Evolution of sexual size monomorphism: the influence of passive mate guarding

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Abstract

Some species have potential for intense mate competition yet exhibit little or no sexual size dimorphism, despite predictions from sexual selection theory. Using a conceptual model, we show the conditions for which passive mate guarding with copulatory plugs can be an alternative and more successful strategy to active (direct) guarding, reducing selection pressure on large male size. The model predicts that copulatory plugs in mammals should be favoured in species for which females have short sexual receptivity periods. Using data on 62 primate species and a phylogenetic regression approach, we show that, as predicted, copulatory plugs are negatively associated with degree of sexual dimorphism and females' sexual receptivity length. Penile spines are also significantly associated with plug use and short receptivity periods suggesting a possible offensive role in sperm competition. Results highlight that life-history characteristics, such as sexual receptivity lengths, may alter the costs and benefits of alternative male strategies and thus alter the strength of sexual selection.

Introduction

Male-biased sexual dimorphism in size is generally viewed as a product of male contested competition for mates (Darwin, 1871; Ralls, 1977). When male reproductive success is limited by how many females they can inseminate, variation in reproductive success occurs if some males can exclude others from accessing females through agonistic competition and mate guarding, often favouring large male size. Although the degree of mate competition explains much of the pattern of male-biased size dimorphism among diverse taxa (Clutton-Brock *et al.*, 1977), it fails for some species which have potential for intense male competition for mates yet exhibit little or no size dimorphism of the sexes (e.g. muriqui monkeys, Strier, 1990; lemurs, Kappeler, 1991; equids, Linklater, 2000; hyraxes, Koren *et al.*, 2006).

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Large male size is expected to be favoured when the spatial and temporal distribution of sexually receptive females allows large males to monopolize multiple mates while excluding smaller males (Ims, 1988; Shuster & Wade, 2003). If oestrous cycles of females are extremely synchronized, or females are spatially very dispersed, even large males will be unable to monopolize and mate with multiple females, thus reducing the advantage of large male size and weaponry related to mate guarding (Ims, 1988; Shuster & Wade, 2003). Understanding why some species display little or no sexual size dimorphism despite having temporal and/or spatial distributions of females that are expected to favour mate guarding requires an exploration of possible alternative male strategies. We explore one potential strategy here.

Several explanations (not mutually exclusive) have been offered to explain lack of sexual size dimorphism in species which are expected to be under strong selection for traits related to male mate guarding. Among others, these include constraints on mate guarding due to diet and foraging behaviour (Janis, 1982), phylogenetic

inertia (Berger, 1988; van Schaik & Kappeler, 1996) and environmental constraints on male body size (Wright, 1999) and/or positive selection for female body size (e.g. fecundity selection) that perfectly balance sexual selection pressures for large male size (Kappeler, 1990). Although these represent possible mechanisms, we focus on an additional potential mechanism for the evolution of monomorphism that has received less attention, particularly in the mammalian literature: passive mate guarding. There are male characters subject to selection through male mating competition that do not involve body size or weaponry because they are used for copulatory or seminal combat rather than aggressive encounters between competitors (Simmons, 2001; Shuster & Wade, 2003; Arnqvist & Rowe, 2005). For example, structures such as copulatory plugs used to inhibit successful inseminations from other males appear to be common among diverse taxa and have evolved independently in several different lineages (e.g. mammals, Koprowski, 1992; reptiles, Shine et al., 2000; insects, Mikheyev, 2003). Unlike scramble-type sperm competition which relies on the relative number of sperm inseminated by each male, the use of copulatory plugs may be used as an alternative, passive form of mate guarding to interfere with the sperm of other males, thus representing interference-type sperm competition (Voss, 1979; Dickinson & Rutowski, 1989; Koprowski, 1992; Takami et al., 2008).

Although the exact plug structure varies among groups, in many species they serve to reduce or prevent a subsequent male's probability of fertilization success (Walker, 1980; Chapman, 2001; Poiani, 2006). Such male–male competitive functions of copulatory plugs include physically blocking sperm from the genital opening (chastity enforcement) (Voss, 1979; Matsumoto & Suzuki, 1992), increasing handling time, decreasing female attractiveness (Orr & Rutowski, 1991), inducing a delay in female re-mating (Baer et al., 2001) or combinations thereof (Takami et al., 2008). However, additional or alternative functions of copulatory plugs have also been noted including enhancing female nutrition and facilitating sperm placement and transport (Toner et al., 1987; Chapman, 2001). When copulatory plugs are used as a passive mate-guarding strategy as an alternative to active mate guarding (e.g. aggressive encounters between male competitors), it may reduce selective pressure on male body size because the contest would rely less on physical combat that favours large male size.

