

The High Price of Success: Costs of Mating Effort in Male Primates

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Abstract While males are generally the low investing sex when it comes to offspring care, males of many species experience intense and persistent mating effort. Mating effort incurs a variety of costs which are expected to have non-negligible effects on fitness, as well as how reproductive tactics are selected and investment in mating activity is moderated over time. This special issue features contributions investigating the costs of male mating effort across primate species. Here, we place these exciting new works in context, addressing the specific types of mating effort expected for male primates and the significance of these costs for our understanding of primate life histories and socioecology.

Keywords Reproductive strategies · Glucocorticoids · Energetics · Life history · Male-male competition · Testosterone

Introduction

A fundamental premise in mammalian socioecology is that females are burdened with disproportionately high costs of reproduction in comparison with males. Female reproductive success is, therefore, predicted to be limited by access to energetic resources while male reproductive success is limited primarily by access to mates (Bateman 1948; Trivers 1972). While this paradigm has tremendous power to predict sex differences in behavior and other aspects of biology, it has skewed how male and female reproductive strategies are examined. Studies of females tend to focus on reproductive *costs* and how they are managed (e.g., resource competition, seasonality, birth spacing), whereas studies of males tend to focus on quantifying and predicting reproductive *benefits*. The primate literature, in particular, has overlooked the costs that

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males incur in the pursuit of reproductive success. This is a departure from the literature on non-mammalian species, as well as the broader spheres of life history theory, in which reproduction is recognized to carry significant physiological costs (Bell 1980; Roff 1992; Stearns 1992; Zera & Harshman 2001), and sexual selection theory, in which costs of male displays occupy a central role (Zahavi 1975, 1977; Andersson 1986; Johnstone 1995; Höglund & Sheldon 1998).

Many primates are highly social and long-lived, meaning that males experience intense and persistent mating effort during their lifetimes. Mating effort can entail direct aggressive competition with other males, indirect forms of competition such as physical, vocal, and behavioral displays, increased vigilance, altered travel and grouping patterns, and persistent or coercive interactions with females (Dixon 2013). These activities can be predicted to drive a variety of costs, including risk of injury, reduction in energetic condition, physiological stress, and the tradeoffs associated with diverting resources toward obtaining status and mating opportunities (Kappeler & van Schaik 2004). Ultimately, the costs needed to reproduce successfully can fundamentally constrain the fitness potential of males and may be, in some cases, proportionately higher or more prohibitive than the costs experienced by females (Key & Ross 1999). However, basic data on the costs of reproduction in male primates are scarce.

To remedy this shortcoming, we invited a diverse group of scholars to consider this problem in a symposium at the 82nd Annual Meeting of the American Association of Physical Anthropologists in Knoxville, TN on April 12, 2013 (Georgiev & Emery Thompson 2013). The symposium, co-sponsored by the Human Biology Association, featured 13 speakers bringing multi-disciplinary approaches to the costs of reproduction in a range of primate species, including humans. This special issue comprises nine papers from that symposium, with two additional contributions. These include studies providing detailed empirical evidence for specific costs of mating effort, evaluations of hormonal mechanisms regulating male life history tradeoffs, and evidence-based comparative models for how costs can be expected to vary across different primate mating systems and taxonomic groups. We present here an overview of the ways in which mating effort may be costly for primate males, contextualizing the contributed papers with one another and with the existing mammalian literature. This culminates in a discussion of the theoretical and empirical challenges raised by this new work, providing prospects for future research.

What Are the Costs of Mating Effort?

