# SAPTENT

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# LETTER FROM THE EDITOR

On behalf of my fellow editors, I am thrilled to present to you the sixth volume of *Sapient*, the Undergraduate Journal of Biological Anthropology. This journal was created to showcase the impressive academic work of undergraduate students, and to foster community and intellectual curiosity across all domains of Biological Anthropology: namely Human Variation and Genetics; Evolutionary Theory and History; Primate Behavior and Ecology; and Paleoarcheology and Morphology.

This year, the editorial board has continued to integrate students from various departments and schools in and around Columbia University. We worked closely and holistically with all contributing authors throughout the editing process, which continues to enrich our intercollegiate community. On behalf of the entire *Sapient* board and our faculty liaison, Professor Jill Shapiro, I am eager to announce the relaunching of the *Sapient* website come September 2018. This reinvigorated presence, both online and on campus at Columbia and beyond, will be elevated by new events and opportunities for editorial writing throughout the school year.

We hope that you will continue to follow our evolution as an academic and extracurricular hub, and that you enjoy the sixth volume of *Sapient* as much as we loved creating it.

- Max Rose Zimberg

# **TABLE OF CONTENTS**

Paleoarcheology and Morphology



**Evolutionary Basis of the Honing Premolar in Female** *Cercopithecus* Luke Fannin, The Ohio State University

# Human Variation and Genetics



*To the Bone*: Impacts of Anorexia Nervosa on Bone Health in Adolescent Girls Amen Wiqas, Barnard College

Primate Behavior and Ecology & Evolutionary Theory and History



**Explicating Female Promiscuity in Non-Human Primates** Sofia Schembari, Columbia University

# *"That's not fair!"*: An Empirical Survey of Inequity Aversion in Non-Human Primates

25 Max Rose Zimberg, Columbia University

# **Evolutionary Basis of the Honing Premolar in Female** *Cercopithecus*

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# **INTRODUCTION**

### Canine dimorphism

Dental dimorphism is a characteristic of many primate taxa, with males tending to possess larger, more projecting maxillary canines than females (Leutenegger and Kelly 1977; Plavcan and van Schaik 1993; Plavcan 2001). A prominent hypothesis is that large male canines evolved through sexual selection as result of intense intrasexual competition for mates (Leutenegger and Kelly 1977; Harvey et al. 1978; Walker 1984; Leutenegger and Cheverund 1985; Kay et al. 1988; Kappeler 1990; Plavcan and van Schaik 1992; Plavcan et al. 1995; Plavcan 2001). Because male fitness is largely dependent on the number of females he can inseminate (Trivers 1972), it would be selectively advantageous for a male to possess traits that help monopolize mating access to females by winning competitions (Plavcan and van Schaik 1992; Plavcan et al. 1995). Furthermore, recent studies have been able to relate large male canine length to high dominance rank (Galbany et al. 2015) and increased numbers of offspring sired (Leigh et al. 2008), suggesting that the sexual selection hypothesis plays a major role in the exaggeration of male canines to increase reproductive output.

Nevertheless, sexual dimorphism is a function of both male and female traits (Plavcan et al. 1995). Across primate species, female canine length exhibits just as much variation as is present in males (Plavcan 1990) and many authors have reported females engaging in intense (sometimes lethal) intrasexual aggression that results in canine-inflicted wounds (Gust and Gordon 1991; McGraw et al. 2002; Payne et al. 2003). Plavcan and colleagues (Plavcan and van Schaik 1993; Plavcan et al. 1995; Plavcan 1998) showed that across 94 primate species, female canines were larger in those species that engage in intense female-female competition (either between or within groups). Only females that compete intensely in coalitions exhibited a lack of canine reduction, because having more allies reduces the need for individual contribution in aggressive contest (Plavcan et al. 1995). If larger canines benefit females competing for access to resources (a driver of female fitness; see Wrangham

1980), then selection is expected to favor enlarged female canines as weapons to win contests, much like the male pattern (Plavcan *et al.* 1995). Overall, these studies highlight the need to view primate dental dimorphism as a function of both male and female trait evolution (Plavcan 2001); and to consider how dental variation may have an adaptive role in both sexes before establishing hypotheses for its evolution.

### Canine-premolar honing complex

Hypotheses regarding the adaptive significance of canine length can also inform studies of dental morphology in other areas of primate dentition, as some features may not be readily explained as adaptations of mastication. This study focused such analyses on the lower third premolar (now referred to as P<sub>3</sub>). The primate canine is a single component in what is referred to as the *canine-honing complex*: a mechanism of dental attrition, present in both sexes across primate species (Greenfield 1992), by which the elongated *mesiobuccal surface* of the lower third premolar (i.e. P3 or P2 in New World primates) occludes with the *distolingual surface* of the maxillary canine. This action sharpens the canine surface and maintains its functional utility as a potential weapon (Zingeser 1969; Walker 1984; Delezene 2015).



**Fig. 1:** Examples of the canine-honing complex. **Left:** Male *Cercopithecus diana* (photo taken by author). Arrow indicates occlusion between the upper canine and lower premolar. **Right:** Diagram of the canine-honing complex from Zingeser (1969). Notation "3" represents the *distolingual surface* of the canine tooth, while "III" represents the *mesiobuccal surface* of the P<sub>3</sub>.

Recent research into the canine-honing complex has shown that both the upper canine and the honing P3 exist in what is referred to as a phenotypic module (Delezene 2015). This means that during the coevolution of traits for which the module is defined, a change in the dimension of one dental trait will result in a proportional change in the other trait. In terms of the canine-honing complex, the evolution of a longer canine would require a longer premolar honing surface to maintain its functional utility (Zingeser 1969; Delezene 2015). Delezene (2015) showed that, across a sample of anthropoid species, a significantly positive correlation exists for both males and females between upper canine height and P3 honing cusp length. This conclusion, that the canine-honing complex is selectively maintained in both sexes, contradicts previous studies (e.g. Greenfield 1992), which posits evolutionary significance in only male individuals.

### Why Cercopithecus?

Guenons (pertaining to those monkeys in the genus Cercopithecus) are a species rich group of medium-sized African monkeys that tend to live in single-male, multi-female social groups (Jaffe and Isbell 2011). Although Cercopithecus is a sexually dimorphic genus, both males and females are active participants in between-group dynamics, including aggression (Jaffe and Isbell 2011). Female guenons exhibit high levels of territorial inter-group aggression because females are the main participants in territorial defense, while unit males take on secondary roles in territorial calling and mate defense during the breeding season (Cheney 1981; Cheney 1987; Hill 1994; Jaffe and Isbell 2011). In addition, several researchers have described females inflicting fatal wounds on extra-group females using their upper-canines (McGraw et al. 2002; Payne et al. 2003). McGraw et al. (2002) posited that the variation in female canine height across Cercopithecus could be explained by differences in between-group competition and aggression, although no extensive behavioral data were provided. Such evidence exposing lethal aggression and repeated biting between unit female guenons and extra-group females supports the potential selective advantage of large, weaponized canine teeth in females (Mc-Graw et al. 2002; Payne et al. 2003). Among guenon taxa, less is known about the correlations between P<sub>3</sub> honing cusp enlargement and other characteristics like elevated canine height and aggressive behaviors, such as intense contest competition. Hypotheses and predictions

Although several studies have investigated the relationship between variation in upper canine tooth size and in levels of intrasexual contest competition among *Cercopithecus* females (Plavcan *et al.* 1995; McGraw *et al.* 2002), few studies have investigated lower third premolar honing cusp length variation, intrasexually, within this genus to see if this pattern is maintained. The author's study is interested in determining if the P<sub>3</sub> is potentially capable of revealing similar insights into competitive regime studies, given its modular integration with the canine. If the honing complex forms a modular system and selective variation in the height of female upper canines can be related to the intensity of contest competition among females (Plavcan et al. 1995; McGraw et al. 2002), then it can be hypothesized that the P3 should also reflect this selective canine variation. Specifically, one could predict that patterns of female P<sub>3</sub> length among Cercopithecus females should emulate the pattern seen in the upper canine teeth, and variation among females should be significantly different. Since males have been shown to display similar trends in modularity (Delezene 2015), male differences will also be assessed with the same aforementioned predictions. We predict that P<sub>3</sub> dimorphism among *Cercopithecus* species should also be similar to upper canine dimorphism, if male and female differences are similarly reflected in both teeth of the module. If female premolar honing cusp lengths significantly differ across Cercopithecus species, and this variation generally follows the same pattern as the height of the upper canine, then the lower  $P_3$  honing cusp could potentially be used, along with the upper canine, to inform predictive competitive regime studies among both extinct and extant Cercopithecus spp.

# **METHODS**

### Materials

*Cercopithecus* spp. skeletal materials were utilized from three separate collections: The Field Museum of Natural History, Chicago, Illinois; Harvard University Museum of Comparative Zoology, Cambridge, Massachusetts; and The Ohio State University Department of Anthropology, Columbus, Ohio. Specimens were chosen based on whether the lower P3 honing cusp was fully intact or mildly worn; individuals with broken, chipped, or moderately to extremely worn cusps were not measured. In total, 158 crania from 7 *Cercopithecus* species were measured and used for analysis, with similar sample sizes of males (n=77) and females (n= 81) (Table 1).

### Process

Digital calipers were used to measure honing cusp length (mm) for both the left and right  $P_3$ , following the measurement protocol outlined in Delezene (2015). These measurements were averaged for each individual to produce an overall  $P_3$  honing cusp length for that specimen. Average mesial-distal lengths of the lower second premolars (M<sub>2</sub>) were used as a proxy for body size (Gingerich 1977) and average  $P_3$  honing cusp length was scaled to this measure to produce a relative  $P_3$  honing cusp length to use in statistical analyses. These scaled measurements were also used to calculate sexual dimorphism in relative  $P_3$  honing cusp length for each species, defined as relative male length/relative female length (Greenfield 1992; McGraw *et al.* 2002).

Same-sex mean comparisons across multiple species in relative honing cusp length were carried out with non-parametric Kruskal-Wallis tests, due to violations of normality and low sample sizes for some species. For all species-level statistical analyses, *Cercopithecus preussi* females were omitted due to the small sample size; however, this species still contributed to overall descriptive statistics presented in the paper. For all analyses,  $\alpha$  was set at 0.05 for significance.

Species	Males	Females	Total	
C.diana	4	7	11	
C.ascanius	6	4	10	
C.preussi	4	2	6	
C.mitis	30	34	64	
C.aethiops	10	13	23	
C.nictitans	12	17	29	
C.cephus	11	4	15	
Total	77	81	158	

Table 1: Species and sample sizes for all measured Cercopithecus crania.

Table 2: Relative dental measures (mm), paired comparisons, and sexual dimorphism in Cercopithecus taxa analyzed.

Species	Male Relative C <sup>1</sup> Height <sup>1</sup>	Male Relative P₃ Honing Cusp Length	Female Relative C <sup>1</sup> Height <sup>2</sup>	Female Relative P3 Honing Cusp Length	Sexual Dimorphism in C1 Height <sup>2</sup>	Sexual Dimorphism in P3 honing cusp length
C. ascanius	0.408	1.40	0.195	1.32	1.56	1.06
C. cephus	0.428	1.46	0.049	1.14	1.77	1.28
C. diana	-	1.66	0.262	1.14	1.62	1.46
C. mitis	0.396	1.51	0.029	1.06	1.97	1.42
C. aethiops	0.421	1.46	0.093	1.12	1.81	1.30
C. nictitans	0.371	1.46	0.191	1.09	1.61	1.34
C. preussi	-	1.53	0.146	0.981	1.77	1.56





**Fig. 2:** Lower right  $P_3$  of a female *Cercopithecus diana*. Arrow depicts where honing cusp measurement was taken in (mm). Note the particularly worn mesial-buccal face and wear facet.

# RESULTS

Across all taxa, males possessed larger relative honing cusp lengths than females, which is cosistent with previous studies that have described similar trends in P3 among primate species (Greenfield 1992; Plavcan 2001). Male relative honing cusp length ranged from 1.66mm in C. diana to 1.40mm in C. ascanius and female relative honing cusp length ranged from 1.32mm in C. ascanius to 0.981mm in C. preussi. Relative P3 honing cusp length patterns did not follow similar trends observed in relative upper canine lengths caluclated in other studies (Table 2). Overall, P3 dimorphism indices across all taxa were generally similar in magnitude, ranging from 1.06 in C. ascanius to 1.56 in C. preussi (Table 2); however, like relative P3 honing cusp length, none of these dimorphism values closely matched simlar dimorphism calculations for the upper canines of these species (Mc-Graw et al. 2002). Within males, there is no significant mean difference between honing cusp length across the seven species

compared ( $\chi^2$  =7.07, p=0.3142; Fig. 3); the same trend was also observed in females across the six species compared ( $\chi^2$ =6.13, p=0.2941; Fig. 4).

# DISCUSSION

Our prediction, that species with larger canine lengths would have larger premolar honing cusp lengths, was not found to be consistent across both sexes and did not align with a strict modular change hypothesis (Table 2). While there was variation in P<sub>3</sub> honing cusp length across guenon male and females (Fig. 3; Fig. 4), this variation was not significant. Additionally, for all guenons, honing cusp length showed little sexual dimorphism compared to canine heights (Fig. 2); moreover, males and females exhibited more similarity in premolar honing cusp length (as indicated by lower levels of dimorphism) than they did in upper canine height. As per the strict canine-honing complex modularity hypothesis, it is expected that both dental components would show similar degrees of sexual dimorphism across all of the species measured, reflecting coordinated changes in length between both teeth.