Previous authors have noted the potential of copulatory plugs for influencing size dimorphism and sexual selection (Elgar, 1998; Shuster & Wade, 2003; Miller, 2007). However, analysis of potential evolutionary consequences of copulatory plugs for sexual dimorphism (but see Miller, 2007) and the specific conditions for which copulatory plugs might be favoured over active guarding has been limited. To do this, we must first examine the advantages of both strategies.

A male which can successfully guard a female throughout her sexual receptivity period has a high probability of fertilization success. For a roving male to be successful, he must exceed this reproductive success by increasing his number of mates and/or his fertilization rate per female (Shuster & Wade, 2003). In populations where female receptivity periods show limited overlap (i.e. where there is a chance of encountering additional unmated females), these requirements could be accomplished with the use of copulatory plugs (mating plugs) as a form of passive mate guarding. They can enhance a roving male's fertilization success for female mates he abandons by inhibiting or reducing successful insemination by subsequent males (Shuster & Wade, 2003). The male can then use time normally spent guarding to search for additional mates. If a passive mate-guarding strategy is effective at increasing a male's reproductive output relative to other strategies, it is likely to increase in the population among future generations and may become the dominant competitive strategy. Assuming that males using this strategy spend more time searching for females instead of guarding (e.g. as observed in ground squirrels, Koprowski, 1992), selection on male traits involving locomotor agility and relating to copulatory plugs (offensive and defensive) may be favoured rather than sexual size and weaponry if the need for active mate guarding is reduced. Such conditions may explain sexual size monomorphism of some taxa for which males are expected to invest in mate-guarding strategies. However, to the best of our knowledge, this has not been explored empirically and, for mammalian taxa, copulatory plugs have been rarely considered as a possible factor in the evolution of sexual dimorphism. This may partly stem from the lack of theoretical models that explicitly predict conditions (i.e. life-history traits) where copulatory plugs are favoured over active mate guarding.

The aim of this study was to test the hypothesis that passive mate guarding in the form of copulatory plugs may help explain sexual monomorphism in some mammalian taxa with polygynous systems and male-biased operational sex ratios. To explore this idea, we first develop a conceptual model to predict the conditions for which active vs. passive mate-guarding strategies should prevail in such taxa. As numerous studies have focused on the conditions favouring investment in scramble-type sperm competition (sperm number) vs. mate guarding (see Shuster & Wade, 2003 for review), our model focuses on species for which mate guarding is already expected to be advantageous. The model predicts the circumstances under which males should rely on copulatory plugs as a mate-guarding strategy rather than allocating energy to staying with a female to guard her from other males. We then used primate taxa as a model system to test our model predictions. We gathered data from the literature on 62 primate species and performed phylogenetically controlled statistical analyses to deter-

mine if the association of primate characteristics, predicted by our model, holds across the primate order.

Active vs. passive mate guarding: a model

Previous models have considered the question of when a male should mate guard rather than leave a female and rely on scramble-type sperm competition (e.g. Alonzo & Warner, 2000; Shuster & Wade, 2003). However, these studies have usually focused on 'active mate guarding' (i.e. a male stays with a female to defend her from other males) and have not examined in detail the situation in which a male, under conditions that favour mate guarding, is likely to allocate energy to a strategy of 'passive mate guarding' such as copulatory plug formation (which differs from scramble-type sperm competition). The advantages of passive mate guarding with copulatory plugs depends on a variety of factors, including the cost and effectiveness of active vs. passive mate guarding and the probability of impregnating additional females (Shuster & Wade, 2003). Our conceptual model, focused on mammals, expands upon the application of sexual selection theory to male strategies by showing that passive mate guarding with the use of copulatory plugs should be favoured over active guarding in species with short periods of female sexual receptivity.

First, consider the reproductive advantage of guarding a female throughout her receptivity period, T^*, vs. leaving her to find new mates. Let w_g represent the probability of a male impregnating one female if he guards her throughout her sexual receptivity period, with $0 \leq w_g \leq 1$. Thus, if he successfully impregnates her by preventing all other males from mating with her, $w_g = 1.0$. The reproductive value of that strategy is given by the probability of impregnating her and the number of sired offspring. For simplicity, we follow previous models by assuming that females are on average equal in reproductive output, but differences across females could easily and explicitly be integrated into the model when necessary. Let w_l be the probability of impregnating the female when leaving the female (i.e. without active mate guarding) and aN_f, the number of additional successful matings he is capable of acquiring from the time saved not guarding the female. The number of additional matings depends on the average number of sexually receptive females that the male encounters during the period T^*, N_f, and on the average probability of inseminating each additional receptive female encountered, a. Note that both mated and unmated females can contribute to aN_f, if plug effectiveness is < 100%. Although the number of unmated females decreases over time, aN_f is always greater than zero if there is limited overlap in receptivity (complete synchrony would make it impossible for males to monopolize females). N_f decreases with the proportion of T^* males spend handling/guarding females vs. searching for females. Given these assumptions, a male should not spend energy and time physi-