Physical Injury

A primary cost of male competition is the risk of injury. Among male primates, this risk is exacerbated by selection for large body size and elongated canine teeth (Plavcan & van Schaik 1992; Mitani *et al.* 1996). Not surprisingly, the species with the most dimorphic canine teeth experience high rates of wounding. For example, gelada baboons (*Theropithecus gelada*) receive severe injuries in about one-quarter of all fights, chiefly in the context of harem defense (Dunbar 1984). In Tibetan macaques (*Macaca thibetana*), 71 wounds and 3 deaths were recorded among 36 study males during a single 3-month mating season (Zhao 1994). A high incidence of wounding has

been reported in mandrills (*Mandrillus sphinx*: Setchell & Wickings, 2005), gorillas (*Gorilla beringei*: Robbins, 1996), baboons (*Papio cynocephalus*: Drews 1996; *Papio anubis*: MacCormick *et al.* 2012), and various other species (Arlet, Carey, & Molleman 2009; Smuts 1987). While wounding events are often not observed and thus cannot be directly attributed to male-male competition, most studies report higher rates of wounding during the breeding season, among males relative to females, among low-ranking or subadult individuals relative to dominants, and in locations consistent with observed male-male combat (e.g., canine slashes to the face). Among arboreal primates, fights may also lead to accidental falls from trees (Arlet *et al.* 2009). While primates are rarely directly killed in male-male combat (Newton-Fisher & Emery Thompson 2012), wounds may persist for several weeks (Archie *et al.* 2012). Aside from the risk of infection, wound healing can involve compromised foraging or traveling efficiency, withdrawal from social groups, and loss of status (Drews 1996). In this volume, Stone (2014) reports that male squirrel monkeys experience an increased prevalence of wounds, including broken bones and severe gashes, associated with concentrated male-male agonism in the mating season.

Along with the risk of injury or death from intraspecific aggression, mating investment can increase the probability of predation by reducing vigilance or by altering normal grouping patterns (Magnhagen 1991). While systematic evidence for this in primates is lacking, the risk of predation figures heavily in determining primate group sizes (van Schaik 1983; Janson & Goldsmith 1995) and may be assumed to pose an increased risk to individuals whose attention is focused on mating.

Physiological Stress

Primates exhibit elevations in glucocorticoids (chiefly, cortisol) in response to a wide range of environmental and social stressors, enabling the “fight-or-flight” response, a critical adaptation that allows an animal to produce a quick and coordinated response to a potential threat (Sapolsky 1992, 1998). While this response promotes survival, it can have damaging collateral consequences. The stress response diverts energy away from the body’s regular somatic maintenance processes, such as immune function and cellular repair, towards the immediate needs for cardiovascular and muscular performance. By straining some systems and reducing investment in others, chronic activation of the stress response can lead to a variety of adverse long-term health impacts, including cardiovascular disease, immune disorders, accelerated aging, and reduced cognitive performance (Sapolsky 1998, 2004, 2005).

Advances in non-invasive methodologies have triggered a profusion of research on stress in wild primates, with many studies asking how social status affects glucocorticoid levels. Social subordination, which often entails resource limitations and increased targeting for aggression, was assumed to be the more stressful circumstance, and in many cases it is. However, this relationship is inconsistent across species, and contradictory results are reported within the same species or even within the same group over time (Creel 2001; Abbott *et al.* 2003; Honess & Marin 2006). The behavioral correlates of dominance rank, and their variance with context, are probably more salient than rank itself. Of particular interest are studies that find that during periods of hierarchy instability the glucocorticoid levels of dominant males, who experience frequent challenges and invest more heavily in aggression, meet or exceed those of subordinates (Sapolsky 1983; Bergman *et al.* 2005;

Higham *et al.* 2013; Setchell *et al.* 2010). This suggests that investment into attaining and maintaining dominance rank, often an important determinant of priority of access to females, entails significant physiological costs. It also hints that the behaviors involved in mating competition in many primates engender stress.

Other studies, including some in this volume, have assessed more directly the influence of mating investments on glucocorticoid levels. For example, in seasonally-breeding redfronted lemurs (*Eulemur fulvus rufus*: Ostner *et al.* 2008b), tufted capuchins (*Cebus apella nigrilus*: Lynch *et al.* 2002), and Assamese macaques (*Macaca assamensis*: Ostner *et al.* 2008a), glucocorticoid levels of males were higher during the mating season than at other times. In this volume, Schoof *et al.* (2014) used hormonal information to identify the days on which white-faced capuchin (*Cebus capucinus*) females were near ovulation, finding that male glucocorticoid levels were significantly elevated when such females were present.