Our results indicate that a strict modular hypothesis does not explain the variation (or lack thereof) in P3 honing cusp length across Cercopithecus spp. Several alternative hypotheses can be proposed, such as the theory of mosaic or non-modular evolutionary change (Delezene 2015). Interestingly, Delezene (2015) noted that while modular change in the honing complex is a significant trend across a wide range of anthropoid primates, there is still some variation in P<sub>3</sub> length that cannot be fully explained by canine height. He reasoned that this represents the complex components' ability to evolve mosaically in some primate groups, by which changes in canine height may not lead to a corresponding change in P3 honing length (Delezene 2015). As displayed in Fig. 3 and Fig. 4, both male and female guenons retain a general monomorphism in relative honing cusp length across species, while previous studies have found their canines more variable in expression (McGraw et al. 2002). Explanations for why both males and females exhibit similar patterns of variation across species was not investigated in this study; however, one could hypothesize that such variation results from the different roles that the upper canine and the honing P<sub>3</sub> play in the weaponized function of the honing complex. For example, canines are the most prevalent weapons used in competitive interactions and can inflict lethal wounds (Gust and Gordon 1991; McGraw et al. 2002; Payne et al. 2003). By contrast, the premolar honing surface plays a more passive role, as it primarily functions to maintain the canine (Zingeser 1969; Walker 1984). Perhaps the asymmetry in dental function, coupled with the potential for mosaic, non-modular change in this complex (Delezene 2015), renders the canine more evolutionarily sensitive to intensifications in between-species competition for male and female guenons alike. Overall, this could explain why marked height differences in the upper canines of many female guenons were not similarly reflected in honing cusp length.

Alternatively, the lesser degree of dimorphism in the P<sub>3</sub> honing cusp, as compared to the upper canine height (Fig. 2), could be the result of a potential correlated response in females, which may prevent the P<sub>3</sub> length and upper canine size from changing proportinally to one another (Lande 1980; Greenfield 1992; Greenfield and Washburn 1992). Lande (1980) proposed that if the genes for a given trait are not located on a sex chromosome, then selection for a trait in one sex could also inadvertenly lead to the expression of that trait in the other sex; once the trait becomes unfavorable to maintain, however, there will be genetic decoupling of the trait between the sexes (Plavcan 2001). Previous studies (Greenfield 1992; Greenfield and Washburn 1992) hypothesize that the enlarged female P<sub>3</sub> condition in cercopithecids is due to a correlated response via selection to increase the length of the male P3 to match an enlarged upper canine. Additionally, Delezene (2015) implies that the correlated response may represent a source of potential P<sub>3</sub> length variation in female Cercopithecids that is not explained by the upper canine. It is possible, at least among females of tested Cercopithecus species, that a correlated response mechanism explains reduced levels of dimorphism in the P<sub>3</sub>, as well as the subsequent lack of strict modular coordination with the canine. In contrast, it is more difficult to explain why males of different Cercopithecus species in this study are also monomorphic in P<sub>3</sub> honing length; perhaps the P<sub>3</sub>'s nonsuceptibility to external selective pressures, given the aforementioned supporting role the P<sub>3</sub> plays to the canine, explains why males do not show similar coordinated changes. This could be coupled with a correlated response mechanism in females, resulting in both sexes being relatively monomorphic.

Notwithstanding the wide range of relative canine length across both sexes in Cercopithecus spp. (Plavcan et al. 1995; Mc-Graw et al. 2002), relative P3 length did not differ significantly among females in the six species tested herein (Fig. 3; Fig. 4). Moreover, although Plavcan et al. (1995) and McGraw et al. (2002) hypothesize that female maxillary canine height differences across various primate species (including Cercopithecus spp.) could be the result of varied competition intensity between social regimes, results from this study suggest that the P3 honing cusp cannot be used to make these same distinctions or evolutionary interpretations. Unfortunately, the social relationships and competitive regimes of many of the female guenons used in this study are still unknown, which means this hypothesis cannot be verified (McGraw et al. 2002). Regardless, the data support the conclusion that P3 honing cusp length, even if appropriate behavioral data were present, is less informative than the upper canines in regard to competitive regime differences, due to their general monomorphism across species. Future studies

Future experiments should collate  $P_3$  honing cusp measurements with observed levels of competition, both among *Cercopithecus* spp. and species of other genera, in order to fully understand if P3 morphology is truly unrelated to documented levels of competition. The increasing amount of studies on female competitve regimes across *Cercopithecus* spp. should facilitate this comparison. Furthermore, species-level studies that

Males: Relative P3 Honing Cusp Length vs. Species 2.0 1.8 1.6 1.4 Relative P3 Honing Cusp Length 1.2 1.0 0.8 0.6 0.4 0.2 C.aethiops C.ascanius C.cephus C.diana C.nictitans C.preuss Species

Females: Relative P3 Honing Cusp Length vs. Species



Fig. 3: Box-and-whisker plot, illustrates the distribution of honing cusp lengths between different **male** *Cercopithecus* spp. Mean differences across species were not significant when subject to statistical analysis.

**Fig. 4:** Box-and-whisker plot illustrates the distribution of honing cusp lengths between different **female** *Cercopithecus* spp. Mean differences across species (excluding *C. preussi*) were not significant when subject to statistical analysis.

emphasize premolar variation in relation to social competition should help to enlighten fossil studies of primate dentition; knowledge of the broad framework of extant dental variation and its relation to social variables may be helpful in interpreting the variability in dental morphological that exists among fossil specimens.

# Implications for hominin studies

Notably, independent changes within the canine-honing complex have been extrappolated to other dental reduction patterns in hominins (Delezene 2015). Specifically, multiple studies have supported mosaic changes in the honing complex in early members of the lineage (Ward et al. 2010; Manthi et al. 2012; Delezene 2015), which hypothesize that selection has targeted different aspects of each tooth in the complex seperately. For most early hominin taxa, patterns of dental morphology seem to indicate that reduced maxillary canine crown height preceded any functional changes in the P<sub>3</sub>; this is evident in early hominin species like Ardipithecus ramidus (4.4 mya), which posseses a sectorial P<sub>3</sub>, despite a lack of honing wear and significantly reduced canine height (Delezene 2015). Major changes in P<sub>3</sub> occusal morphology, including advanced molarization, are not seen until the Australopithecus anamensis to Australopithecus afarensis transition in geologically younger fossils (Delezene and Kimbel 2011). It seems there were significant portions of hominin evolution where the P<sub>3</sub> remained stable, while the upper canine was able to evolve and reduce in size, which aligns with other investigators' hypotheses of mosiac evolutionary change (Ward et al. 2010; Manthi et al. 2012; Delezene 2015). The relative independence of these two teeth, even in the context of this current study, is helpful in further explaining the independent

functional paths of both canine and premolar variation in the evolution of early members of the hominin lineage (Delezene 2015). Further speculations can be made about how changes in the hominin social system, among females in particular, may have driven this change in the honing complex; for example, how changes in competitive regimes can influence selection pressures on canine teeth and their ultimate reduction in size. P3 reduction may not be equally affected by competitive regime changes; however its increased molarization during hominin evolution may be related to dietary changes that occurred after intial canine reduction (Delezene and Kimbel 2011). As such, future studies must investigate how the P<sub>3</sub> might be used in extant primates for non-honing purposes, including mastication, to model independent selective pressures that could have reshaped the hominin P<sub>3</sub> away from a sole honing function. For instance, several species of extant monkeys (e.g. Cercocebus atys) use their premolars to access hard objects in their diets (Daegling et al. 2011; McGraw et al. 2011), so further research into primate diets and oral processing behaviors could be useful in interpreting the selection patterns and potential implications of P<sub>3</sub> processing on the evolution of later hominin dentition.

# **CONCLUSION**

Canine dimorphism in *Cercoptihecus* spp. (i.e. guenons) has been hypothesized to be a function of canine height evolution in both males and females. Variation in male canine height across *Cercopithecus* spp. has been related to intense competition for mates, while variation in female canine height among *Cercopithecus* spp. has been related to the intensity of contest competition between social groups for resources. Structurally, the  $P_3$  exists in a honing complex with the upper canine, and both components are hypothesized to exhibit coordinated evolutionary changes as a phenotypic module. Unlike the upper canine, however, the  $P_3$  in *Cercopithecus* does not appear to be a useful marker for gauging potential competitve regime differences in females between species.  $P_3$  variation patterns do not strictly match observations in the upper canine, and moreover do not differ significantly across species. Hypotheses that predict  $P_3$  stability in social interactions and/or a potential correlated response to male  $P_3$  length may explain the  $P_3$ 's lack of evolutionary plasticity and its strict adherance to modular change among female *Cercopithecus*.

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# *To the Bone*: Impacts of Anorexia Nervosa on Bone Health in Adolescent Girls

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# **INTRODUCTION**

Anorexia nervosa, often referred to as simply anorexia, is an eating disorder characterized by food restriction and significant weight loss. The diagnostic criteria for anorexia include the restriction of food, fear of weight gain, and distorted body image (Hudson et al. 2007). Anorexia is quite prevalent, with 0.9% of American women suffering from it during their lifetime (Hudson et al. 2007). Those who suffer with anorexia are at a higher risk of premature death, marked by a standardized mortality rate of 10.5, or the ratio of observed to expected deaths (Birmingham et al. 2005). Anorexia dramatically affects various morphological structures, ranging from the cardiovascular to the pulmonary and gastrointestinal (Mehler and Brown 2015), and namely, the skeletal system. This article will describe the pathogenesis and effects of anorexia nervosa on bone density and bone metabolism, specifically among adolescent girls. Finally, this article will discuss the processes of bone recovery during and after treatment, as well as current treatment options for anorexia symptoms.

# **METHODS AND RESULTS**

Adolescence, which is characterized by the onset of puberty, is an important period in bone development (Bailey 1996). A notable increase in bone mineral density is observed in girls between the ages of 11 and 14 (Theintz *et al.* 1992), and approximately 90% of bone mass is achieved by the time one reaches 18 years of age (Bailey *et al.* 1996). Increase in bone mass occurs most rapidly during adolescence, with 25% of the peak bone mass being acquired during the two-year period surrounding peak height velocity, which for girls is at roughly 12 years of age (Bailey *et al.* 1999). Furthermore, the greater the peak bone mass achieved as a young adult, the more an individual can afford to lose bone mass in old age without getting a fracture, thus reducing the individual's risk of developing osteoporosis (Stagi et al. 2013). Osteoporosis is the condition of reduced bone mass, resulting in increased fragility of the bone and a higher risk of fractures (Misra and Klibanski 2006). A low peak bone mass may lead to a higher risk of osteoporosis and its complications such as fractures (Stagi *et al.* 2013). Given the importance of this period in bone development, it is important to understand the short-term and long-term effects anorexia has on bone density and bone metabolism.

One of the major consequences of anorexia is low bone mineral density (BMD). Low BMD is a result of bone loss, reduced bone formation or a combination of both (Misra et al. 2016). Several studies (Bachrach et al. 1990; Jagielska et al. 2002) have consistently demonstrated a correlation between low bone mineral density and anorexia in adolescent girls. An early study (Bachrach et al. 1990) indicated that 12 adolescent girls with anorexia (n=18) had lumbar bone mineral density more than two standard deviations below lumbar spine BMD of the control group. It is important to note that over half of the girls who demonstrated this degree of low bone density had exhibited symptoms of anorexia for less than a year; underscoring the large impact this condition can have on adolescent girls even in a short amount of time (Misra and Klibanski 2006). Another study (Jagielska et al. 2002) measured lumbar spine BMD as well as total body bone density, in girls (n=61) aged 14.7±2.16 years who suffered with anorexia for a duration of 12.9±15.1 months, which the authors considered a relatively short period of illness, undernutrition, and secondary amenorrhea. Despite the short duration of symptoms, 24% of patients experienced a reduction of total body BMD and 37% showed a reduction of lumbar BMD (Jagielska et al. 2002). In another study (Misra et al. 2004) of adolescent girls (n=60) with an average duration of 10.5±9.8 months, measures of BMD in the lumbar spine, hip, and femoral neck were all significantly lower in girls with anorexia than in control subjects. All of these studies emphasize the speed at which anorexia can make a dramatic impact on bone mineral density.

In order to study changes in bone metabolism in young female anorexia patients, several studies (Lennkh *et al.* 1999; Soyka *et al.* 1999; Soyka *et al.* 2002) have measured biochemical markers of bone metabolism and compared these levels to healthy controls. In one study (Soyka *et al.* 1999), these markers included osteocalcin (OC), bone specific alkaline phosphatase (BSAP), C-terminal propeptide of type I procollagen (PICP), deoxypyridinoline (DPD), and aminoterminal cross-linked telopeptide of type I collagen (NTX). All of these markers are involved in the process of either bone resorption or bone formation, being either the products of osteoblasts or collagen types (Seibel 2005). OC and BSAP were significantly lower in anorexia patients than in controls, while DPD and NTX did not significantly differ between the groups (Soyka et al. 1999). Because OC and BSAP mark bone formation and DPD and BSAP indicate bone resorption, this study suggests that, deficits in bone formation lead to weakened bone, rather than to an increased rate of resorption. However, a follow up study (Soyka et al. 2002) discovered that baseline levels of OC, BSAP, DPD, and NTX in adolescent female anorexia patients were significantly different from control levels, suggesting that dysregulation of both bone formation and bone resorption are involved in the resulting low BMD. Research by Lennkh et al. (1999) also identified divergent levels of both bone resorption and bone formation markers, and therefore concluded that anorexia patients experience increased bone resorption and decreased bone formation.

The lower BMD and lack of bone turnover in adolescents with anorexia leads to questions about the impact of these factors on fracture risk in these patients. In a study (Faje *et al.*2014) following 310 adolescent girls with anorexia along with healthy controls, researchers found that the occurrence of fractures was 59.8% higher in those with anorexia as compared to healthy controls (Faje *et al.* 2014). This demonstrates that adolescents suffering from anorexia are not only at higher risk for fracture at later ages, but during their current developmental stage as well.