cally guarding a female throughout her receptivity period if

$$w_g < w_l + aN_f. \tag{1}$$

In other words, instead of active mate guarding, a male should leave a female with which he has just mated, if the potential value of actively guarding her from other males, w_g, is less than the combined probability of fathering the female's offspring when he leaves without active guarding, w_l, plus the number of additional successful matings he is capable of acquiring from the time saved not guarding, aN_f. For simplicity, the model assumes that the costs of the two strategies to a male are comparable. However, cost asymmetries between both strategies could easily be integrated into inequality 1.

If the male is incapable of physically or passively guarding his female then his probability of impregnating a female if he leaves her after mating, w_l, will be

$$w_l = \frac{1}{1 + N_m(T^*)} \tag{2}$$

where $N_m(T^*)$ is the number of additional males with which the receptive female is likely to copulate if not guarded by a male and is an increasing function of the length of her receptivity period (T^*) (i.e. $\delta N(T^*)/\delta T^* > 0$). This makes the standard assumption of random sperm mixing and equivalent sperm production among males.

If males are capable of passively guarding a mate through copulatory plug formation and placement, this will reduce the probability of subsequent males impregnating her. In the simplest case, which assumes equivalent sperm contribution and mixing among males, w_l then becomes

$$w_l = \frac{1}{1 + N_m(T^*)[1 - p(T^*)]} \tag{3}$$

where $p(T^*)$ is the probability of inhibiting another male's insemination success with a copulatory plug and is a declining function of the female's receptivity time, T^*. Copulatory plugs in mammals are generally short lived (17–76 h) (Murie & McLean, 1980; Williamsashman, 1984) and eventually dissolve in a female's reproductive tract. Thus, the effectiveness of plugs as a guarding strategy declines over time. This also means that longer sexual receptivity periods of females make passive guarding with plugs a less effective strategy (plugs would only be effective in passive guarding for a small proportion of the receptivity period). Combining equations 1 and 3 indicates that with higher effectiveness of the copulatory plug [i.e. large $p(T^*)$], males receive less benefit from actively guarding mates. If $p(T^*) = 1$, males should always leave females as long as there is a small chance of impregnating another female (i.e. $aN_f > 0$). The effectiveness of the plug, $p(T^*)$ is driven by both intra- and intersexual conflict. If females

and competing males are capable of counteracting the effects of plugs (i.e. increased handling time, decreased female attractiveness, delay in female re-mating and/or chastity enforcement), through removal or other mechanism, then $p(T^*)$ declines. Conversely, the relative benefits of plugs in passive mate guarding can increase when the probability of insemination success for active mate guarding (w_g) is reduced. For example, the benefits of passive guarding are enhanced in a system in which females actively resist being guarded and seek out new mating partners.

In some systems, competing males may remove copulatory plugs after some effort and displace sperm of previous males (e.g. Parga, 2003). Such displacements may violate the model assumption of equivalent sperm contribution and mixing. Accounting for an unequal sperm contribution by competing males reduces the threshold of receptivity period, T^*, for which copulatory plugs are the beneficial strategy. The lower the ratio of sperm contribution between the first and later matings, the faster is the decline in benefit of copulatory plugs with longer receptivity periods. If the use of copulatory plugs as a defensive strategy is not impervious to competitors, it does not mean that it cannot be a beneficial strategy, as long as inequality 1 still holds. Thus, even 'imperfect' copulatory plugs (i.e. $w_1 < 1$) which are subject to displacement by females or male competitors can be beneficial as long as they reduce the probability of insemination by subsequent males to some extent and aN_f is large enough so that inequality 1 still holds.