A key feature of the endocrine stress response is that it is highly generalized across contexts. Importantly, the fundamental effect of glucocorticoids is to increase the circulating levels of glucose should energy be needed to mount a behavioral response to a challenge (Sapolsky 1992; Genuth 1993). Thus, in addition to the potential psychosocial stress associated with elevated aggression, mating effort can also increase glucocorticoids by creating energetic stress (Bercovitch & Ziegler 2002; Muller & Wrangham 2004). This may explain why males in species such as muriquis (*Brachyteles arachnoides*) experience elevated cortisol during mating periods despite low levels of overt male contest (Strier *et al.* 1999). Accordingly, male golden lion tamarins (*Leontopithecus rosalia*), which engage in energetically-taxing paternal effort, have moderately higher levels of glucocorticoids during the birth season than during mating periods (Bales *et al.* 2005). In this volume, Schülke *et al.* (2014) report that glucocorticoid levels did not increase with mating effort in wild Assamese macaques, and mate-guarding did not impose measurable energetic costs. Finally, while Girard-Buttoz *et al.* (2014a) did find higher glucocorticoids in association with mating effort in long-tailed macaques (*Macaca fascicularis*), the effect was greater when males were guarding low-ranking (less desirable) females, when males fed less, than when guarding high-ranking females, when males were more vigilant and aggressive. Further research on mating effort and stress should follow these examples in attempting to disentangle energetic from psychosocial stressors. This is particularly important when mating seasons coincide with periods of reduced food availability.

Energetic Stress

Mating effort can bring about energetic stress in a number of ways. First, the intensity of male mating competition is a key predictor of body size dimorphism in primates (Mitani *et al.* 1996; Plavcan & van Schaik 1997). In highly dimorphic species (when males are at least ~60% larger), the extra costs of male body mass can actually raise the daily energy expenditure beyond that experienced by lactating females (Key & Ross 1999). This is before any consideration of energetically-costly behaviors associated with mating effort. Studies of other mammals suggest these costs may also be quite substantial. For example, in the minimally-dimorphic North American red squirrel (*Tamiasciurus hudsonicus*), total energy expenditure (assessed with doubly-labelled water) of males approximated that of lactating

females; expenditure was predicted by mate search effort, which was in turn constrained by low resource availability (Lane *et al.* 2010).

Several primate studies note that male mating effort reduces foraging effort, particularly when males are guarding or following females (*Papio cynocephalus*: Alberts *et al.* 1996; Rasmussen, 1985; *Macaca fuscata*: Matsubara, 2003; *Macaca fascicularis*: Girard-Buttoz *et al.* 2014b; *Macaca mulatta*: Higham *et al.* 2011). This need not indicate a reduction in caloric intake if males are able to compensate by eating foods of higher nutritional quality (c.f., lactating females: Dufour & Sauther 2002), nor does it necessarily lead to loss of condition (Girard-Buttoz *et al.* 2014b), though this is a likely consequence. As reported by Higham and Maestripieri (2014 this volume, see also Higham *et al.* 2011), high-ranking male rhesus macaques spent more time consorting, and less time feeding, during the breeding season than did low-ranking males, and suffered energetic consequences; while dominant males began the breeding season with relatively high C-peptide of insulin levels (indicating positive energy balance: Girard-Buttoz *et al.* 2011), they ended with significantly lower levels than subordinates. An analogous process may occur in squirrel monkeys wherein seasonal fattening of males predicts increased time in association with breeding females and reductions in feeding time (Stone 2014 this volume). Seasonal weight gains in some seasonally-breeding primate males may serve to buffer the high costs associated with mating effort, or may be a way to avoid paying the high metabolic costs of maintaining a robust physique year-round.