# Hormonal markers of anorexia

The process by which altered bone metabolism and low bone density occur in anorexia is not completely understood. Nevertheless, many studies (Manolagas 2000; Misra et al. 2003; Misra et al. 2004; Misra et al. 2005; Misra et al. 2007) have analyzed various hormonal changes in patients with anorexia to determine the mechanisms for these differences. Because anorexia is a state of severe energy deprivation, many endocrine axes are disturbed in order to conserve energy and increase energy intake and mobilization (Misra et al. 2016). The disruption of these axes has many harmful consequences on bone (Misra et al. 2016). Evidence of altered functioning of hormonal axes, including the hypothalamic-pituitary-gonadal (HPG) axis, the growth hormone-insulin-like growth factor-1 (GH-IGF-1) axis, and the hypothalamic-pituitary-adrenal (HPA) axis, during anorexia results in changes in bone metabolism and subsequent low bone density (Misra et al. 2016). Additional hormones that demonstrate dysregulated functioning and contribution to low bone density in anorexia are adipokines, such as leptin and adiponectin; appetite regulating hormones, such as lepin, ghrelin, and peptide YY; as well as other proteins (Misra et al. 2016).

The HPG axis is inhibited as a result of anorexia, resulting in hypogonadism (Misra *et al.* 2016). Hypogonadism refers to

the failure of the gonads to function properly, leading to low levels of gonadal hormones, including estrogen and testosterone (Misra et al. 2016). Both these hormones impact bone metabolism. Estrogen acts to inhibit bone resorption, meaning that a deficiency of estrogen will lead to increased resorption (Manolagas 2000). One mechanism by which estrogen inhibits bone resorption is through the secretion of inflammatory cytokines and receptor activator of nuclear factor kappa-B ligand (RANKL), which increase osteoclastic activity. Estrogen also increases the secretion of osteoprotegerin (OPG), which in turn inhibits osteoclasts (Riggs 2000). Lower ratios of OPG and RANKL have been reported in patients with anorexia (Ostrowska et al. 2012). Thus, low levels of estrogen may result in increased osteoclast activity and increased bone resorption. Lower levels of testosterone have been observed in adolescent girls suffering from anorexia (Soyka et al. 2002). Testosterone has been shown to reduce bone resorption and has a positive effect on bone formation (Manolagas 2000); therefore a deficiency of testosterone has a negative effect on bone density.

Another endocrine axis affected in anorexia is the GH-IGF-1 axis (Misra *et al.* 2003). GH is secreted by the pituitary gland and stimulates IGF-1 secretion in bone and both GH and IGF-1 are involved in the bone formation (Misra *et al.* 2003). Along with gonadal hormones, GH and IGF-1 are involved in the rapid addition of bone during puberty (Misra *et al.* 2003). Adolescent patients with anorexia have increased basal GH secretion, likely a compensatory reaction (Misra *et al.* 2003). Despite these higher levels of GH, there is no positive correlation between bone turnover markers and GH levels, suggesting a resistance to GH (Misra *et al.* 2003). There is decreased expression of the GH receptor in patients with anorexia leading to GH resistance in these individuals (Misra *et al.* 2003). This results in low levels of IGF-1 and lower rates of bone formation in anorexia patients.

The HPA axis is the third major endocrine axis affected (Misra *et al.* 2004), specifically cortisol levels—though the molecular mechanism by which cortisol impacts bone formation is not well understood (Misra *et al.* 2016). High amounts of cortisol are thought to inhibit the HPG axis, the effects of which were previously described (Misra *et al.* 2016). Moreover, high cortisol levels increase gluconeogenesis, thus increasing the amount of energy available for vital functions. This hypercortisolemia is also associated with anorexia (Marchili *et al.* 2016) and suppressed bone formation, which contributes to low BMD in adolescent females with anorexia (Misra *et al.* 2004). In general, cortisol levels were inversely correlated with markers of bone turnover (Misra *et al.* 2004), and high quantities of cortisol have been shown to have negative effects on bone (Abad *et al.* 2001).

Other hormone concentrations that are altered in anorexia include leptin, adiponectin, lepin, ghrelin, and peptide YY, which all impact bone health (Biver *et al.* 2011; Cornish *et al.* 2002; Misra *et al.* 2007). Patients with anorexia often have lower levels of leptin, a hormone that inhibits appetite (Misra *et al.* 2007). In addition, leptin increases osteoblastic activity and bone formation and has been shown to reduce bone fragility (Cornish *et al.* 2002), whereas low leptin levels correlate with low bone density and increased fracture risk (Biver *et al.* 2011). In contrast, adiponectin is harmful to bone, and high adiponectin in any fat mass present in anorexia patients is associated with lower bone density (Misra *et al.* 2007).

Ghrelin has also been shown to be high in adolescent girls suffering from anorexia nervosa (Misra *et al.* 2005). Although ghrelin is positively correlated with bone density in healthy adolescent girls (i.e. higher ghrelin is associated with higher bone density), this association was not shown in patients with anorexia because of their lower bone density; in fact, anorexic patients showed higher ghrelin levels than healthy controls, which suggests that patients had developed a resistance to the hormone (Misra *et al.* 2005).

Peptide YY is another hormone shown to regulate bone remodeling by promoting the breakdown of bone (Wong *et al.* 2012). Adolescent girls suffering from anorexia have been shown to have higher levels of this hormone, along with lower levels of bone turnover markers and lower bone density, suggestive of a possible association (Misra and Klibanski 2006). Similar to the case of cortisol, the molecular mechanisms behind the effects of these hormones on bone are not well understood.

# DISCUSSION

### Recovery options for anorexia

Given that adolescent anorexia dramatically impacts bone in a period of rapid bone accrual, an important question emerges: can adolescent girls who have suffered from anorexia ever fully recover in terms of bone density? A two-year study (Mika et al. 2007) tracking recovering anorexic patients found that while markers for bone turnover were normalized, bone mineral density remained low at the end of the study; however, by the end of the study, these patients exhibited a pattern in bone turnover markers similar to that of healthy controls two years earlier. This suggests that while these patients could not recover their BMD in two years, later adolescent-like patterns of bone growth could lead to bone mineral accrual in early adulthood (Mika et al. 2007). Research by Hartmann et al. (2000) examined the bone density in 19 adult women who had previously suffered from anorexia and had been fully recovered for an average of 21 years. The age of onset for these women was between 14 and 17 years old (Hartmann et al. 2000). The study found that bone mineral density in previously anorexic patients was lower than in the control group in both spinal and femoral measurements. This study found no correlation between bone mineral density measurements and duration of illness or age of onset. It is promising to note that only two of the patients demonstrated a history of fractures (Hartmann et al. 2000).

Many treatment options geared towards restoring bone health and preventing the development of osteoporosis in later age have been explored while the patient is still suffering from anorexia (Munoz and Argente 2002; Strokosch *et al.* 2006). One possible treatment option is estrogen replacement therapy, given that hypoestrogenism is commonly seen in anorexia patients and can be harmful to bone mineral density levels (Manolagas 2000); however, estrogen replacement therapy alone is not effective in reversing or preventing bone loss in adolescent patients who are recovering from anorexia (Munoz and Argente 2002; Strokosch *et al.* 2006). Munoz and Argente (2002) followed 20 adolescent girls recovering from anorexia with an average age of approximately 15 years and found no difference in the BMD of a group receiving oral estrogen and an untreated group. Another study (Strokosch *et al.* 2006) following 112 recovering anorexia patients, ranging from ages 11 to 17, found a similar result; there was no significant difference in the lumbar spine and hip bone mineral densities in patients taking an oral contraceptive versus those taking a placebo.

Another treatment option is the use of recombinant human IGF-1, since levels of this hormone are low in patients suffering from anorexia. Research conducted on a group of adolescent girls with anorexia showed that administration of recombinant human IGF-rincreased levels of the bone formation marker PINP, while no effect on the bone resorption marker CTX was observed (Misra *et al.* 2009). This is a promising treatment option, given the short time it takes for effects to be observed (Misra *et al.* 2009); however, there are still a number of limitations to this study. For example, the research was not randomized and the duration of medication was only seven to nine days. This short duration does not reveal the long-term effects of recombinant human IGF-1, which could be potentially harmful, as it is involved in a number of other biological functions.

# Limitations in the literature

Although scientists have conducted considerable research (Bachrach et al. 1990; Jagielska et al. 2002; Lennkh et al. 1999; Soyka et al. 1999; Soyka et al. 2002) and some progress has been made in understanding the effects of anorexia on bone density and how these effects can be mitigated, it is important to point out the limitations of these studies. The first major weakness is the majority of the research does not track adolescent anorexia patients into adulthood to determine the long-term effects of anorexia. As a result, this article primarily explores patients in the process of recovery instead of fully recovered patients. Moreover, these aforementioned studies have been, for the most part, conducted on girls who are referred to as Caucasian. These are girls of European descent, making it difficult to generalize the conclusions to other ancestral groups. Further, the research lacks a uniform definition of the term 'adolescent' and the chronological age of the subjects in these studies ranges from 11 years to 19 years. It is reasonable to question whether the effects of anorexia are similar in those who fall in different parts of this spectrum, since hormonal changes occur rapidly in this phase of life.

### **CONCLUSION**

Although scientists have a much better understanding of the effects of anorexia on bone health, we still have not made much progress in understanding the proximate mechanisms underlying these effects. For example, while the hormonal changes in anorexia have been elucidated, the role of these changes in increasing bone fragility is still not well understood. To make truly meaningful progress that can be clinically relevant in understanding and managing anorexia, investigators must expand their research to other ethnic groups and stratify the subjects in terms of chronological age. Finally, a better understanding of the mechanisms that lead to bone effects in anorexia, such as the breakdown of existing bone and the process of bone reconstruction, is imperative to designing safe and effective therapies for anorexia, particularly within the vulnerable subgroup of adolescent females.

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# **Explicating Female Promiscuity in Non-Human Primates**

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# **INTRODUCTION**

Promiscuity in female primates, defined in this paper as mating with multiple partners, is a puzzling phenomenon because its practice does not necessarily increase one's number of offspring. Rather, female fitness depends on a mother's ability to provide for her offspring and should not increase with greater access to mates (Soltis 2002). From an evolutionary standpoint, the benefits of a behavior must outweigh the associated costs for the behavior to persist. Females in the primate order invest heavily in each pregnancy, and each mating is costly in terms of energy and vulnerability, yet female promiscuity persists among human and non-human primates (Nunn et al. 2000; Dixson 2012; Huchard et al. 2012). Individuals must gain a net benefit from costly promiscuous behavior, which calls into question the evolutionary origins and biological markers of female promiscuity across primates. This article will explore extant hypotheses about why female promiscuity still persists, ranging from adaptive and non-adaptive explanations and encompassing the primary costs-benefits at play-namely infanticide avoidance as a strong selective force for female promiscuity.

# **METHODOLOGIES**

## Measuring female promiscuity

Promiscuity can be measured through direct observations of females engaging in copulations with multiple males, such as the western lowland gorillas in a study by Doran-Sheehy *et al.* (2009), to be discussed. While this method can be effective, there is potential for researchers to miss copulations without continuous monitoring of every individual female, which is impractical. As a result, researchers often rely on proxies to determine the number of matings in which a female participates. In this article, the term mating refers to an event where a female and male engage in sexual intercourse.

One possible proxy for female promiscuity is female solicitation of multiple sexual partners, free from the coercion of males (Stoinski *et al.* 2009). In some species, like the Bornean orangutan and bonnet macaque, male coercion sometimes overpowers female choice, meaning that female mating behavior does not always reflect female choices or strategies (Dixson 2012). If observed, influence of male restraint and aggression would be a confounding variable in explaining female promiscuity (Soltis 2002). Female copulatory solicitation is therefore a useful proxy because it ensures that the observed behavior actually reflects a female's choice, ruling out the possibility of male coercion as the driving force of female promiscuity. An experimental study by Huchard *et al.* (2012) showed that female mouse lemurs do exert control over mating choices, despite the sexual dimorphism in the species. Moreover, female solicitation displays do not always result in copulation, so observers must be mindful that solicitation and actual mating behavior, such as promiscuity, are sometimes separate matters.

Another possible proxy of female promiscuity is male testes size, which is an indicator of sperm competition (Nunn 2000). Sperm competition refers to the contest among sperm from multiple males to fertilize a female's egg, and results in selection for increased production of sperm and high volume ejaculations in males (Dixson 2012). In monogamous species where male-male competition is infrequent, sperm competition and therefore large testes are unnecessary. For example, humans generally live in monogamous pairs, and the testes of males are only 0.06% of total body weight (Harcourt et al. 1981). In polyandrous species, in which females mate with multiple males and sperm competition increases, testes size should also increase with the amount of female promiscuity (Hrdy 1995). Accordingly, polyandrous cotton-topped tamarins have testes that weigh 0.65% of total body weight (Harcourt et al. 1981). Though this method is not exact and applies to a whole species rather than its individual members, the data that Harcourt et al. (1981) present show a general trend of larger male testes size in polyandrous species.

Estrus, or the duration of a female's sexually receptive period, could also indicate level of promiscuity, because a longer period of receptivity would generally allow the female to mate with more partners. In many animals, including some primates such as chimpanzees, the period of sexual receptivity in females is strictly limited to times in the menstrual cycle when the female can actually conceive (Hrdy 1995). In contrast, the period of receptivity is continuous or almost continuous in many species of primates, such as langurs, meaning that females are sexually receptive even at points in the menstrual cycle when they cannot actually conceive (Dixson 2012). Prolonged periods of receptivity and the loss of sexual swellings to advertise ovulation likely evolved so that females would not have to limit their sexual activity to a short period around ovulation. Consequently, females gained an expanded window of time to engage in multiple matings and sexual activity separated from solely conceptive purposes (Hrdy 1995).

