receptive females increases (figure 4b).
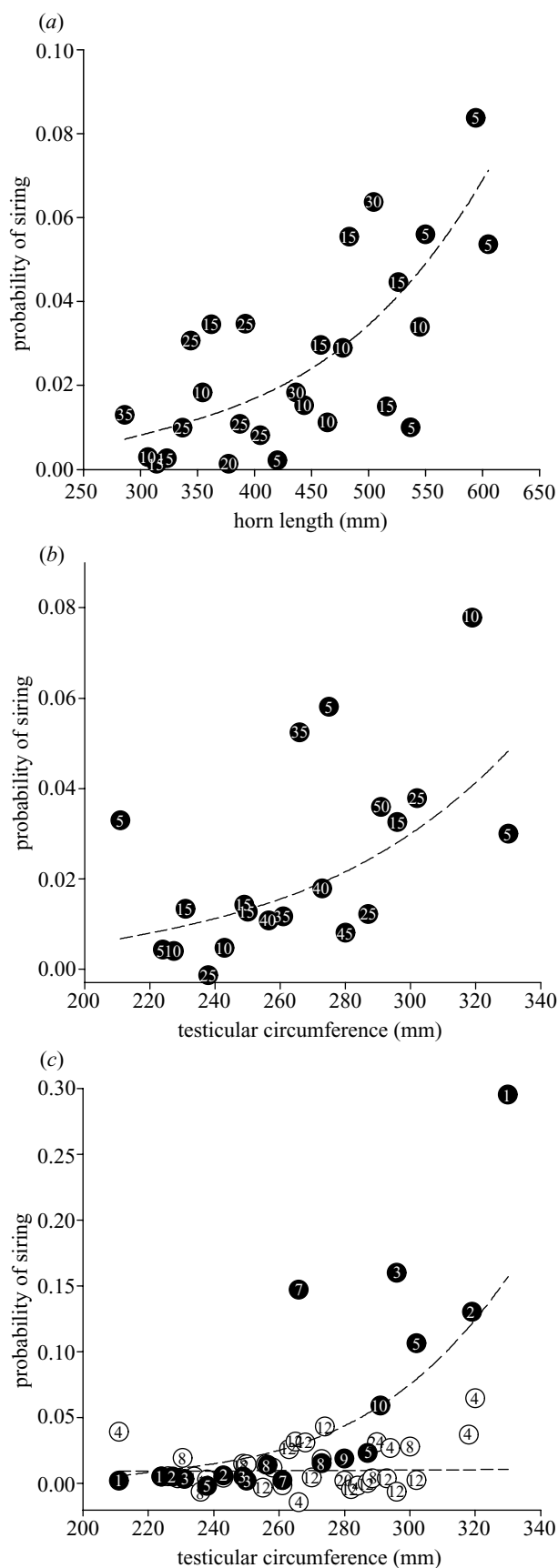
(a)

(b)

(c)

Figure 3. Predictors of male siring success. The probability of being assigned a paternity on any given day of a week against (a) horn length and (b) testicular circumference ($n = 340$, effect = 0.0168, s.e. = 0.007 22, d.f. = 1, Wald statistic (χ^2) = 5.42, $p = 0.02$, controlling for significant effects of the number of females conceiving and male horn length). (c) An illustration of the effect of testicular circumference on siring success at high (black circles) and low (white circles) female availability. High female availability was treated as the week *in each year* that most females conceived (mean $n_{females} = 92$); low female availability was the remaining weeks in the analysis (mean $n_{females} = 25$). (a) and (c) are controlled for terms remaining in the minimal model (see table 2 for details of the analysis); fitted lines are plotted from model predictions. For illustrative purposes, data are grouped at 10 mm intervals of horn length and 5 mm intervals of testicular circumference; numbers on data points indicate the number of observations grouped.

successive ejaculations within a day (Salamon 1962; Tomkins & Bryant 1976; Thwaites 1994). For example, rams who ejaculated 11 times daily for a period of 5 days showed a 70% decline in sperm numbers between the first and last ejaculates within a day (the ejaculates were collected using an 'artificial vagina'; Salamon 1962). The opportunity for Soay rams to inseminate more than one female a day increases with female availability (Preston 2001), and males have been observed copulating with as many as six females, copulating 13 times in all, within 8 h (Grubb 1974). Thus, limits on sperm production within a day may be an important constraint on male success in sperm competition at high female numbers. If this were the case, then high sperm production rates and large reserves would be at a premium. In support of this, we find that males with larger testes copulated at higher rates whilst in consort (table 1; figure 2), which may be the result of a greater availability of sperm. Constraints on sperm production across the rut have already been identified, with the sperm reserves of frequently copulating dominant rams becoming depleted as the rut progresses (Preston *et al.* 2001).