Primate males may also increase their energetic expenditure during mating effort. For example, if mates are dispersed, as in gray mouse lemurs (*Microcebus murinus*: Eberle & Kappeler 2004) or orangutans (*Pongo pygmaeus*: Knott & Emery Thompson 2013), male search effort can be costly and dependent on maintaining adequate condition. Male aggression and physical display can also be energetically costly (Muller & Wrangham 2004). Direct data on the energetic costs of aggression are rare for primates, but are elegantly shown in experimental studies of lizards (*Sceloporus jarrovi*: Marler & Moore 1988) and invertebrates (*Acheta domesticus*: Hack 1997).

For some species, energy may be every bit the constraint on male reproductive success that it is for females. Across mammals, most evidence for the energetic effects of mating arise from seasonally-breeding species, suggesting that costs might be most apparent when males experience concentrated periods of reproductive effort (e.g., *Cervus elaphus*: Clutton-Brock *et al.* 1982; *Mirounga lionina*: Galimberti *et al.* 2007; *Macaca mulatta*: Higham *et al.* 2011). However, this volume contains one study of a seasonally-breeding species (*M. assamensis*) in which males actually fed more when mate-guarding, and in which mating effort was unrelated to body condition (Schülke *et al.* 2014). By contrast, in aseasonally-breeding chimpanzees (*Pan troglodytes*), mating opportunities, and specifically aggression and copulation rates, predicted reductions in feeding time (Georgiev *et al.* 2014 this volume). In contrast to seasonal breeders, species like chimpanzees appear to experience more persistent costs over time with fewer opportunities to recover their condition.

Immune Function and Somatic Health

Reproductive effort can affect the immune system and somatic maintenance in at least two ways. First, investments in behavioral and morphological aspects of reproductive effort divert resources away from the immune system, cellular repair, and similar

survival-enhancing processes (Lochmiller & Deerenberg 2000; McDade 2003; Schmid-Hempel 2003; Harshman & Zera 2007). Second, the steroid testosterone, which promotes reproductive effort, can directly inhibit components of the immune system (Folstad & Karter 1992; Klein 2000; Schmid-Hempel 2003), a phenomenon that has received considerable attention.

Most confirmatory evidence for immune suppression by testosterone derives either from *in vitro* studies or from experimental manipulations of testosterone. Data on naturally-occurring variation *in vivo* are minimal, particularly for primates, and provide mixed evidence that testosterone (or reproductive effort writ large) impairs immunity (Muehlenbein & Bribiescas 2005; Harshman & Zera 2007). Many studies, such as the paper in this volume by Gettler *et al.* (2014), who examined intraindividual variation in Filipino men, find a positive correlation between testosterone and measures of immune function. Such positive associations may, in fact, reaffirm the costliness of testosterone, if it is the case that only high-quality males can afford its costs (Folstad & Karter 1992). In this volume, Prall and Muehlenbein (2014) provide an updated review of the literature on testosterone and immunity in primates, pointing out methodological issues, such as the challenge of accurately characterizing immune health (see also Roberts, Buchanan, & Evans 2004; Muehlenbein & Bribiescas 2005; Harshman & Zera 2007). They highlight the potential role of individual energetic condition as a mediator of trade-offs, implicate the likely potentiating effects of other hormones such as glucocorticoids, and note a significant problem with causality in that immunological challenges can themselves suppress testosterone. Several authors propose that, while testosterone can play a mediating role, sex differences in immunocompetence are the result of long-term selection on male life histories to invest in reproduction at the expense of maintenance (Klein 2000; Zuk & Stoehr 2002; Nunn *et al.* 2009).