### Costs of female promiscuity

Multiple matings are costly because, with each mating, a female expends energy, exposes herself to diseases, and risks harassment from other individuals. She also invests time that could otherwise be spent on other tasks, or may become distracted and therefore more vulnerable to predation (Soltis 2002). Other costs of promiscuity include distance travelled to reach a sexual partner and vulnerability to attacks by other individuals during copulations (Kowalewski and Garber 2010). Additionally, all of these costs may accumulate with each promiscuous mating.

Huchard et al. (2012) demonstrate the energetic cost of mating in their experimental study of mouse lemurs, in which females were kept under two different conditions: one group received a sufficient amount of daily food, while a calorie-restricted group only received 20% of that amount. It is also important to note that mouse lemurs are nocturnal and breed seasonally-an example of noncontinuous sexual receptivity. On the first day of estrus during the mating season, researchers placed a female into a cage with three males and videotaped the cage to record any mating behavior at night. They also weighed each female at the same time each evening and morning to determine any change in body mass, which would indicate net energy expenditure. Results show that females on the calorie-restricted diet mated with only one partner and did not solicit additional matings. In contrast, well-fed females tended to mate with multiple partners, and their weight loss increased directly with the number of matings. While promiscuous mating might benefit females in some circumstances, these results indicate that low energy conditions may deter females from mating promiscuously (Huchard et al. 2012).

Promiscuous mating is also costly in terms of exposure to pathogens. Nunn *et al.* (2000) found that white blood cell (WBC) counts in females were higher in species whose females mated promiscuously; in this study promiscuity was measured in terms of estrus duration and testes mass. Because WBC count generally increases if an individual is exposed to infection, Nunn *et al.* (2000) used it as a proxy of exposure to disease. Ultimately, the researchers concluded that female promiscuity correlates with exposure to disease and is thus costly.

Lemaitre and Gaillard (2013) investigated the effects of female promiscuity on longevity, a life history variable that they chose to reflect disease burden. When they found no relationship between female longevity and male testes size, they concluded that female promiscuity has no cost to female health. Longevity may not directly indicate exposure to disease, however, because females might engage in counterstrategies, such as genital grooming, to combat disease risk (Lemaitre and Gaillard 2013). Thus, WBC count is a better measure of disease exposure than longevity, as used by Nunn *et al.* (2000). It is important to note the different proxies used to gauge female promiscuity and other variables because they may explain conflicting reports about the costs of promiscuity in the scientific literature.

# DISCUSSION

## Non-adaptive explanations for female promiscuity

Despite these associated costs, there are several hypotheses to explain why female primates engage in promiscuous matings. The first group of hypotheses includes non-adaptive explanations, which imply that female promiscuity is simply a byproduct of other advantageous traits selected for through natural selection.

Arnold and Halliday (1986) propose that female promiscuity has coevolved with advantageous male promiscuity. In males, promiscuity is expected to be beneficial because mating with multiple females directly increases reproductive success. The authors suggest that selection for promiscuity in females derives from selection for promiscuity in general.

Advantageous male promiscuity is related to Bateman's principle, which summarizes the idea of an 'eager male' and a 'choosy female,' based on limiting resources (Soltis 2002). In mammals, males invest relatively little in offspring compared to females, so their strategy should be to mate with as many females as possible to maximize their reproductive success. On the contrary, females invest heavily in each offspring, meaning that they need enough resources to support themselves and their offspring; a lack of resources negatively influences the offspring's well-being and the female's ability to reproduce. Therefore, increased access to mates does not affect females' reproductive success, because access to mates is not the limiting resource.

According to Arnold and Halliday (1986), there could be a genetic correlation between the sexes, and selection on male mating is stronger than selection on female mating. In fruit flies, for example, selection for male mating speed has affected female mating speed (Arnold and Halliday 1986). By this logic, female promiscuity may be a byproduct of natural selection for male promiscuity. This argument could also be used to explain the female orgasm as a consequence of male ejaculation; the former has no reproductive value of its own, while the latter is necessary for fertilization (Hrdy 1995). Small (1988) rightfully questions whether this proposed correlation between the sexes actually exists in primates, because no study has quantified selection between male and female sexual behaviors within the primate order.

Another non-adaptive explanation is that female promis-

cuity is a byproduct of pleasurable sex (O'Neil 1988). According to this explanation, sexual activity should be pleasurable to ensure that individuals actually mate and reproduce. Because pleasure is an immediate reward of copulations, regardless of the number of partners or potential functional benefit, female promiscuity might be merely incidental to selection for pleasure (O'Neil 1988).

Furthermore, continuous sexual receptivity may be correlated with this pleasure-based hypothesis. If the only purpose of sex is to conceive, then females should engage in copulations only around ovulation. For example, galagos conspicuously display sexual receptivity with hormone dependent swellings and only mate during those advertised fertile periods. In contrast, langurs and bonobos have concealed ovulation or swellings that can appear at other points in the menstrual cycle, allowing them to mate at points in their menstrual cycles when conception is unlikely or impossible (Hrdy 1995). These traits would be difficult to explain without acknowledging some push for nonconceptive matings, because prolonged estrus and concealed ovulation do not necessarily promote mating during times when females are fertile, and thus do not necessarily promote reproductive success. Because females can experience pleasure regardless of whether the mating increases fitness, pleasure is a plausible nonconceptive benefit to sex.

Non-adaptive explanations fail to account sufficiently for the costs associated with multiple matings. A behavior that decreases an individual's reproductive success must also provide significant benefits for the actor—enough to overwhelm the costs of the behavior and give the individual a net benefit. In sum, these non-adaptive explanations of female promiscuity do not provide enough of a benefit to overwhelm the costs a female incurs from promiscuous matings.

# Adaptive explanations to female promiscuity

There are also several evolutionary explanations that account for female promiscuity. These hypotheses suggest ways in which females benefit directly from having multiple sexual partners, ultimately increasing their reproductive success and allowing natural selection to act upon these behaviors.

Small (1988) hypothesizes that females mate promiscuously to ensure fertilization. While Bateman's principle states that resources, rather than access to mates, always limit females, this assumption might not hold true in all cases. For example, males experience refractory periods after each copulation during which they cannot mate. Sometimes groups have a high female-to-male ratio or polygynous social structures, which limits females' access to mates. Seasonal breeding might also result in female competition for a male's attention. Furthermore, sperm varies in quantity and quality; so not all ejaculations guarantee fertilization, and some males are infertile altogether (Small 1988).

In contrast to Bateman's principle, Small (1988) argues that sperm is sometimes in short supply; accordingly, females should be expected to maximize their reproductive success by maximizing their access to good sperm. Depending on the situation, females might enact multiple strategies: they might mate with multiple males to increase their chances of fertilization, compete with other females over access to mates, or choose to mate with the most fertile male. Nevertheless, there is no evidence that primates can detect the fertility of potential mates by external factors, rendering the latter strategy implausible. Thus, in cases when sperm is limited, female primates might strategize by mating with multiple partners (Small 1988).

In response to Small (1998), Thornhill (1988) argues that if sperm is sometimes the limiting resource for females, other role reversals should be apparent. For example, one would expect females to be larger and more aggressive, and to engage in direct conflict with other females, as males often do when they compete for females. Small (1988) responded by noting other physiological factors, such as gestation and lactation, that would limit female size regardless of competition. Furthermore, in her response, Small (1988) explicitly defines a limiting resource as one that has a higher demand than supply, as opposed to a resource over which individuals compete directly and aggressively.

Regardless, sperm is usually not a limiting resource by any definition. Even in situations where sperm might be in short supply, such as the ones Small (1988) describes, other factors may have a stronger effect on reproductive success. Studies in langurs and macaques, such as those of Sommer *et al.* (1992) and van Noordwijk and van Schaik (1999), have shown that females take longer to conceive in groups that have many more females than males. These findings seemingly support Small's (1988) argument that sperm can be a limiting resource affecting females' reproductive success.

In contrast, Hrdy (1995) proposes that females take longer to conceive in large groups not because of limited sperm supply, but because of social and nutritional stresses caused by an increased group size, regardless of the sex ratio. Small (1988) fails to take these potentially confounding variables into consideration. Furthermore, if a female's goal of mating promiscuously is to ensure fertilization, then she should mate only or primarily during ovulation (Kowalewski and Garber 2010). Promiscuous or not, mating during nonfertile periods is hard to attribute to ensuring fertilization.

Thus, while Small's argument might be reasonable in very specific situations, it does not seem to hold up to others' criticisms (O'Neil 1988; Thornhill 1988). Her hypothesis would be difficult to test in a field setting, and no study concretely supports her idea of promiscuity as a method to ensure fertilization (Doran-Sheehy *et al.* 2009).

Small (1988) briefly addresses the idea of female-female competition as another explanation for female promiscuity. By engaging in promiscuous matings, a female depletes the sperm supply, harming others' fitness with cost to herself. Small (1988) calls this behavior spiteful because promiscuous mating is energetically costly for the actor, but the behavior more significantly decreases other females' reproductive success. The actor thus increases her reproductive success relative to that of other females affected by her sperm-depleting sexual behavior, despite associated costs.

Scientists appear to have observed such behavior in gorillas.

Doran-Sheehy *et al.* (2009) and Stoinski *et al.* (2009) have both observed female gorillas engaging in sexual activity at times when conception was impossible. Doran-Sheehy *et al.* (2009) observed pregnant western lowland gorillas who engaged in sexual activity, despite the fact that they were already pregnant and therefore not cycling. Copulation while pregnant obviously has no direct reproductive benefit, but both Doran-Sheehy *et al.* (2009) and Stoinski *et al.* (2009) propose that female gorillas use post-conceptive mating as a way to minimize male sexual interest in other females.

This type of competition benefits the actor on three levels. First, females compete sexually by reducing the amount of competition for sperm, in case sperm is a limiting resource as Small (1988) suggests. Second, by reducing other females' access to the alpha male silverback gorilla, for example, a high-ranking female can reinforce her rank in relation to other lower-ranking females. Finally, by reducing other females' access to mates, a promiscuous female indirectly protects her future offspring from competition among other potential infants (Stoinski *et al.* 2009).

Doran-Sheehy *et al.* (2009) predicted that females' nonconceptive copulations would depend on the sexual behavior of other females in the group; specifically, pregnant females should only mate with males when other fertile females also mated with those males. To test this hypothesis, the researchers followed wild male and female gorillas intermittently over the course of a four-year study and recorded in detail any copulations they observed. They found that pregnant females mated on days when other females mated—a pattern which supports their hypothesis.

Stoinski *et al.* (2009) performed a similar study on captive western lowland gorillas at Zoo Atlanta, expanding their hypothesis to include all females rather than just pregnant females. Likewise, Stoinski *et al.* (2009) found that females mated more frequently on days when other females also mated, which indicated a non-random pattern throughout the reproductive cycle that could not be accounted for simply by individual variation (Stoinski *et al.* 2009).

This mating behavior in gorillas, observed by both Doran-Sheehy et al. (2009) and Stoinski et al. (2009), corresponds with Small's (1988) description of spiteful behavior. According to Small (1988), spiteful behavior decreases the reproductive success of others at a personal cost to the actor in terms of fitness; costs of female promiscuity include energy expenditure and increased vulnerability, as discussed earlier. Unlike selfish behavior, spiteful behavior increases the actor's reproductive success while spitefully reducing the reproductive success of others (Small 1988). Because spiteful behavior does involve costs to the actor herself, it would be difficult for such behavior to evolve. Moreover, in medium to large-sized groups, it would be especially costly for the actor to behave spitefully towards all group members, and individuals who did not participate in or receive spiteful behavior would benefit the most in the group (Soltis 2002). By engaging in promiscuous mating, a female repeatedly subjects herself to the costs of mating. As such, the benefits of depriving other females' access to sperm are unlikely to outweigh the costs or to explain female promiscuity as spiteful behavior. Soltis (2002) proposes that sperm depletion is sometimes a side effect of female promiscuous mating, but not a cause as Small (1988) suggests.

Furthermore, the explanations of post-conceptive sex as a form of female-female competition or mate guarding might more appropriately describe social situations in which only one male has reproductive access to females. Western lowland gorillas live in one-male, multi-female groups, meaning that a single female probably will not have the opportunity to mate with multiple partners (Doran-Sheehy *et al.* 2009). Though this study does provide a potential explanation for nonconceptive sex, this phenomenon is not always the same as promiscuous mating. To date, no study has specifically demonstrated that females' use of promiscuous sex is a form of female-female competition. Consequently, there is insufficient evidence to accept sperm depletion or female-female competition as an explanation of female promiscuity.

Another possible explanation for female promiscuity is that females and their offspring gain genetic benefits when females mate with multiple males. This explanation is based on the idea that, especially during times of instability, a mother will benefit most by having genetically diverse offspring able to withstand multiple types of environments (Kowalewski and Garber 2010).

Kowalewski and Garber (2010) observed black and gold howler monkeys in South America and recorded individuals involved in sexual interactions. The researchers expected the genetic diversity hypothesis to apply to howler monkeys because adults of both sexes disperse—meaning that both males and females leave their natal groups once they reach a certain age so individuals of both sexes must be able to survive many types of forest environments. Additionally, animals in that region of South America often face unexpected environmental disasters such as floods (Kowalewski and Garber 2010).

If females are capable of having litters sired by multiple fathers, the genetic diversity hypothesis might be a good explanation for female promiscuity. Birds and mammals, including some primates such as mouse lemurs, are indeed capable of having litters of mixed paternity (Huchard et al. 2012). However, most primates tend to have singleton births, meaning that mating with multiple males during a single estrus period would provide no genetic diversity benefits to a female (Wolff and Macdonald 2004). Rather, the genetic diversity explanation could apply to a situation in which a female primate mates with a single male during a single estrus period, gives birth to an infant sired by that male, and then mates with a different male during the next estrus period after weaning the first infant. This strategy would result in successive offspring being sired by different males, increasing the diversity in the mother's progeny and maximizing the chance that her offspring will survive changing environments or unstable situations. Nevertheless, the genetic diversity hypothesis does not adequately explain the type of promiscuous behavior that Kowalski and Garber (2010) observed, where females mate with multiple males during a single estrus period.