Our findings provide the first, to our knowledge, empirical evidence that larger testes provide a reproductive advantage to males within populations of mammals that experience sperm competition, which is likely to be the result of their role in sperm production and their association with larger ejaculates. We thus provide support for the interpretation of numerous comparative analyses that have found an association between testes size and estimated sperm competition intensity across mammalian species (e.g. primate and ungulate species; Harvey & Harcourt 1984; Ginsberg & Rubenstein 1990) and other taxa (e.g. fish and bird species; Stockley *et al.* 1997; Møller & Briskie 1995).

In conclusion, it appears that reproductive success is achieved through both overt and covert mechanisms in Soay sheep. Large horns, greater body size and good condition enable males to gain and maintain access to receptive females, and it is most likely that this is mainly the result of their importance in overt male contests. Our results also provide direct quantitative support for the

A further mechanism may have acted to increase the influence of large testes at high female availability. Several studies of domestic sheep demonstrate that the number of sperm ejaculated by males declines dramatically with
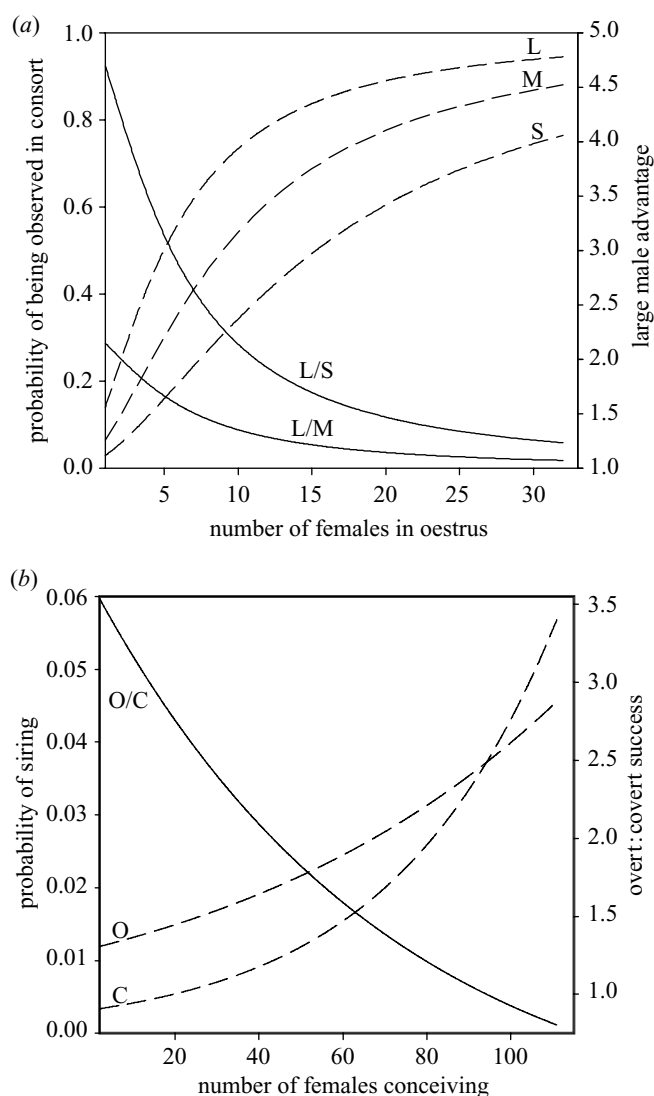
Figure 4. Overt and covert success as a function of female availability. (*a*) Predictions of behavioural success for small (S), medium (M) and large (L) males (dashed lines), and the advantage gained by large over small (L/S) and medium (L/M) males at increasing female availability (solid lines). Predictions are formed from GLMM analysis of consort success reported in table 1 using S, lower quartile; M, mean; L, upper quartile measurements of horn length and weight in the adult population. (*b*) An illustration of the relative influence of overt and covert competition on siring success with increasing female availability. Predictions of siring success (dashed lines) are for two hypothetical males, one of which makes a greater investment in overt contest competition (O), whilst the second makes a larger investment in covert sperm competition (C). Predictions for the O competitor are calculated using the upper quartile measurement of horn length and the lower quartile measurement of testes size in the adult population; for the C competitor the situation is reversed. The relative success of each tactic (O/C) with increasing female availability is also plotted (solid lines). Predictions are based on the GLMM analysis of siring success reported in table 2.

theories that larger testes have evolved through sexual selection, and that the intensity of selection will be dependent upon the relative magnitude of overt contest competition and covert sperm competition.

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