In addition to its potential effects on the immune system, reproductive effort can increase an organism's vulnerability to other kinds of somatic stress, including both external sources (e.g., toxins, environmental stress) and internal sources (e.g., cellular damage) (Harshman & Zera 2007). A growing literature, primarily from birds and insects, focuses on oxidative stress as a potential cost of reproduction. Oxidative stress is the result of an imbalance between the damage produced by reactive oxygen species and the body's ability to repair or prevent that damage. Accumulated oxidative stress appears to be integrally involved in the aging process (Finkel & Holbrook 2000; Sohal & Weindruch 1996). Reproductive effort could increase oxidative stress via an increased rate of damage, decreased antioxidant activity, decreased investment in repair, or a combination of these (Monaghan *et al.* 2009). Studies of zebra finches, for example, associate male reproductive effort with a reduction in antioxidant activity (Alonso-Alvarez *et al.* 2004, 2006). More broadly, mating effort that involves physical exertion is expected to increase oxidative damage (Powers & Jackson 2008), though other evidence suggests that the caloric restriction experienced by many breeding males could reduce long-term oxidative stress (Sohal & Weindruch 1996). The literature on oxidative stress parallels that on immune function in that: (a) testosterone and/or glucocorticoids are suggested to mediate oxidative stress during reproductive efforts (Alonso-Alvarez *et al.* 2007; Metcalfe & Alonso-Alvarez 2010; Costantini *et al.* 2011), (b) most studies employ only limited measures of oxidative stress, (c) few naturalistic studies have been conducted, (d) the long-term health effects of oxidative stress

accrued during breeding are unknown (Costantini 2008; Monaghan *et al.* 2009). Studies evaluating oxidative stress as a cost of mating effort in free-living primates have not yet been conducted.

Infectious Disease Exposure

Just as mating effort may increase susceptibility to pathogens, it can also increase exposure to pathogens. Mating behavior can most obviously increase transmission of sexually-transmitted diseases (STDs), but may also influence ordinary infectious disease transmission if social contacts are increased during breeding or if alterations in ranging patterns affect exposure to fecal parasites (Moller *et al.* 1993; Altizer *et al.* 2003; Nunn *et al.* 2011; Rushmore *et al.* 2013). In this volume, Nunn *et al.* (2014) refine predictive models for STD prevalence in primates, integrating the interspecific variation in the influences that age and rank have on relative male mating success (see also: Thrall *et al.* 2000; Nunn & Altizer 2004).

Social Costs

In many primates, males use alliances with other males to improve rank or mating access, to defend access to mates or resources, or to engage in other cooperative efforts (e.g., vigilance: Rose & Fedigan 1995; hunting: Watts & Mitani 2002; intergroup aggression: Wilson & Wrangham 2003). Primate males often must balance the benefits of these relationships against individual success in intragroup mating competition. Thus, a cost of mating effort in multi-male groups can be strain on affiliative or cooperative relationships within groups, threatening these relationships or necessitating increased investment in relationship maintenance (de Waal 2000; Aureli *et al.* 2002; Muller & Mitani 2005). Such costs can be difficult to evaluate and to interpret, particularly when alliances are used to facilitate mating access for one or both partners (Chapais 1995; Watts 1998; Duffy *et al.* 2007). For example, in gelada baboons (*Theropithecus gelada*) males with subordinate male followers lose a share of matings to these males but benefit by maintaining a longer tenure (Snyder-Mackler *et al.* 2012).

Tradeoff with Parenting Effort

Papers in this issue focus on the mating component of male reproductive effort. However, many primates invest in some form of parenting effort, such as feeding, carrying, play, or protection (Wright 1990; Fernandez-Duque *et al.* 2009). Paternal care can promote the health and survival of offspring, but, like mating effort, consumes time, energy, and attention. While at least some forms of paternal effort can double as mating effort (van Schaik & Paul 1996), male primates generally face tradeoffs between seeking new mating opportunities and investing in current offspring (Smuts & Gubernick 1992). Testosterone appears to mediate this tradeoff, increasing during times of high mating investment and decreasing during offspring care (Wingfield *et al.* 1990; Muller & Emery Thompson 2012; Gettler *et al.* 2014).