Sapient Undergraduate Journal of Biological Anthropology | Spring 2018 | Volume 6

Genetic benefits might also include genetic compatibility. This hypothesis is based on the assumption that monogamous species have more failed pregnancies than promiscuous species; however, there is no evidence that genetic incompatibility is the cause of failed pregnancies, or that potential genetic incompatibility results in a significant difference in reproductive success between promiscuous and monogamous species (Wolff and Macdonald 2004).

Another hypothesis to explain female promiscuity is that female primates use sex as a commodity to exchange for other services, such as alliance building or grooming. Biological market theory refers to cooperative social exchange, and can be applied to individuals who use sex as payment for other social acts, such as grooming (Noë and Hammerstein 1994; Gumert 2007). This explanation is based on the assumption that by mating with multiple males, a female can accumulate benefits from each sexual partner.

In baboons, lasting friendships between a male and a female are common. These relationships involve close association, mutual grooming and protection, but do not necessarily require mating. Even when sex is involved, the female does not mate exclusively with that male, and the male's probability of siring any of the female's offspring is low. Nonetheless, the male protects her infant and continues to associate with the female without any evident reproductive benefits, such as increased access to mating opportunities (Taub 1984). Even when sexual interactions are observed as a major aspect in baboon relationships, there is no clear evidence that males or females mate to gain the benefits of an alliance or to maintain a relationship with a current ally (Smuts 1985). Therefore, the sex-for-allies explanation is not applicable to female primate promiscuity.

Females might also trade sex for grooming. Gumert (2007) predicted that if this were the case, males should direct grooming efforts toward sexually receptive females in particular, and that grooming should increase the probability of the recipient female mating with the male groomer. To gain insight on this hypothesis, researchers observed a group of longtailed macaques in scattered 10-minute focal sessions over the course of almost two years (Gumert 2007). They recorded sexual activity, including actual copulations, female presentation, and genital inspection, as well as grooming acts. They found that males directed 89% of grooming acts towards sexually receptive females; 57% of male-female grooming acts were related to any type of sexual activity; and 37% of male-female grooming acts occurred within three days of an actual copulation between the pair. Problematically, Gumert (2007) makes the assumption that sexual activity as distant as three days from grooming is still related to a grooming act, which implies strong cognitive capacity for which Gumert (2007) does not provide evidence. It is also questionable whether individual of any species can actually differentiate who is fertile at a given time (Small 1988).

Overall, the sex-as-trade explanation does not seem to apply generally to female promiscuity. Additionally, it is unclear whether some of the exchanges described above are actually examples of trade, or simply coincidence. Furthermore, there is no evidence of a female soliciting multiple sexual partners to make an exchange for something she wants.

Another hypothesis posits that female primates mate promiscuously to secure paternal care from multiple males. For example, female Barbary macaques mate very promiscuously, and males often care for infants in the group, favoring one or two particular infants (Taub 1984). This phenomenon, called facultative polyandry, refers to situations in which females mate with multiple males, and each of those males participates in caring for the offspring. Facultative polyandry generally applies to species with large infants or twins, which would be difficult for a mother to support by herself (Dixson 2012).

Male primates can sometimes increase their own offspring's fitness by protecting and caring for the infant and its mother (Smuts 1985). According to Soltis (2002), however, paternal investment does not usually have a significant impact on offspring survival, giving males little motivation to invest in paternal care rather than more mating opportunities. Even if paternal care by one male substantially increases an offspring's well-being, paternal care by a second male is not likely to have a significant effect (Soltis 2002). Accordingly, paternal care is generally associated with monogamous species, in which fathers are relatively certain that they are investing in their own progeny. On the contrary, in promiscuous species, fathers have a reduced probability and certainty of paternity, and therefore less motivation to protect potential offspring (Wolff and Macdonald 2004). Additionally, bystander males who mate with females but do not invest in offspring might benefit the most; while bystanders are able to solicit more mating opportunities for themselves, other males unknowingly care for the bystander male's offspring (Soltis 2002). The paternal care hypothesis does not withstand such criticisms, and probably does not explain female promiscuity.

# Adaptive explanation: female promiscuity as infanticide prevention

The final and most convincing explanation to female promiscuity is that mating with multiple males can confuse paternity and thereby reduce the risk of infanticide. The term infanticide refers to any act that leads to the death of an infant of the same species (Palombit 2015). Specifically, female primate promiscuity protects against sexually selected infanticide, which is committed by males who are not the father of the infant. If a male is not the father of a particular infant, it is in his best interest to mate with the mother to increase his own reproductive success, regardless of the success of the mother and her offspring. Lactating mothers experience a period of lactational amenorrhea, during which they are not cycling and not sexually receptive. By killing an infant, a male truncates the mother's lactational amenorrhea, allowing him to mate with her sooner than if she were still nursing her infant. Because there is no way for males to determine definite paternity, they should commit infanticide based on probability of paternity, which in turn should be based on mating history (van Schaik 2000).

Sexually selected infanticide is common after male takeovers (i.e. when a new male usurps the highest-ranked male and becomes the dominant male of the group) (Dixson 2012). Vulnerability to infanticide can also depend on the presence of seasonal breeding, the rate at which an offspring matures, and the length of time that an infant is wholly dependent on its mother (Huchard *et al.* 2012). Comparing durations of lactation and gestation is another good indicator of vulnerability to infanticide, because species in which lactational periods are long will likely have higher rates of sexually selected infanticide (Palombit 2015).

Furthermore, female primates invest a great deal of energy in carrying an infant to full term, giving birth, and lactating until the infant gains nutritional independence. For example, to meet the energetic demands of both herself and her infant, a baboon mother increases her time spent feeding from 43%at birth to 60% five months after giving birth (Altmann 1980). Such immense cost is manageable if the outcome is a healthy and viable offspring, but a female would suffer a great deal if she lost her offspring. Thus, females should be expected to develop strategies to protect their offspring from infanticide, such as paternity concentration or confusion, which would maximize their own reproductive success (Soltis 2002).

One strategy against infanticide is paternity concentration, in which a female mates with a single, high-ranking male to ensure his protection of her future offspring. The success of paternity concentration depends on the group's social structure, such as that of hamadrayas baboons (Swedell and Saunders 2006); in this species, the high-ranking male has a relatively stable dominant position and can easily defend infants from the infanticidal efforts of other males.

Alternatively, females in other primate species might use promiscuous mating as a means of paternity confusion, in which females obscure paternity by mating with multiple partners to gain protection from infanticide from multiple males (Swedell and Saunders 2006). A male's decision to commit infanticide should depend on the probability that he has sired that particular infant, because killing his own offspring obviously would not be beneficial to his reproductive success; this type of situation often arises in periods of dominance shifting. During times of social instability, females should be expected to mate promiscuously to protect their future offspring from the possibility of infanticide (van Schaik 2000).

The main critique of the infanticide avoidance hypothesis is that infanticide is rarely observed in the wild, especially in certain species such as howler monkeys. Researchers who have noticed the lack of observed infanticide have concluded that because infanticide occurs seemingly infrequently, it must not be a significant threat (Kowalewski and Garber 2013); however, other factors can influence frequency of observation. For instance, effective counterstrategies, avoidance behaviors, and observational errors could also account for lack of observation of infanticide. Essentially, a low rate of infanticide occurrence does not mean that the risk of infanticide is minor or that infanticide is a weak selective force (Sommer 2000). Infanticide is such a strong a selective force, and the costs of infanticide to a female are so great, that many behaviors stem from infanticide avoidance, such as early rearing of infants and female promiscuity.

Though promiscuous mating is costly, losing an infant to infanticide is even more costly. Thus, the infanticide avoidance hypothesis provides a high enough benefit to balance the costs of female promiscuity. It also can explain female promiscuity toward both in-group and extra-group males, female mating at all times during the reproductive cycle, and mating with multiple males during a single estrus period (Soltis 2002).

## **CONCLUSION**

To explain female promiscuity in nonhuman primates, it is vital to examine both non-adaptive and adaptive hypotheses. Generally, female promiscuity in mammals is unexpected because it does not obviously contribute to the production of more offspring, but scientists have observed promiscuous mating in several species of primates and other animals. The hypotheses discussed herein attempt to explain possible nonprocreative benefits that a female might gain from mating promiscuously, despite costs associated with multiple matings.

Non-adaptive explanations state that female promiscuity is a byproduct of another advantageous trait that has been selected for, such as male promiscuity or pleasure. Though these hypotheses provide a possible benefit with which female promiscuity might be associated, they do not account for the high costs associated with female promiscuity. These costs include energetic expenditure, exposure to disease, and risk of predation (Nunn *et al.* 2000; Dixson 2012; Huchard *et al.* 2012).

Adaptive explanations to female promiscuity include ensuring fertilization, competing with other females by depleting the sperm supply, gaining genetic diversity, trading for other benefits, gaining paternal care, and reducing the risk of infanticide. Most of these studies cannot apply to female promiscuity broadly, but only to specific social situations or mating behaviors. For example, a female's chances of fertilization do not increase with number of matings, barring specific social situations when sperm is a very limited resource. Female promiscuity to deplete the sperm supply usually costs a female more than she benefits from the behavior. The genetic diversity hypothesis does not explain mating multiply during a single estrus period. The sex-as-trade hypothesis also does not seem to apply to female promiscuity because females do not consistently use sex at the same time as they reap other social benefits. Likewise, paternal care is rare among primates, making the paternal care hypothesis another unlikely explanation to most instances of female promiscuity. Only the infanticide inhibition hypothesis can broadly apply to female promiscuity across a variety of social, environmental, and reproductive conditions.

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# *"That's not fair!"*: An Empirical Survey of Inequity Aversion in Non-Human Primates

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# **INTRODUCTION**

Inequity aversion (IA) in human primates is associated with game theory, utilitarian decision-making, and social cooperation (Fehr and Schmidt 1999); yet there is limited evidence of IA in non-human primates (NHPs) or other species. IA has become an increasingly popular area of study for biologists, ethologists, economists, psychologists, and philosophers alike, followed by many studies on its evolutionary origins (Chen and Santos 2006; Braüer, Call, and Tomasello 2009; Neiworth et al. 2009; Brosnan and de Waal 2014). Sociologically defined as the resistance to inequitable outcomes, IA demonstrates how humans are willing to give up some material payoff in the interest of more equitable outcomes (Fehr and Schmidt 1999). In the primate order, one would expect those species predisposed to IA to have high levels of cooperation and sociality, and thus clear expectations for the distribution of payoffs they receive (Dugatkin 1997).

More specifically, Fehr and Schmidt's (1999) model delineates two types of IA: The first is disadvantageous IA or first-order IA, in which the actor receives 'the short end of the stick' and may manifest in the actor's willingness to sacrifice a potential gain to block their partner from receiving a superior reward. On the other hand, in advantageous IA, the actor may receive 'the better end of the deal,' but still feel inequity averse by virtue of unfairness or a similar ethical dilemma (e.g. over-benefitting) (Fehr and Schmidt 1999); the forestalling of which would be considered second-order IA (Brosnan and de Waal 2014). In contrast to earlier definitions of IA in humans, Brosnan and Bshary's (2016) more recent definition of IA in NHPs is primarily situated in the context of social and coalitionary behavior, such that IA is a negative behavioral response to receiving less than a partner; nonetheless, this definition does not imply that NHPs understand IA in terms of fairness, as humans do (Brosnan and de Waal 2004). Researchers Brosnan and de Waal (2004) predict that humans' moral inclinations to IA may have evolved over a series of simpler, rudimentary steps that would have incrementally increased an individual's relative fitness in social scenarios—in other words, maligned individuals may react strongly enough to terminate a current inequitable relationship, perhaps in search of a 'better deal' that would increase his or her fitness/net gains.

IA is also influenced by other social variables and structures, such as kin selection theory and Hamilton's rule; dominance rankings; individual personalities and cheating; and/or Noë and Hammerstein's (1995) notion of the biological market, which many studies cited herein have cross-referenced (Brosnan 2006; Chen et al. 2006; Massen et al. 2012). Because of the clear social component of IA, which is also important for other behaviors like social learning or coalitionary foraging (Brosnan, Schiff, and de Waal 2005), experiments designed for NHP species will test individual primates' recognition and evaluation of others' rewards as compared to their own (i.e. first-order IA, or relative gains versus absolute gains). However, constraining IA to this social framework and experimental design leaves a myriad of other, less domain-specific functions and possible adaptations for detecting inequity, which could help to explain IA's evolutionary origins.

Brosnan and de Waal's seminal experiment (2003) can be credited with prompting and shaping the scientific conversation of IA in NHPs, specifically by spurring many procedural replications and critiques. This article will examine the original experimental design, complemented by a brief chronology of methodological improvements and critiques, followed by a more theoretical discussion on the evolutionary origins and implications of IA. In this regard, Brosnan and de Waal believe that advantageous IA developed *after* the evolution of disadvantageous of IA, so their research focuses on the precursors of negative inequity and first-order IA by testing how Capuchin monkeys (*Cebus apella*) react if they receive different food rewards than those of a conspecific.