Now, consider the relative advantages of the different reproductive strategies for a male in a polygynous system in which females have some limited overlapping receptivity and are clumped in space (such as many of the primates we are investigating). In this case, without considering passive mate guarding, sexual selection theory predicts that leaving a female after mating is typically more disadvantageous than mate guarding (Shuster & Wade, 2003), although specific conditions can alter the ability of males to monopolize females (Switzer et al., 2008). Thus, under conditions for which active guarding is likely to allow some males to monopolize female mates, strong sexual selection on male size is likely to result in sexual size dimorphism. However, if the use of copulatory plugs is an available and effective defensive strategy for males, passive guarding is expected to be more advantageous than active mate guarding if females have a short sexual receptivity period (Fig. 1, eqns 1 and 3). Below a certain threshold in receptivity length, the advantage of depositing a copulatory plug as a passive guarding strategy increases because its effectiveness throughout receptivity is likely to be high, and a male can leave to seek out additional matings. In that scenario, the time spent guarding receptive females is reduced and sexual selection is expected to act on traits such as male mate-searching ability and traits associated
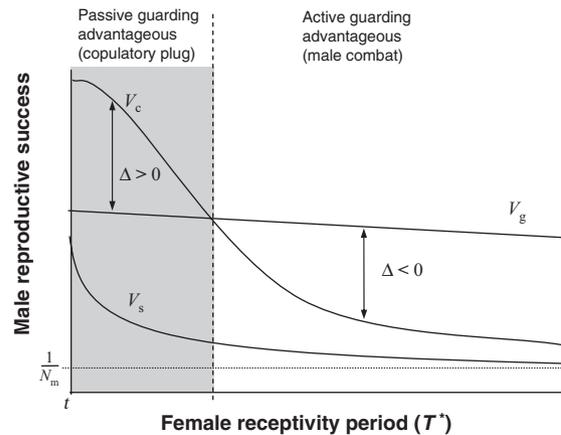
Fig. 1 The graph demonstrates the value of different male strategies in a system that is assumed polygynous with a male-biased operational sex ratio. The graph explores the values of active mate guarding, V_g, passive mate guarding through copulatory plug placement, V_c, and no form of mate guarding, V_s as a function of sexual receptivity length in females. N_m is the number of reproductive males a female is likely to encounter. The graph starts at receptivity time t, at which multple matings are possible (if multiple matings are not possible, there would be no point at mate guarding, which is not of interest in the present study).

with copulatory plug use (both offensive and defensive) rather than male body size.

Methods

Study system

Primates are particularly useful for studying the evolution of sexual size dimorphism in mammals because despite being amongst the most sexually dimorphic mammalian taxa (males generally larger than females) (Weckerly, 1998), there are several species with inexplicably weak or lacking sexual size dimorphism within both haplorrhine and strepsirrhine suborders (Appendix S1). The strepsirrhine primates (including lemurs) are unusual in this regard, exhibiting amongst the lowest sexual size ratio found in mammals (Weckerly, 1998). Because of this, most research and discussion on sexual size monomorphism in primates has been focused on lemurs despite several examples within the haplorrhine suborder.

Empirical studies indicate that sexual size dimorphism in primates is primarily driven by intrasexual selection on male size (Clutton-Brock et al., 1977; Gaulin & Sailer, 1984; Harvey & Harcourt, 1984; Mitani et al., 1996; Lindenfors & Tullberg, 1998), making them a useful group for examining the influence of male competitive strategies on the evolution of sexual size dimorphism. Given this trend, however, the lack of dimorphism found in some polygynous primates is surprising because it cannot be predicted based on social structure or

operational sex ratios (Kappeler, 2000). Many strepsirrhines of Madagascar and several monomorphic haplorrhine species live in multimale/female groups such that females are clumped in distribution with a low degree of temporal overlap in female oestrus (e.g. Pereira, 1991; Schwab, 2000; Lawler *et al.*, 2003; Pochron & Wright, 2003) and thus are predicted to exhibit strong male–male competition and selection on large male body size (Shuster & Wade, 2003).

The conundrum is why these species have not evolved substantial sexual differences in size or canine weaponry given the wide range of variability among species in physical characteristics and the numerous life-history traits thought to be important for driving sexual size differences in other species (Jenkins & Albrecht, 1991). This paradox has resulted in much discussion in the literature (van Schaik & Kappeler, 1996; Pochron & Wright, 2002; Thoren *et al.*, 2006; Kappeler & Schaffler, 2008), but proposed explanations (for review, see Wright, 1999; Kappeler, 2000) have remained unsatisfactory among researchers (Tan *et al.*, 2005; Kappeler & Schaffler, 2008) and/or the predictions do not hold across primates (Plavcan *et al.*, 2005). Although copulatory plugs have been reported for several primate species (Dixson & Anderson, 2002), their function and potential role in passive mate guarding (but see Eberle & Kappeler, 2004b) and in influencing size dimorphism within this order have been largely neglected.

Testing model predictions in primates

Hypotheses

The model suggests that the presence/absence of sexual size monomorphism in polygynous mammalian taxa could be related to the length of sexual receptivity periods which affects advantage of passive vs. active mate guarding. If, in primates, very short receptivity periods create conditions for which passive mate guarding with copulatory plugs can be more beneficial than active mate guarding, the following predictions should be upheld: (1) the use of copulatory plugs should be associated with shorter receptivity periods across primate taxa and (2) primates with copulatory plugs and the shortest receptivity periods should exhibit little to no sexual dimorphism in size across primate taxa. Our model formulation was carried out before data assembly and statistical analyses of primate traits across suborders. Although general observations within lemurid strepsirrhines did influence our formulation and should be considered when interpreting our results, we were unaware if the predictions above were likely to hold across strepsirrhines or across primate taxa as a whole.