Costs of Insemination

Sperm may also not be as cheap as widely assumed, though this is difficult to assess because sperm production is often concurrent with other kinds of effort. This has clearly been assessed in a non-primate species, the adder (*Vipera berus*), for which reproduction is divided into two delimited phases: an initial period of spermatogenesis and immobility followed by a phase of active mate search and reproductive competition. Male adders lost as much weight during sperm production as they did in the more active components of mating effort (Olsson *et al.* 1997). Aside from spermatogenesis, ejaculate production may also carry energetic costs. Using caloric analysis of ejaculates, Thomsen *et al.* (2006) estimated that, depending on male size and frequency of copulation, male Japanese macaques (*Macaca fuscata*) spend between 0.8% and 6% of their basal metabolic rate producing ejaculate during the breeding season. Sperm production is also rate-limited, meaning that effort used to inseminate one female may constrain the ability to inseminate others (Small 1988; Wedell *et al.* 2002).

Costly Signaling

Aside from direct investments in mating effort, males of many species invest in behavioral displays, vocalizations, and ornaments that can aid in signaling competitive ability, physical condition, or genetic quality to both male competitors and potential female mates (Zahavi 1977; Folstad & Karter 1992; Andersson 1994). These signals function effectively only if they are costly, thus the investment required to develop and maintain such traits are assumed to limit their expression to those males who can afford to produce them. While condition-dependence suggests that investment in mating displays should not be disproportionately costly to any male, this does not negate the importance of these expenditures in male life history tradeoffs. Furthermore, whereas the affordability of incremental costs, such as energetic investment, might reasonably be calibrated based on recent condition, risks – such as injury, predation, or death from opportunistic infection – cannot be as easily forecast.

Ornamental signals of mate quality are less pronounced in primates than in some other taxa, such as birds, perhaps because female choice is so often undermined by male-male competition or sexual coercion (Clutton-Brock & McAuliffe 2009). Similarly, status badges in primates are less important than in species where individuals lack social knowledge of others (e.g. ungulates). However, signals that reflect the current state of individuals, augmenting past knowledge, are expected to be important (Bergman & Sheehan 2013). Loud wahoo-calling ‘contests’ among chacma baboons are a well-documented example: they are hypothesized to indicate fighting ability (‘stamina’) as their intensity decreases with age and fatigue (Fischer *et al.* 2004) and males use them to assess potential rivals (Kitchen *et al.* 2013). A variety of species exhibit colored ornaments that correlate with social status (e.g., blue scota in vervets (*Cercopithecus aethiops*), Gerald 2001; red chest patches in gelada baboons: Bergman *et al.* 2009), female preference (red faces in rhesus macaques: Dubuc *et al.* 2014; Higham & Maestripieri 2014 this volume), or both (mandrills: Setchell & Dixson 2001; Setchell & Wickings 2005; Setchell 2005). Red skin is linked to androgen levels in at least some

species, waxing and waning with mating effort and/or rank instability (Setchell *et al.* 2008; Dixson 2013). While often integrated with red, blue coloration does not follow the same patterns (Dixson 2013; Setchell & Dixson 2001). Darker blue scrotal coloration was instead reported to reflect serotonergic activity in vervets, potentially marking bearers as targets for aggression (Gerald & McGuire 2007; Gerald 2001). In most cases it is not yet known how condition-dependent such traits are, what their proximate costs are, or what particular aspects of male condition they reveal.

Multidimensional Costs

It is important to recognize that the specific costs of mating effort, as outlined above, are often not independent of one another. For example, when mating effort induces a glucocorticoid response, this can also affect the immune system, increasing susceptibility to disease and impairing the wound healing process (Sapolsky 2005; Christian *et al.* 2006; Segerstrom 2007). This may explain why, over a 27-year observation period at Amboseli, low-ranking male baboons were ill more often and suffered slower recovery time from injuries than high-ranking males (Archie *et al.* 2012). In long-tailed macaques, low social status predicted susceptibility to respiratory infection following experimental exposure (Cohen *et al.* 1997). Similarly, any reductions in energy budget could lead to multiple, diverse effects on somatic health.