# **METHODS AND RESULTS**

# Original experiment by Brosnan and de Waal (2003)

Brosnan and de Waal (2003) gave female brown capuchin monkeys (n=5) tokens (small rocks) to trade with a single human experimenter for a food reward; based on the predetermined rules of each trial (4 methods; 25 trials total), the subject would either receive a grape (preferred food, PF), or a cucumber piece (less preferred food, LPF), with preference evaluated by a dichotomous food-preference test beforehand (Brosnan and de Waal 2003b). As noted, the experiment consisted of four types of trials depending on the dissemination of foods to both the actor (i.e. the model) and their partner (i.e. the witness): the equity trial (ET), in which both the subject and the partner received cucumbers; the inequity trial (IT), in which the subject continually received a cucumber while the partner received grapes; the effort control trial (EC), in which the partner did not exchange a token for a grape, followed by the subject exchanging a token for a cucumber; and the food control trial (FC), in which the partner monkey was absent, but the subject witnessed a grape being placed (and accumulated) in the adjacent cage where the partner usually sat. Grapes were present in a bowl near the human experimenter in all trials except for the ET, although the researchers claim neither monkey knew which food she would receive before each trial. The researchers measured the rate and latency of successful token-exchange, while unsuccessful exchanges fit into two categories: failure to return token (no token, NT), or failure to eat or accept the PF (reject/refuse reward, RR). Despite commonalities between these scenarios, such as aggressive rejections of the LPF (i.e. throwing food out of the chamber), researchers defined each exchange as NT or RR exclusively.

Already there are four main concerns with the experiment: First, the sample size is extremely small with no intrasexual variation; this poses extreme limitations on the data and the scope of any conclusions. Second, the EC and FC are not controls in the traditional sense of the term because there is no separate sample group (Wynne 2004); in fact, this methodology likely whetted the subjects' appetite and signaled that the PF was available. Given the high capacity for memory formation in the primate order, prior receipt of PFs could lead to intensified frustration or contrast effects (Dubreuil et al. 2006; Roma et al. 2006) and increase NT or RR results. Consequently, Brosnan and de Waal's experimental design renders it difficult to parse out frustration effects from true inequity discernment and second-order IA. Third, capuchin monkeys are generally known for being extremely tolerant and prosocial, especially in regards to food sharing, so this fact may have influenced the results and limits replicability of the experiment across species. Lastly, IA responses are so individually varied that streamlining them into successful and unsuccessful exchanges (i.e. NT, RR) is somewhat subjective and oversimplified-especially given the small sample size. In fact, negative reactions (e.g. frustration, agitation, begging, etc.) should not automatically be equated with displays of IA, as these reactions can also be independent of IA or related motivations.

Although Brosnan and de Waal (2003) acknowledge that behavior may generally change over the course of a test, they do not name frustration or contrast effects specifically; rather, they posit that subjects may not recognize inequity immediately (thus explaining increasing RR; the case in ET, IT, EC tests), or that subjects may have gradually 'settled' over-time for the LPF (thus explaining decreasing RR; as in FC). In fact, Brosnan and de Waal hypothesize that the lack of a partner in the FC made it easier for the subject to accept the LPF (i.e. less social pressure/comparison of relative gains) and/or eventually 'settle' for the LPF. Nevertheless, this explanation of the FC anomaly is widely disputed by primatologists who think this is a clear example of frustration effects (Dubreuil et al. 2006; Roma et al. 2006), which, depending on affective idiosyncrasies can manifest as increased or decreased RR. The significant disparities in rates of successful exchange across the four conditions underscores this individual variation-bolstered by the high values of both unsuccessful exchange types (NT and RR, 45.4% and 54.6%, respectively), and the fact that NT is typically a rare occurrence among these trained capuchins (Brosnan and de Waal 2003).

Notably, subjects reacted vehemently to cucumbers (a food that is regularly accepted at the Yerkes primate center), which suggests that subjects were in fact comparing their food rewards relatively. More specifically, subjects compared their food reward to the mere presence and availability of the PF (Wynne 2004), not necessarily the food rewards of their partners as Brosnan and de Waal suggest. To support their social inequity claim, Brosnan and de Waal cite the low number of RRs in the ET; however, the anomalous absence of grapes in the ET (a product of experimental design) actually supports Wynne's (2004) parsimonious counter-explanation, that the mere presence of grapes (or lack thereof) is what triggered an inequity response, rather than true disadvantageous IA (i.e. the "reward availability" hypothesis). Furthermore, Brosnan and de Waal (2003) rule-out positive conditioning as the source of NT behavior in the IT and control trials because cucumbers were accepted in the ET, but because there were no grapes present in the ET, NT data should not be extrapolated across trials.

To explain increasing RRs in the three inequity trials, Brosnan and de Waal anticipate subsequent interpretations (e.g. Chen and Santos 2006; Neiworth et al. 2009), which claim that if the subject anticipated a better reward or (i.e. experienced a violation of expectations known as contrast effects) she would be more likely to reject the LPF; however, Brosnan and de Waal deflate this hypothesis based on the subjects' reward history at Yerkes, concluding that there is no reason that a subject receiving a cucumber should expect anything else during the same test. Given the limitations inherent to assigning a mental state unto other non-human beings (i.e. theory of mind), to accurately gauge IA in NHPs, baseline expectations must originate from the visible presence of inaccessible PFs. To explain the inverse scenario (i.e. decreasing RRs in the FC trial), Brosnan and de Waal conclude that subjects form expectations vis-à-vis seeing a partner receive and/or eat the PF, rather than the mere presence of PFs. This is simply not true given what is known about NHPs high capacity for long-term memory, coupled with their ability to adjust expectations based on relative versus absolute terms (Melis *et al.* 2009). Finally, because of the limited sample size, monkeys were tested in all four trials on consecutive days, which is certainly not enough time to neutralize memory of past trials.

In terms of rate of exchange, Brosnan and de Waal (2003) found that capuchins completed exchanges most quickly in the IT, and more slowly in the control tests (i.e. FC and EC) than in the ET. From this data, the researchers concluded that the mere presence of grapes did not excite rates of exchange in the control trials; however, as noted, any frustration or contrast effects at play could just as well slow subjects' rates of exchange. Lastly, the rate of NT in the IT (43.00%) is about equal to the rate of RR in the FC (49.00%), suggesting that monkeys were just as likely to refuse LPF with or without partner influence. Wynne (2004:140) aptly invokes Occam's razor here: "There can be nothing iniquitous about receiving an [LPF] if nobody is receiving anything better." In fact, Wynne (2004) claims that a graph in the original experiment (see Brosnan and de Waal 2003; Fig. 2), which depicts increasing RR in IT and EC tests, as well as declining RR in FC trials, was incorrectly calculated in the original experiment (confirmed via personal conversations with Brosnan and de Waal; Wynne 2004). The validity of Wynne's (2004) reanalysis (which showed neither an increase of RR in IT and EC, nor a decline of RR across FC trials) and Brosnan and de Waal's (2003) data is still not clear; further, Brosnan and de Waal response (2004), published beside Wynne's commentary, was conservative and circumlocutory. They stated that the primary goal of the study was admittedly narrow, but with major implications-to show that NHPs would recognize inequity if presented with it, which would point to IA as a possible evolutionary precursor to fairness.

Given the complex nature of fairness and reciprocity, to be discussed in a later section on Evolution of IA, Brosnan and de Waal's conclusion seems fairly reductionist and unsupported. Put simply, to merely recognize inequity does not mean to exhibit characteristics of first or second-order IA. Furthermore, Brosnan and de Waal's (2004) reanalysis of their (2003) data (in response to Wynne's [2004] claims) sought only to reaffirm their original conclusions, without acknowledgement of possible frustration and contrast effects (given short delta-t between trials), or more parsimonious "PF reward-availability" rationales. Interestingly, Brosnan and de Waal (2004) admit that their experimental paradigm did not allow monkeys to actually avoid inequity, but that their recognition of negative inequity was enough to prove IA. Ultimately, the researchers conclude that IA in capuchin monkeys is guided by social emotions-exacerbated by perceived differences in effort (i.e. highest RR in EC) and influenced by the presence of a partner/their PF (i.e. decreasing RR in FC).

There is an additional assumption that underlies Brosnan and de Waal's experiment, as explained in de Waal's TED Talk video (2013), "Moral Behavior in Animals," in which he presents the original experiment (2003). De Waal claims that the capuchin subject "happily accepts" the cucumber (LPF) in the first exchange of the IT-until her partner receives the grape (PF)so to say that the omnipresence of grapes in the experimenter's PF bucket had no effect on the initial exchange. Without breaching the limitations of theory of mind, it is hard to know if, prior to the unequal distribution of 'pay,' this monkey was fully contented by the cucumber. In reality, this is highly unlikely given that cucumbers were the LPF in a dichotomous preference test (Brosnan and de Waal 2003b) and that subjects had recently received grapes during other trials. Rather, monkeys in the IT could have held a 'hopeful expectation' for a grape (PF), and thus passively accepted the LPF. Once again, this could the result of residual expectations from prior trials and/or feeding patterns at the Yerkes primate center (NT is a highly unusual response among these trained capuchins; Brosnan and de Waal 2003: 298). In their conditioned environment, monkeys might develop expectations analogous to: "I'll take what I can get"; "Something is better than nothing"; or "I'll wait it out to get something better." Lastly, because the bucket of grapes (PF) was visible during this first LPF-exchange in the IT, it is more realistic to assume that the subject has seen and/or considered the presence of the PF before accepting the LPF, than it is to imply that the psychological mechanisms behind IA only begin once the partner has exchanged her token for the PF-implying first-order IA (i.e. comparing relative pay-offs).

The chronology of Brosnan and de Waal's experiment seeks to confirm interactional evidence of IA; however, as stated, one cannot assume that: (a) the subject accepted the initial LPF without any social comparisons, expectations, or weighing of payoffs (i.e. that the first LPF acceptance was fully unproblematic) or (b) that the witnesses' IA response was totally in reaction to the model's higher relative payoff, rather than an initial expectation (i.e. reference-point, to use the terminology of Chen and Santos 2006) or a general desire for PFs, independent of all social factors (Wynne 2004). In fact, the mere presence of abundant grapes frames anything less preferable as a relative loss. Furthermore, this initial reference-point or brewing frustration is plausibly intensified by a partner's rewards or lack of effort, rather than having been purely prompted by social emotions (i.e. comparing own rewards to the big bowl of grapes, rather than the single grape the partner gets). This suggests that IA is also a matter of reward quantity (in addition to food-reward quality, as measured by LPF vs. PF), which Brosnan and de Waal do not control for. In fact, during the FC trial, there was an accumulation of grapes because the researchers claim it would have been too disruptive to reset food-rewards after each exchange (Brosnan and de Waal 2003). This detail must be accounted for in the data analysis because it is well known that individual monkeys will react negatively to receiving rewards smaller than those they see hidden inside a food container (Tinklepaugh 1928); subsequent experiments have controlled for this caveat by hiding the food-rewards (Dubreuil et al. 2006). In essence, having the bowl of grapes near the human experimenter in all but one trial (ET) is a flaw in the experimental design, as the mere presence of abundant grapes will intensify any reaction to a partner receiving a PF. Thus, IA as a social function is supported only by statistical correlations,

rather than theoretically justified *causations*.

After their 2003 experiment, Brosnan, de Waal, and co-author Schiff (2005) also tested IA in chimpanzees (Pan troglodytes) with a similar methodology (i.e. 4 token-exchange trials [ET, IT, EC, FC]; 2 visible buckets of PF [grapes] and LPF [cucumbers and celery]), but with twice as many trials (50 total) and a larger, mixed-gender sample size (n=20). It is worth noting that the researchers believed any new results would yield even more information on IA's human origins than the 2003 experiment, given the great ape subject and an increased number of trials. Interestingly, Brosnan, de Waal, and Schiff (2005) ran a mixed-model statistical analysis to control for effects of housing regime, sex, dominance status and time on individual refusals to exchange. Like the original experiment, subjects showed far fewer refusals in the ET than in other tests where grapes were present, and the most common display of IA was a refusal to exchange. The pretrial statistical analysis showed that neither gender nor dominance rank have a significant effect on subjects' level of refusals, nor did effort because subjects did not show any variation between the IT and EC trials. In contrast, social and housing conditions affected chimpanzees' willingness to complete exchanges, as the researchers predicted; subjects from pair-housed couples or the same short-term social group (together for 8 years; none born in group) had frequent RRs when their partner received a PF, while members of a long-term social group (together for 30 years; all but one born and reared in group) had virtually no RRs/signs of first-order IA. This discrepancy raises questions about the correlation between kinship/relationship quality and IA, as well as the tendency for IA in a closely bonded group. Based on Brosnan, de Waal, and Schiff's (2005) data, we should expect IA to be uncommon in wild, long-term social groups because of increased social tolerance; however, this does not seem to be the case given that unequal payoffs are common in the wild (e.g. sharing hunted food) and recognition of inequality is important for resource management, survival, and social learning. Furthermore, Melis et al. (2009) found that, among captive chimpanzees, IA was more likely in socially cooperative groups and socially tolerant species. Ultimately, the group size of the pair-bonded subjects (n=4) was too small to definitively tease out the influence of social and housing stability on cooperation or IA.

With results similar to their (2003) experiment, Brosnan and de Waal employed the same fallacious reasoning to conclude that IA is greater when a conspecific received the PF (i.e. in IT), versus when the PF was merely visible (i.e. in FC) (Brosnan, de Waal, and Schiff 2005). On the other hand, decreasing RRs in the FC trial could simply be due to contrast and frustration effects, as critiqued by Roma *et al.* (2006) and Dubreuil *et al.* (2006). For example, in the FC, grapes were held in front of chimpanzees just before placing them on the ground or giving them to the individual. This small act of showing the grape before each trial is akin to 'dangling a carrot on a stick,' as if to incite IA in subjects before each trial begun, thus interfering with this trial as an effective food control. One would assume that the dichotomous preference pretest would signify cucumbers and celery as the LPF, barring the need to disrupt the base-equity of each trial by showing a grape (PF).

# Chronology of methodological improvements

Several interesting replications and methodological improvements have been published in response to Brosnan and de Waal's original claim (specifically the 2003 experiment). Most replications also feature capuchin monkeys (*Cebus apella*) (Chen *et al.* 2006; Dubreuil *et al.* 2006; Roma *et al.*2006; Dindo and de Waal 2007), while other studies examine IA in great apes (Bräuer, Call, and Tomasello 2009), cotton-top tamarins (Neiworth *et al.* 2009), and long-tailed macaques (Massen *et al.* 2012). Nevertheless, two common themes remain from the original 2003 study: (1) the presence (or deliberate absence) of the token-exchange paradigm or similar work-related task; and (2) using food-rewards (with a similar LPF/PF model) to test IA.