We also examined the association of keratinized penile spines or papillae with copulatory plugs and receptivity period. Such keratinized structures are frequent within the primate order (Dixson & Anderson, 2002) and are a potential offensive agent against copulatory plugs as they

are often distally positioned and posteriorly oriented. Other roles may be in sensory feedback (Eberhard, 1985; Dixson, 1991), reducing re-mating attempts (Stockley, 2002), ovulation induction (Milligan, 1979; although unknown to occur in primates) or genital locking (Dewsbury & Hodges, 1987).

Data collection

To investigate predicted associations, we gathered data on primate traits from the literature including female sexual receptivity length, level of sexual size dimorphism, presence of copulatory plugs, presence of keratinized penile spines or papillae, mating system, body size and testis mass (Appendix S1). The references used for these data are given in Appendix S2.

Female sexual receptivity was categorized by the number of days in which females were receptive to matings. When a range of receptivity lengths was given in the literature, the average of the upper and lower values was used for the analysis. All primate species with receptivity periods of less than 1 day were rounded to 1 day for the analysis. We used the log-transformed ratio of the average male vs. female body mass as a measurement of sexual size dimorphism. We also collected data on the presence and absence of copulatory plugs, defined as a firm, solid coagulation of seminal fluid that forms in the vaginal tract after copulation. Keratinized penile structures including spines and papillae were also noted as either present or absent for each taxon. In addition, where data were available, we used relative testis mass as a measure for scramble-type sperm competition (Kenagy & Trombulak, 1986). As testis mass scales allometrically to body mass (Kenagy & Trombulak, 1986), we used residuals from a least squares linear regression of log-transformed data of testis mass and male body mass as our measure of relative testis mass (Gage, 2003). For studies in which testis volume (based on dimension) was available but not mass, we used the calculation: mass $(g) = 2 \times$ volume $(cm^3) \times 1.1$ g cm^{-3}, where 1.1 is the conversion factor (as in Moller, 1991; Harcourt *et al.*, 1995; Schwab, 2000). Harcourt *et al.* (1995) tested the validity of this method for primates with 14 genera with both measurements and found a slope near one, very close agreement of measurements and no directional bias; thus, we felt comfortable combining the two forms of data.

Statistical analysis

The potential confounding effects of shared ancestry in comparative studies mean that data from individual species cannot necessarily be considered as independent observations (Felsenstein, 1985; Pagel, 1992). To control for phylogenetic nonindependence in the data, we employed general linear models with log-likelihood statistics corrected for phylogeny with the software PHYLO.GLM v0.7 for SAS (Grafen, 1989). This analysis uses phylogenetic degrees of freedom and avoids use of

species as independent data points to assure independence of observations and to correct for phylogenetic restrictions. The phylogeny for the analysis was constructed after Purvis & Webster (1999). Receptivity periods and dimorphism values were log transformed for all analyses to meet normality assumptions.

Results

Receptivity length and copulatory plug use

Haplorrhine primates were found to have periods of female sexual receptivity averaging 11.8 days (± 8.12, $n = 30$), which is significantly longer than for strepsirrhine primates which average just 1.8 days (± 1.28, $n = 19$) ($F_{1,13} = 5.8$, $P = 0.03$). All species in our data set with female receptivity periods less than 4 days also formed copulatory plugs (Fig. 2). There were only three species, *Pan troglodytes*, *P. paniscus* and *Macaca arctoides*, with female receptivity periods greater than 4 days (14, 15 and 29 days respectively) which also had copulatory plugs. We found female sexual receptivity in primates (17 Haplorrhini and 11 Strepsirrhini) to be negatively associated with copulatory plug presence ($F_{1,11} = 10.5$, $P < 0.01$) (Fig. 2).

The degree of sexual dimorphism was significantly lower in species with copulatory plugs across primate taxa ($F_{1,8} = 7.4$, $P < 0.03$; note that the low degrees of freedom in all tests results from the phylogenetic correction), based on 55 species, including 35 haplorrhine and

Fig. 2 Relationship between copulatory plug presence and the length of female sexual receptivity in primates. The level of a species' sexual size dimorphism is coded according to the following ♂/♀ size ratios – strongly dimorphic (SD): > 1.5; dimorphic (D): 1.3–1.5; weakly dimorphic (WD): 1.1–1.3; monomorphic (MM): 0.9–1.1.