Exciting and Unresolved Questions

How Do the Costs of Mating Effort Impact Male Fitness?

While males clearly suffer a variety of short-term costs associated with mating effort, a critical question remains whether these costs, particularly when accrued over time, are significant enough to affect long-term survival or fitness. Long-term consequences are difficult to measure directly, but are supported by comparative analyses. Whereas males and females have similar mortality schedules in monogamously-breeding species, males live much shorter lives than females in polygynous species, where male competition for mates is more intense (Allman *et al.* 1998; Bronikowski *et al.* 2011). This may be a simultaneous consequence of the accumulated costs of reproduction and weaker selection on longevity, owing in part to the greater potential payoffs for reproductive effort and greater limitations on breeding tenure in males versus females (Clutton-Brock & Isvaran 2007). However, the timing of mortality events in primates is telling and reveals a proximate role for mating effort in male mortality. In rhesus macaques, females die at higher rates during the birth season, when their costs of reproduction are highest, whereas males die at higher rates during the mating season (Hoffman *et al.* 2008). A similar clustering of male deaths during the mating season is observed in gray mouse lemurs (Kraus *et al.* 2008).

The costs of male mating effort can also affect fitness by constraining reproductive lifespan. Across mammals, breeding tenure decreases as the degree of polygyny increases (Lukas & Clutton-Brock 2014). Whereas low female numbers and low birth rates generally signal greater intensity of male competition (Mitani *et al.* 1996), more frequent mating opportunities and a higher number of females predict short tenure

length in cross-species comparisons (Lukas & Clutton-Brock 2014). This suggests that the frequency, rather than the intensity of mating effort, may limit male reproductive lifespan. In similar fashion, Higham and Maestripieri (2014 this volume; Higham *et al.* 2011) propose that male fitness in rhesus macaques is determined by the ability to endure repeated mating competition over time (c.f. Andersson 1994).

How Do Costs of Mating Effort Influence Male Mating Tactics?

Male mating tactics vary in both costs and benefits, covarying with individual features such as competitive ability, energetic condition, and age, and with contextual factors, such as the number of competitors and of sexually-available females, and the availability of food (Dominey 1984). A high payoff strategy may entail costs that are prohibitive for some males. Additionally, the efficacy of many tactics is rank-dependent, meaning that males must invest in status competition over a long period of time to succeed. Thus, primates frequently adopt alternative mating tactics that offer a low-cost possibility of siring infants (Setchell 2008; Taborsky *et al.* 2008; van Schaik *et al.* 2004). Examples include the use of sneaky copulations (e.g., *Cebus apella nigrilus*: Alfaro 2005) and consortships (e.g., *Pan troglodytes*: Wroblewski *et al.* 2009) by subordinates in mating systems in which competition is high and alpha males secure the majority of matings. In an extreme example, many orangutan males exhibit prolonged developmental arrest, which may be a strategy to delay the high costs associated with the large-bodied, flanged phenotype that females prefer (Knott *et al.* 2010; Knott & Emery Thompson 2013); while retaining a smaller stature, these males avoid the high costs of direct competition with flanged males and can afford to range more widely in search of females. Variation in male mating tactics across species might also be predicted to correspond with costs of mating effort. For example, male hamadryas baboons (Swedell & Schreier 2009) and chimpanzees (Muller *et al.* 2011) use conditioning aggression towards females to increase the effectiveness of mate-guarding. By directing aggression towards smaller females and altering their behavior, males minimize the costs of riskier conflicts with competing males. Female choice, when it is not predicated on male dominance, can also alter the costs and benefits of specific types of mating effort (Qvarnström & Forsgren 1998; Soltis *et al.* 1997). We suggest that a more comprehensive understanding of primate mating behavior may be gained by closer attention to the costs, and not just the benefits, associated with pursuit of different male mating tactics. A particularly promising opportunity for future long-term research is an assessment of how the costs of mating effort interact with individual condition to predict the adoption of different tactics by an individual male over his lifetime.