Roma et al.'s (2006) experiment was published in direct response to the original experiment, although Brosnan and de Waal (2006) deemed it a "non-replication" because of its lack of token-exchange (i.e. food rewards were 'up for grabs' from the human experimenter's hand). Roma et al.'s study also lacked intrasexual and organizational variety (all females; one social group), but had a slightly larger sample size (n=8) than the original, so that four subject/partner (i.e. model/witness) pairs were rotated together with less overlap than the original experiment. Most significantly, witnesses had never seen PF to control for "reward degradation." In addition, these capuchins were separated from their primary social group during testing, unlike the capuchins of Brosnan and de Waal's original study, who were paired with members of their long-term social group. These are minor, yet important improvements, because Roma et al. (2006) sought to control for the frustration effects they critique in the original experiment (2003). The methods were similar to the original procedure in that there were four trials; however these consisted of two ITs (trials 1 and 3; PF [grape] and LPF [cucumber]) and two ETs (trials 2 and 4; in which both monkeys got LPF). Naturally, Roma et al. predicted higher RRs in trials 1 and 3 than in 2 and 4, as the former offers an unequal distribution of food-rewards. To convincingly highlight the frustration effects in Brosnan and de Waal's (2003) procedure, Roma et al. predicted three specific results: First, their capuchin witnesses, as compared to Brosnan and de Waal's subjects, should have lower RRs in the ITs (trials 1 and 3) because they are not exposed to the PF condition at all (i.e. do not experience "reward degradation" which could impart contrast/frustration effects). Second, witness rejections should stay constant because they never received grapes (note presence of a traditional control group); therefore their rejections would not be dependent on what the model got, but rather on their history of food received (cucumbers, LPF). Third, models should have higher RR than witnesses in the ETs (trials 2 and 4) because they experienced "reward degradation" from grapes (PF) to cucumbers (LPF)which would disprove the presence of IA in Brosnan and de Waal's (2003) experiment and suggest a more parsimonious explanation. In essence, if Roma et al. (2006) found that models have high RRs in ETs 2 and 4 (where no grapes were present, as in original experiment), then the only difference between the ET in Brosnan and de Waal's (2003) and Roma *et al.*'s (2006) experiments (besides general lack of token-exchange) is the "reward degradation" that models experience before the ET—highlighting the role of contrast effects and history of food received.

Roma et al. (2006) found that cucumber rejection was infrequent among witnesses, unlike the elevated rates in Brosnan and de Waal's (2003) experiment. Their study was met with a direct reply by Brosnan and de Waal (2006), in which they issued "partial support for a non-replication," given that the experimental design was so different and intended to prove something entirely different. The partial support comes from the acquiescence that there may be some frustration effect, but Brosnan and de Waal argue that this effect is not greater than the presence of IA. In fact, they conclude that Roma et al.'s study further supports IA in capuchin monkeys because RRs were higher in IT than ET-however, Roma et al. (2006) explicitly stated this expectation (that RRs should be higher in IT and less in ET, as compared to Brosnan and de Waal's findings) to demonstrate that the frustration effect is stronger than that of IA. Ultimately, Roma et al.'s experiment cannot disprove the methodology or conclusions of Brosnan and de Waal's (2003) study, because without a token-exchange element, the experiments' dependent variables are too disparate and may have changed the value of food reward (i.e. traded versus given for free) (Brosnan and de Waal 2006). Furthermore, none of the capuchins who witnessed the PF being eaten in Roma et al.'s (2006) ITs had actually eaten grapes themselves (to control for contrast effects/reward-degradation); however, this palate whetting may have intensified frustration effects via partner 'envy.' Regardless, these results cannot fully imply the presence of frustration effects within Brosnan and de Waal's 2003 data, given that this control was novel to Roma et al.'s experimental design. Instead, Roma et al. should have constructed two different sample groups to compare and parse out inequity effects versus frustration effects, rather than tailoring experimental design to evidence the latter in the guise of an attempted replication.

One month later, in response to Roma et al. (2006), Brosnan and de Waal (2006) conducted another reanalysis of their (2003) data to disprove any frustration effects. They used their same small sample size (n=5), yet bottlenecked the data even further by only reanalyzing those trials (3 total) where subjects (i.e. witnesses) had not previously received a grape. They recalculated mean RRs (see Brosnan and de Waal 2006; Fig. 1) from the 2003 data, illustrating that individuals naïve to grapes were not more likely to display IA than they would after having seen a grape; however, this still does not account for long-term memory or contrast effects prior to that specific day of testing. Also, frustration effects may be embedded into the RR and NT responses of the original experiment (2003), just by nature of compelling monkeys to trade tokens incessantly. Brosnan and de Waal (2006:75) admit that the sample size and data set are too small to draw any significant conclusions, yet they also claim the figure provides enough evidence for one "to get an idea of the direction of the data." Their conclusions thereafter hinge upon this flimsy data, which they could have omitted and still made a strong argument against Roma *et al.*'s claims (2006).

Similar to Roma et al., Dubreuil et al. (2006) sought to indirectly challenge Brosnan and de Waal's original claim by showing that capuchins' rejections are influenced by, perhaps more so than true IA, the frustration of seeing and not obtaining the PF; this also includes food available in bowls set near the human experimenter, as well as possible "audience effects" in which the human experimenter may influence refusal/acceptance behavior. Capuchins (n=6; 2 males, 4 females) were tested in four trials: three alone and one with a partner in adjacent cage. It is worth noting that the primates in this laboratory received a wide diversity of foods on a regular basis, so naturally preferences varied more: LPF (apple slices for all) and PF (raisin n=4; peanuts n=2); monkeys also received a snack 20-30 minutes before testing so as to maintain mild hunger, which is an interesting precaution not mentioned in the other methods and could have possibly suppressed hunger, though this was not measured.

The four trials varied as such: (I) Control trial, in which two pieces of LPF were shown to the capuchin and one was hidden-the remaining piece moved towards the subject to take; (2) Hiding condition, in which the LPF and PF were initially visibly available, but the PF was subsequently hidden-the LPF tray was then moved towards the subject to take; (3) Accumulation condition, similar to Brosnan and de Waal's (2003) food control (FC) trial—but the LPF was moved towards the subject to take while the PF accumulated in adjacent cage; and (4) Partner condition, in which the partner in an adjacent cage received the PF, while the LPF tray was moved towards the subject to take. This experimental design, while intentionally not a replication of the original experiment, is certainly a methodological improvement because there are clearly delineated control groups and extreme attention to detail-ensuring that capuchins are well-trained in experimental conditions, which was a critique of Roma et al. (2006) by Brosnan and de Waal (2006). Hiding the PFs is meant to control for the aforementioned hypothesis that the mere presence of PF causes IA (rather than a purely social mechanism); though the act of initially presenting the PF in the hiding condition (i.e. 'dangling the carrot') before concealing it may skew the frustration effects. Lastly, Dubreuil et al. measured the latency of NHPs to take and eat the LPF across all conditions; problematically, it is unclear what effect pushing the LPF bowl towards the capuchins, almost as a proposition, might of had on acceptance/refusal behavior, as well as how this convention compares to the efficacy of token-exchange or open-hand provisioning.

In all cases where the preferred reward was shown (regardless of the partner's presence in the adjacent cage), Dubreuil *et al.* (2006) found that capuchins were less likely to initiate a trial for the LPF. Specifically, refusals of LPF were higher when PF was hidden or out of reach (compared to when PF was placed on same tray), which suggests decreased motivation over time. It is curious that Dubreuil and others would call this a clear example of frustration effects, while Brosnan and de Waal (2003) were quick to call this type of behavior 'settling' for the LPF; perhaps Brosnan and de Waal were aware of possible frustration effects in (2003) and included this alternate, more social-oriented hypothesis? On the other hand, Dubreuil et al.'s (2006) study may demonstrate that these two phenomena are not mutually exclusive: Dubreuil et al. also found that, by virtue of seeing a partner eat a LPF, the subject became more accepting of LPF food-rewards and decreased RR (2006)-this effect was emphasized if the PF was not shown, which simultaneously supports the "reward availability" hypothesis (Wynne 2004). Further evidence of frustration and audience effects can be deduced by: (a) the similarity in data between the control and partner conditions and (b) that latencies to initiate a trial (i.e. to take LPF) significantly increased as sessions progressed in the hiding, accumulation, and partner conditions (Dubreuil et al. 2006). In sum, Dubreuil et al.'s experiment sheds important light on Brosnan and de Waal's studies and the social IA hypothesis in general-illuminating some of the aforementioned externalities that could have been problematic in Brosnan and de Waal's (2003) data (e.g. frustration effects, accumulation) by employing controls (e.g. hiding PF) to challenge the need for token-exchange.

Most significantly, Dubreuil et al.'s (2006) decision to test primates solitarily in three of the four trials demonstrates that, while socially facilitated acceptance of LPF is a factor across all studies mentioned herein, it is not the sole influence on acceptance/refusal behavior (or what Brosnan and de Waal would consider definitive displays of IA). Rather, Dubreuil and co-authors (2006) would agree with Brosnan and de Waal that NHPs do consider relative gains and weigh payoffs (which could be an evolutionary precursor to fairness or similar cooperative decision-making mechanisms), yet they might disagree in the sense that primates need not always compare their rewards to that of their partners. Furthermore, there may be factors other than food preference at play when attempting to test IA; for example, unlike Brosnan and de Waal, Dubreuil et al. (2006) were able to test reward-seeking behavior both in terms of quality (LPF vs. PF) and quantity of food available (hidden versus revealed; singular versus accumulated). An important, somewhat unanswerable, question lies herein: Do NHPs consider the bowl of food near the human experimenters to be a part of this quantity of available rewards, or is this food perceived to be exclusively accessible to the experimenter (Kummer and Cords 1991) and thus not available until it properly enters the trial? In addition, is food placed in the adjacent cage (a common fixture among FC experiments) viewed as extra-desirable (in both quantity and quality) given its state of unattainable availability (a hypothesis that could be corroborated by high rates of RR during FCs and the "reward-availability" hypothesis [Wynne 2004]), or alternatively, is this extraneous food perceived to be already dispossessed and thus not a driver of active IA to unequal distribution (a hypothesis that most experiments are not designed to account for whatsoever)?

More recently, Bräuer, Call, and Tomasello (2009) extrapolated Brosnan and de Waal's (2003) original methodology to a study on great apes—chimpanzees (n=4), bonobos (n=5), and orangutans (n=6). Experiments on IA in great apes could potentially uncover more about the evolutionary origins of human IA than prior studies on capuchins have been able to-bolstered by Bräuer et al.'s close attention to patterns of individual variation, just as IA would manifest in humans. Their methods were identical to the original experiment (2003), yet Bräuer et al. (2009) conducted vastly more trials (on chimps, 375; on bonobos, 300; on orangutans 225), utilizing all combinations of partners (as compared to the limited, fixed pairs of the original experiment). This study did not support Brosnan and de Waal's findings because subjects did not refuse to exchange (RR) any more in the IT than in the ET or trials when a partner received a better reward; moreover, this trend did not depend upon relationship quality, as subjects in short-term relationships did not RR more in the IT than the ET (Bräuer et al. 2009). Despite the more expansive sample size of this study, there are still many problems with Bräuer et al.'s. (2009) methodology. Namely, the mélange of species yielded noisy and disparate data, which the authors may have over-synthesized to draw conclusions about great apes in general. As mentioned above, the researchers concluded that RR did not increase significantly in the IT as compared to the ET (and thus claimed no signs of IA as defined by Brosnan and de Waal's parameters); however 2 of 4 orangutans and 5 of 5 bonobos displayed the opposite trend of increased RR in the IT, and bonobos remained an outlier throughout the experiment. Such individual variation among great apes poses concerns about extrapolating IA data across species, especially between monkeys, apes, and human primate species. Lastly, the experimenters seemed to use extremely active solicitations to elicit token-exchange from the apes; these extreme provocations may have significant effects on primate behavior and responses, even beyond possible "audience effects" that benign human experimenters may have on NHP subjects.

Interestingly, in 2007, de Waal co-authored a paper (Dindo and de Waal 2007) that opposed the findings of the 2003 study with Brosnan. Also on brown capuchin monkeys, but with a sample size more than twice the original experiment (n=12), Dindo and de Waal wanted to explore what other factors may affect IA, other than simple token-exchange or social provocation. Like the original study, capuchin pairs were presented with a LPF (cucumber) and a PF (grape)—however there was no task-performance. Instead, provisioning differed across the four trials: ET (LPF); IT (LPF and PF); inaccessible LPF; inaccessible PF. Just four years later, the verdict shifted: brown capuchin monkeys were not displaying negative IA, but rather showed signs of fast-paced, scramble competition for food resources. Social dynamics were still at play, as expected, and capuchins ate the LPF more rapidly if their partners received a PF. Racing to consume the LPF diametrically opposes the inclination to reject the LPF in the 2003 study-thus exposing inherent limitations or skews in the original experimental design. Alternatively, IA could play a different role (and thus manifest differently) when a reward is being exchanged for a task, versus being provisioned. Dindo, de Waal, and others (Neiworth et al. 2009) have proposed exactly this: Whereas an offering task generates foraging strategies (i.e. scramble competition), a barter*ing task* (i.e. token exchange) may induce the weighing of costs, payoffs, and partner takings—triggering hallmark signs of IA as seen in the video footage of Brosnan and de Waal 2003 (de Waal 2013).