20 strepsirrhine taxa. This pattern still holds if logarithmic transformations of testis mass and body mass were included as covariates in the model ($F_{1,6} = 16.3$, $P = 0.007$) suggesting that the pattern was not driven by allometry or level of scramble-type sperm competition. Only body size, however, was a significant covariate ($\chi^2 = 4.9$, $P = 0.02$), whereas including testis mass as a covariate did not improve the fit of the model (i.e. it is not a significant covariate, $\chi^2 = 0.01$, $P = 0.45$). There was no association between plug presence and relative testis mass ($r = -0.08$, $F_{1,6} = 15.4$, $P > 0.01$) indicating that the presence of plugs is unlikely to be driven by the level of scramble-type sperm competition.

All polygynous species in the data set with female receptivity periods less than 4 days and with copulatory plugs were either monomorphic or weakly dimorphic (see Fig. 2 for graph and classification method). These included species from both haplorrhine and strepsirrhine taxa. All other polygynous species with longer receptivity periods were classified as dimorphic or strongly dimorphic except for *M. arctoides* (weakly dimorphic).

Presence of penile spines and papillae

In support of previous work by Stockley (2002), phylogenetic regression showed that primate species with keratinized penile spines and papillae had significantly shorter female receptivity periods (2.6 vs. 13.5 days) ($n = 17$ haplorrhines and 16 strepsirrhines, $F_{1,11} = 5.9$, $P < 0.04$). There was also a significant association of penile spines and papillae in primates with the use of copulatory plugs ($F_{1,6} = 9.6$, $P = 0.02$) based on 23 species including 12 haplorrhine and 11 strepsirrhine taxa and using plug presence as the independent variable. Of the 13 species we could identify with copulatory plugs in this data set, only *Varecia variegata* was known not to have keratinized penile structures; however, it has been described as having highly corrugated and sculpted penile morphology (Hill, 1953). Only one of the 10 species lacking copulatory plugs in the data set had keratinized penile spines (*Hylobates lar*).

Discussion

Passive mate guarding and the evolution of monomorphism

There are many variables that can affect the level of sexual size dimorphism in a species; however, the potential effects of passive mate-guarding strategies have received relatively little attention (Miller, 2007), particularly in mammals. In several species, there seems to be a discrepancy between predictions from sexual selection theory and empirical data of associations between life-history traits and operational sex ratios and sexual size dimorphism (Clutton-Brock, 2007). Our results suggest that a passive mate-guarding strategy may account for

such discrepancies in some species. Sexual size mono-morphism may evolve in polygynous mammals with male-biased operational sex ratios if males use a nonaggressive guarding strategy, which is not expected to favour large male size, to deal with intense mate competition. Thus, species-specific differences in the conditions that favour either active (aggressive interactions between males) or passive (e.g. copulatory plugs) mate guarding could affect the evolution of sexual size dimorphism across species.

Our model predicts that the benefits of copulatory plugs as a passive guarding strategy will be the greatest in species with short behavioural oestrus because mammalian copulatory plugs for most species degrade quickly over time (17–76 h) (Murie & McLean, 1980; Williamsashman, 1984). Under these conditions, benefits of additional matings can make this strategy advantageous over active mate guarding for male reproductive success (Fig. 1). Note that this does not imply the absence of strong male–male competition. Indeed, passive mate guarding is a potential result of such competition, but selection pressure on males is likely to act on agility, locomotor ability (i.e. search ability) and traits involved in plug formation (e.g. accessory genital glands and seminal binding proteins) rather than body size and weaponry.

Although correlation does not imply causation, the hypotheses tested were based on predictions developed from our conceptual model and we hope it encourages further empirical testing of mechanisms. Our analysis of primates confirmed model predictions by showing that copulatory plugs were generally present in species with very short receptivity periods with remarkably few exceptions. These few exceptions may represent combined strategies of active mate guarding and passive guarding with copulatory plugs or alternative plug functions. Combined strategies are outside the scope of our conceptual model but may infer selective advantages in some circumstances. Furthermore, copulatory plugs were significantly associated with short receptivity periods and with lack of sexual size dimorphism (and while accounting for testis mass and body mass) across primate taxa. Strepsirrhines, in which species are monomorphic or weakly dimorphic in size, were found to have sexual receptivity lengths 6.9 times shorter on average than that of haplorrhine taxa in which male-biased sexual size dimorphism is more common. Thus, the combination of copulatory plugs and unusually short receptivity could solve the long-standing enigma of monomorphism in lemurs as well as several haplorrhine taxa such as *Samiri* sp. (Appendix S1).