Evidence for the costs of male mating effort in primates leads to the prediction that males will modulate effort according not only to their own condition but to the quality of mating opportunities available. Thus, just as the costs of producing infants drive mate selectivity by females (Small 1992), the costs of competition and mate guarding should drive a certain degree of selectivity by males. Males may be expected to invest more intensively in mates that have the highest probability of conceiving and raising offspring successfully. Thus, the bulk of available evidence for male choice in primates indicates preferences for high-ranking females, who have preferential access to food resources, and for parous females, who have higher offspring survival rates (Anderson 1986; Keddy-Hector 1992; Muller *et al.* 2006; Setchell & Wickings 2006; Georgiev *et al.* 2014 this volume; Girard-Buttoz *et al.* 2014a).

Recent studies indicate that males in at least some species invest according to the probability that a female will conceive at that time (*Saguinus oedipus*: Ziegler *et al.* 1993; *Macaca fascicularis*: Engelhardt *et al.* 2004; *Pan troglodytes*: Emery Thompson & Wrangham 2008; *Cebus capucinus*: Schoof *et al.* 2014 this volume).

How Do Costs of Mating Effort Contribute to Variance in Male Reproductive Success?

To the extent that costs of mating effort affect the affordability of different mating tactics, these costs can contribute to variance in male reproductive success. Costs therefore figure prominently in evaluating evolutionary models for reproductive skew, and by extension affect the genetic structure of primate groups. ‘Concession’ models posit that dominant males cede a proportion of matings to lower-ranking males as an incentive to keep them in the group or to prevent them from mounting status challenges (Vehrencamp 1983; Keller & Reeve 1994; Reeve & Shen 2013). Central to these models is the assumption that alpha males would otherwise have the ability to completely control access to mates, and this assumption is unlikely to be met in most primates (Clutton-Brock 1998). Alternatively, ‘tug-of-war’ models posit that, at least under some circumstances, alpha males are simply unable to monopolize all mating opportunities (Reeve *et al.* 1998). One key reason that males may lose a share of matings is that they are unable to afford the costs needed to successfully guard all receptive females. While variants on the ‘tug-of-war’ model have some power to predict variation in reproductive skew in primates (Kutsukake & Nunn 2006), the assumptions of these models have also been questioned (Port & Kappeler 2010). In this volume, Port and Cant (2014) question the traditional model specifications which assume that the costs invested in individual mating effort are experienced as a loss of group productivity. They propose a new dynamic tug-of-war model that operationalizes the costs of mating effort in terms of their potential impacts on male survival and considers how these costs covary with the overlap in female receptive periods. Their theoretical work highlights the need for greater detail on the specific costs of reproduction across a range of species in order to test their predictions. Data on strepsirrhines and New World monkeys are particularly needed.

Conclusion

In sum, male mating effort in primates entails significant costs experienced across a number of dimensions and time-scales. The costs of mating effort are often overlooked due to compensating reproductive advantages and the assumption that costs are proportional to individual ability to pay. However, recognition of these costs has important ramifications for understanding the dynamics of primate social groups, including the degree of reproductive skew, the variety of reproductive tactics employed by males, the influence of male mate choice, and the stability of group leadership. Preparing for and bearing the costs of mating can be expected to exert critical influences on male life history in primates. Because most primates live in stable social groups and have slow life histories, males experience persistent competition for status, repeated and intense periods of mating investment, and changing opportunities as ecological and social parameters shift. Thus, successfully managing mating expenditures over the long-term is integral to male fitness. The reproductive challenges faced by male primates differ in both kind and degree from the dominant literatures on

sexual selection in birds and insects, making empirical data all the more essential for revising and refining evolutionary models (Kappeler & van Schaik 2002, 2004). The papers in this volume collectively represent a major contribution to the knowledge about the evolutionary processes shaping primate males and illustrate novel methodologies, syntheses, and theoretical approaches. We anticipate that this volume will stimulate substantial new work in this area and lay the groundwork for new frontiers in primatology.

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