In some systems, the absence of sexual dimorphism can be explained because males are incapable of monopolizing females and thus they invest heavily in sperm production (i.e. larger testes) rather than total body size to cope with sperm competition between males (see Shuster & Wade, 2003 for review). Reliance on such scramble-type sperm competition (sperm production) and mate-searching ability has been suggested as a possible reason for monomorphism in lemurs (Pochron & Wright, 2002; Thoren *et al.*, 2006) despite male-biased operational sex ratios that are expected to make male monopolization of females possible (Kappeler, 2000) and without noticeably larger relative testis mass in relation to other primates. Our results demonstrated no association between relative testis mass and plug use across primates, suggesting that the association of monomorphism with plugs in our sample is unlikely driven by intense male competition in sperm volume or number. This is interesting because copulatory plugs are more common (Dixson & Anderson, 2002), and the evolution of semenogelin 2 (an important structural component of plugs) is accelerated in primates with promiscuous relative to monandrous mating systems (Dorus *et al.*, 2004; Ramm *et al.*, 2008, but see Hurle *et al.*, 2007) (note that plugs do not necessarily prevent mating attempts in mammals, but may only reduce the success of those successive matings). This suggests that copulatory plugs are effective enough in intense male–male competition in these species in that there is not intense selection for larger testis mass (increase in sperm number) as one might predict without considering passive-guarding strategies.

Previous work has demonstrated that the rate of sequence evolution of semenogelin 2 also correlates negatively with body weight dimorphism in primates (Herlyn *et al.*, 2007). This has been interpreted as being driven by increased sperm competition in species which lack enhanced male size. We propose an alternative hypothesis for this pattern; that copulatory plugs may reduce advantages of large male size if plugs are used for interference-type sperm competition. This might explain the lack of a positive association between copulatory plugs and relative testis mass in our study.

Copulatory plugs as an effective method for mate guarding

The premise of the mating strategy we propose requires that, for some species, copulatory plugs reduce the probability of successful insemination by subsequent males. Similar structures found in nonmammalian taxa, including invertebrates and reptiles, are frequently interpreted as having a role in interference-type sperm competition (Dickinson & Rutowski, 1989; Masumoto, 1993; Shine *et al.*, 2000). Mammalian copulatory plugs are generally thought to reduce mating success of subsequent males and/or to stimulate sperm transport and placement (Voss, 1979; Shine *et al.*, 2000; Ramm *et al.*, 2005). Although, in rodents, function of copulatory plugs appears to vary across species, clear evidence of chastity enforcement occurs in some taxa. For example, in guinea pigs (Martan & Shepherd, 1976) intact copulatory plugs were found to completely block spermatozoa from

subsequent matings. For primates, anecdotal evidence suggests that the presence of a copulatory plug in lorises can prevent or reduce a male's successful intromission for hours after the plug is deposited (Schulze & Meier, 1995, H. Shulze, personal communication). However, copulatory plug effectiveness does not have to be as complete as these examples to be advantageous.

In some species with copulatory plugs, including some strepsirrhines, males have been observed to remove plugs from previously mated females (Brun *et al.*, 1987; Schulze & Meier, 1995; Parga, 2003; Eberle *et al.*, 2007). This alone should not be considered evidence that plugs are not used for passive defence of females in the same way that usurpation of a male guarding a fertile female does not mean that active mate guarding is not a beneficial strategy. As our model demonstrates (see inequality 1), the use of passive guarding has only to increase the mating success of males over other strategies to be successful and need not block insemination from all competing males. Even an increased handling time by courting males, an increased refractory period for females or slightly reduced fertilization success of subsequent matings could be enough to make this strategy advantageous.

Plug deposition by males may also cause sexual conflict. Plug removal by female rodents (Koprowski, 1992), primates (Setchell & Kappeler, 2003; Eberle & Kappeler, 2004a) and insects (Takami *et al.*, 2008) has indeed been documented, but its prevalence and importance in altering male mating success and strategies in primates is unclear. Observations of plug removal can also be deceiving. For example, in a study of peccaries (Sowls, 1996) females were consistently observed to remove and consume copulatory plugs, but autopsy revealed that a large solid portion of the plug still remained proximal to the cervix.

Despite the presence of sexual conflict, Parker (1984) suggests that the use of copulatory plugs can be a stable strategy such that the ESS (evolutionarily stable strategy) is likely to be a Nash equilibrium (meaning that males and females are using the best strategies that they can, taking into account the strategies of their opponents). Females still attempt to remove plugs and re-mate if there is an advantage to multiple mating, even if the plugs are sometimes effective against their behaviour. In an empirical example, Takami *et al.* (2008) demonstrated that female expulsion of copulatory plugs in a ground beetle did not negate the importance of plugs to reduce successful copulations by subsequent males. Of course, copulatory plugs may lose their advantage under intense inter- or intrasexual conflict if the guarding efficiency of plugs is reduced such that inequality 1 no longer holds.

Penile spines as adaptation to copulatory plug use?

Our results show that the presence of keratinized penile spines and papillae in primates is significantly associated with copulatory plugs as well as short receptivity periods

(the latter also found by Stockley, 2002). Although male genital structures are commonly thought to be primarily the result of sexual selection by female choice (Eberhard, 1985), they may also function in male–male competition (Waage, 1979) (these explanations are not mutually exclusive). We hypothesize that the association of plugs and penile spines in primates may occur because spines are useful for removing the copulatory plugs of competitors. Defensive and offensive traits for mate competition are expected to co-evolve such that evolution of more efficient defensive traits (e.g. plugs) leads to selection for more effective offensive traits (e.g. spines) and vice versa (Parker, 1984). Although Harcourt & Gardiner (1994) stated that that penile spines in primates are probably 'unimportant' for copulatory plug removal based on an untested assumption that there was no association with copulatory plug use (an idea since perpetuated in the literature), our results suggest that this idea should be revisited.

Although functions differ across taxa, complex penile structures such as spines are known to be adaptive for sperm removal in other taxa (e.g. Waage, 1979; Fincke, 1984). Consistent with our hypothesis, we found that primates that have penile spines without copulatory plugs are exceptional, with only one species in our analysis (*H. lar*). In this species, spines may serve a different function in male reproductive strategies, but its presence does not preclude support for the role of spines in offensive sperm competition by other primate species.

The observed associations between spines, plugs and receptivity could also be due to a combined passive guarding strategy. For example, if spines increase female refractory periods between matings, our model of expected conditions (eqn 3) for plugs to be advantageous would similarly apply to spines such that shorter female receptivity periods would yield higher effectiveness of this strategy in males. The co-occurrence of male strategies could arise as an historical outcome of an arms race between males and females (Chapman & Davies, 2004; Poiani, 2006).

Lemur monormophism

The conundrum of monomorphism in polygynous lemurs has been discussed in the literature for over 20 years, but there is yet to be a hypothesis, satisfactory among researchers, that adequately explains inconsistencies with predictions from sexual selection theory and applies to other primate taxa. Previous explanations such as environmental (see Wright, 1999 for review) or phylogenetic constraints (van Schaik & Kappeler, 1996) have received much controversy and are either in contradiction to patterns observed across taxa (Plavcan *et al.*, 2005) or inconsistent with genetic and physiological studies (Roos *et al.*, 2004; Tan *et al.*, 2005; Kirk, 2006). Invoking female dominance, which is commonly observed in lemurs (Pereira & Weiss, 1991; Richard,

1992; Kappeler, 1993), as a mechanism for the evolution of monomorphic size is troublesome because female dominance is unlikely to have existed before the presence of monomorphic size (see Dunham, 2008).

Contrary to previous hypotheses, our passive mate-guarding hypothesis does not require invoking perfectly balanced natural vs. sexual selection across multiple species with different life histories and habitats (environmental constraints or selection on female size) (Kappeler, 1990; Wright, 1999) or insufficient evolutionary time (van Schaik & Kappeler, 1996) to explain why predicted intense levels of male competition has not led to active mate guarding and selection on male size. As such, passive mate guarding may be a more parsimonious hypothesis and thus invites further testing in primates and other mammalian taxa.

Conclusions and suggested research

Our results have important implications for our understanding of the ecological context of male mating strategies and the evolution of sexually dimorphic characters such as body size. They highlight that life-history characteristics, such as female sexual receptivity length, may alter the costs and benefits of male strategies and influence the strength of sexual selection on male body size even in the presence of male-biased operational sex ratios.

The prevalence of sexual monomorphism in lemurs has been a long-standing enigma in primatology and mammalogy in general. Our hypothesis that passive mate guarding may be a more advantageous strategy in species with short receptivity periods than active mate guarding provides a possible and testable resolution. In this case, sexual selective pressures on males would be focused on traits involved in post-copulatory competition and locomotor agility rather than male body size and weaponry. Empirical research is needed to further test this new hypothesis in primates and other taxa. For primates, information on time latency of plug adhesion, delay of subsequent male matings and effect of mating order on paternity under natural or semi-natural conditions will contribute to our understanding of copulatory plug function and the potential role in passive mate defence.

Acknowledgments

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Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1 Characteristics of 60 primate species taken from the literature. The presence or absence of copulatory plugs and penile spines/papillae are noted with 'Yes' or 'No'. *indicates that testes mass calculations were converted from volumetric measurements

Appendix S2 References used in compiling data on primate traits.

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