Neiworth et al. (2009) sought to study the effects of offering and bartering tasks on IA in NHPs, or the lack thereof-specifically in New World Monkeys other than capuchins, which are known to be uniquely tolerant and sociable. Their study on cotton-top tamarins (n=11; 6 females, 5 males) included three familiar trials (ET, IT, FC), yet each was distinctly repeated using two types of tasks: (I) Bartering task, in which a monkey must place a token inside of a cup and accept a food item by removing it from experimenter's palm, or (2) Offering task, in which the monkey approaches an experimenter's closed hand when their name is called and can accept or reject food. Despite Dindo and de Waal's conclusion about bartering tasks and the obvious need to test this hypothesis, the minutia of Neiworth et al.'s experimental design seemed arbitrary; nevertheless, these work tasks seemed to be more cognitively demanding than the basic token-exchange or no task at all (e.g. Roma et al. 2006). This kind of task-based IA experiment may require a deeper understanding of the existing patterns of inequality among primates, as well as the tradeoffs involved to acquiring the desired reward; once again, this breaches what humans know about NHPs' theory of mind and may only be achieved through longterm conditioning.

For example, Neiworth et al.'s offering task required primates to make a choice between the LPF (grape) and the PF (cereal)-a thought process that is central to IA in action (e.g. cooperative decision-making) and hence its evolutionary precursors too. Interestingly, no previous experiment discussed herein, whether token-exchange or provisioning, had given NHP subjects much choice-other than dichotomous food preference pretests or the 'choice' to participate without troublesome or frustrated behavior (often conflated with signs of IA). This freedom of choice is especially compelling because in Neiworth et al.'s (2009) study, grapes are now the LPF. This begs the question: Is it important to streamline or standardize food-reward values across comparative experiments, or do these idiosyncrasies pose no problem, given that the PF and LPF are specific to the sample via a dichotomous preference test? Furthermore, how important (or perhaps misguided) is the utilization of food as the primary commodity to test IA?

Neiworth *et al.* (2009) ultimately found evidence of IA, but only under conditions of limited resources, and with a work requirement. Subjects in the bartering task (who were required to trade tokens for a reward) rejected far less overall (13.92%) than in subjects in the offering task (50.00%); this average rate of acceptance in the offering task was acquired in nine sessions. Notably, only the bartering task led to IA guided by social inequity, which could suggest a correlation between the presence of a work-related task and tendency not/to cooperate. It could be that monkeys are inclined to accept a LPF after an arduous task because the effort is a sunk cost and any food would help to replenish that expenditure. In the wild, this could manifest as 'settling' or being more 'tolerant' to LPF or unequally distributed resources after running a calorie deficit from foraging or fighting. Fittingly, the aforementioned presence of IA was most severe when tamarins saw others working to receive the PF. Here, the work scenario stimulates the effect of increased competition and thus finer attention to social distribution of rewards, as would be the case in the wild.

Furthermore, rejection of LPFs in the IT increased over time, yet there was no difference in offering task trials-denoting heavy frustration effects of the token-exchange task. In offering tasks or foraging circumstances, tamarins seem to assess differences between expected and obtained rewards; higher RR is a product of this referential mismatch, regardless of social comparisons. Lastly, Neiworth et al. (2009) found significantly more rejections in the FC condition when PF was present but unavailable, suggesting the importance of "reward availability" over presence of a partner with whom to compare rewards. When rewards are scarce, tamarins are motivated to expend greater effort to procure the limited resource. In this case, social facilitation (e.g. partner eating PF) increases RR in "food-getting" situations (e.g. Brosnan and de Waal 2003; Dindo and de Waal 2007), whereas when resources are more available, sociality may facilitate "grab-and-go" scramble competition (Neiworth et al. 2006). In sum, tamarins' sensitivity to level of work, to others' possessions, and to food value is affected only in scenarios where food is limited and effort (i.e. bartering) is required.

Finally, Massen et al. (2012) tested Neiworth and others' (2009) hypothesis about work and cooperation, as well as the effect of rank and relationship quality on IA in long-tailed macaques (n=12)—a very hierarchical, domineering species as compared to capuchins (dominance hierarchy and relationship quality measured as pretests). Massen and co-authors (2012) predicted that if effort is a crucial factor of IA, then inequity responses and effort might also depend on individual motivations of effort (e.g. dominance, role, rank), as relative to others (e.g. kin/maternalistic, non kin, friendships). They had three main hypotheses: (1) That IA will be greater when work is involved (vs. provisioning) and will increase with workload; (2) If IA is domain specific, food versus social paradigms will vary; (3) That cooperation and IA depend on rank. For this method, a gradient of PFs (i.e. mango > apple > cucumber) sat on trays made available through a pulley apparatus weighted to test effort, which diminishes possible stimuli satiation and/or "observer effects," respectively. While no frustration effect was found, subordinate NHPs likely experienced frustration during dominance tests (likely offset or neutralized by data on dominants); there was also a lack of control for the frustration involved in effort exerted to pull the weight (e.g. closeness to body). As such, how does one control for extra frustration effects in work-related or frustration-inducing experiments? Would observer effects offset these frustration effects, insofar as provisioning would actually be more favorable than a self-pulley apparatus?

Only the first two of the aforementioned hypotheses were supported, but with caveats: (1) Dominant subjects expressed IA only if minimal effort was required (no IA with large amount of effort) and subjects seemed cognizant of the amount of effort exerted (also found by Melis et al. 2009); (2) IA response was similar between friends and non-friends, thus rendering IA independent of relationship quality. Although this is somewhat counterintuitive, this finding has been long-standing in the literature (e.g. de Waal and Davis 2003; Melis et al. 2009). Furthermore, just because the degree of kinship or relationship quality is not a significant factor in these IA tests, does not mean kin selection isn't at work in cooperative decision-making at-large. In fact, IA is most notable in species that habitually cooperate-suggesting a possible co-evolution in which relationship quality and rank plays a large factor. Seminal studies have shown that individuals in positive relationships are more averse to getting better rewards than their partners (and are more oriented towards equity) than those in negative relationships (Loewenstein et al. 1989). Additionally, those in close relationships follow communal rules of equity or equality, whereas those in more distant relationships follow more contingent rules (Brosnan and de Waal 2004).

# DISCUSSION

Where are we now? Social theories of IA and the biological market After Brosnan and de Waal's (2003) original experiment, IA has since been demonstrated in humans, some NHPs, corvids, dogs, and wolves (Brosnan and Bshary 2016). In captive NHPs, IA research has continued to use food-reward models to further understand inequity responses, cooperation, and even NHPs' concepts of 'fairness.' Because these replications are homogenized by design, conclusions supporting or refuting IA in NHPs should be evaluated with cautionespecially given the lack of consistent observational studies in the wild. It is recommended that future research considers other arenas in which inequity and IA could be readily observed in nature, such as observations of operational foraging, sexual selection/assortative mating, or cooperation and partner choice in a biological market (Noë and Hammerstein 1995). In such scenarios, it would be relatively easy for observers to control for mutualism and shared-benefit interactions, parsing out the natural distributions (e.g. clustered, unequal, rank-based, etc.) of commodities (e.g. food, mates, protection, etc.), which could manifest in IA behavior and strategies (e.g. partner swap, aggression, sharing/tolerance, etc.). Moreover, these market models are all highly prone to cheating (Noë and Hammerstein 1995), which may be especially fruitful for collecting IA data because NHPs have been shown to use IA as a mechanism to stabilize cooperation in times of cheating (Brosnan and Bshary 2016). In simple terms, cheating and IA both require the comparison of personal gains to those of others and the subsequent recognition of unequal outcomes, so we would expect these scenarios to be related in occurrence, especially in the case of negative inequity aversion (i.e. disadvantageous IA [Fehr and Schmidt 1999]).

While cheating and IA are not characteristic of all biological markets, both phenomena are associated with perceptive, yet anti-social behavior—which entails the weighing of future expectations (e.g. temporal discounting for delayed 'profits' or future punishment), and the weighing of risk, rank, and relationship quality (i.e. risk of losing extra rewards or an ally is likely a function of the players' degree of relational asymmetry). Given this overlap, guarding against cheating, which is regularly observed in cooperation among unrelated conspecifics (Noë and Hammerstein 1995), could be an indirect or anticipated form of IA.

Experiments that use a two-player, reward-based model may not apply to biological market situations or more complex inequity scenarios in the wild. Relevant examples of these models include the (2003) original experiment and the game theory scenario known as the Prisoner's Dilemma; the latter is often applied to NHPs to describe why two players may not cooperate beyond the principles of "rational thought" (Fehr and Schmidt 1999). In these two-player models, the sole alternative to interaction (e.g. with partner, experimenter, or LPF) is no interaction at all (e.g. no token (NT) or reject reward (RR) in Brosnan and de Waal 2003; refusal to pull tray for food in Melis et al. 2009). Still, these scenarios neither encompass the manifestations of IA in multi-player models, nor when audience effects are lessened. In both the Prisoner Dilemma (wherein if both prisoners kept silent, they would get a better prison-sentence than if one betrayed the other for freedom [Fehr and Schmidt 1999]), and in Melis et al.'s (2009) experiment with chimpanzees (dominant/subordinate pairs were given two trays that could be cooperatively pulled to obtain food rewards [tray 1 split evenly  $\{5/5\}$ ; tray 2 split unevenly  $\{10/1\}$ , but if they didn't work together, they got o rewards), pursuing an individual reward is equated with a betrayal of the other, insofar as staying silent or not pulling tray 2 would reap better, more equal rewards for both players. There are two main takeaways from these examples: First, in the Prisoner's Dilemma (Fehr and Schmidt 1999), humans display a systemic bias towards cooperative behavior that is much higher than predicative models of 'rational' self-interested action suggests. Second, in Melis et al. (2009), chimpanzees most often pulled tray I {5/5} or neither tray, suggesting that relative gains are more important than absolute gains (i.e. the subordinate would rather get nothing than get substantially less than the dominant). Whether this tendency is a direct product of IA or 'fairness' is debatable; however, the data are consistent with the idea that IA (and the concept of relative, equitable gains) are more closely linked to cooperative decision-making than pure dominance rank-as supported by the role of fairness/utilitarianism in the Prisoner's Dilemma and other NHP studies (Brosnan et al. 2006; Massen et al. 2012). Nevertheless, chimpanzees in Melis et al.'s (2009) experiment were shown to prefer and preferentially recruit more tolerant partners/better sharers. This is natural among humans too-demonstrated by the general importance of reputational effects.

In a similar experiment (Brosnan *et al.* 2006), capuchins pulled a heavy counterweight tray to obtain 1 of 2 gener-

ally preferred foods (1st PF grape; 2nd PF apple slice) and could determine which partner pulled for which outcome. Although monkeys always benefitted (i.e. grapes and apples, both PF), they did not always cooperate-specifically when a partner got a grape, further underscoring the importance of relative versus absolute gains. Notably, this non-cooperation was not changeable on a trial-by-trial basis; rather, the IA partner refused to cooperate in all conditions-not just the ones where said subject expected or received a relative disadvantage. By the same token, those who were successful in the long-term (i.e. consistently received grapes) continued cooperating even in times when they pulled for an apple slice, suggesting that IA is a product of long-term 'bookkeeping,' rather than an immediate, trial-by-trial reflex. If long-term relationships are important to IA, one may predict that kinship, sex, or group stability would have an effect on perceived tolerance in both humans and NHPs. While the original experiment (Brosnan and de Waal 2003) claims that only females reacted differently to the various equity trials, subsequent studies have shown that sex and kinship have no effect on IA (de Waal and Davis 2003; Brosnan et al. 2006; Massen et al. 2012). In fact, Brosnan and de Waal's original claim (2003) was moot to begin with, as the data only represented females because male capuchins were unable to successfully complete all trials. In terms of group stability, the aforementioned study by Brosnan, de Waal, and Schiff (2005) shows that willingness to cooperate and displays of IA are related to social stability and housing conditions (i.e. long-term social group virtually never refused rewards).

One could argue, however, that in these cooperative decision-making tests, IA is simply a product of study design and the pressure to perform, rather than an indication of fairness, social utilitarianism, or other (second-order IA) moral considerations. Moreover, in wild biological markets, there may also be additional costs (Noë and Hammerstein 1995), which could offset this apparent degree of inequity sensitivity and/or aversion strategies. This qualification goes both ways: on one hand, game theory suggests that IA is a valid interpretation of NHPs' refusal to cooperate because there is an individualistic weighing of rewards beyond "rational thought". On the other, token-exchange experiments may skew evidence for IA by creating a perfect paradigm for refusal-exacerbated by audience and frustration effects (Roma et al. 2006; Dubreuil et al. 2006)-which may not be as severe in wild or candid multi-player scenarios. It is also worth noting that results from experiments that omit a token-exchange or work-related element (Roma et al. 2006; Dubreuil et al. 2006) could not support the original claim. Finally, Massen et al. (2012) found that positive results of IA are closely related to work-related tasks, as noted above.

Without doubt, the original experiment and its methodological flaws have spurred a conservative backlash to labeling NHPs as inequity averse; but falsifiability is logically stronger than verifiability. Beyond what can be verified by human observation, IA may be an intrinsic part of social living and non-mutualistic cooperation in the wild. As such, the prototypical food-reward for token-exchange experiment may not be the most apt way to test IA in a NHP species—especially for species that do not share food as their main 'commodity' in the wild, but rather grooming, mating, protection, etc. Future studies of IA should consider biases in the current literature and also strive to incorporate more observational data (perhaps of wild behavior), although it is undeniably difficult to test and control for motivations in nature.

# Evolution of IA: "Domain-general" theories of IA

Brosnan (2006) and others (e.g. de Waal; Neiworth et al. 2009) hypothesize that fairness, in the human sense, has its phylogenetic origins in NHP inequity aversion (IA). As the original experiment and aforementioned cooperative theories of IA indicate: IA, in its present-day observable form, is an adaptive social function. Brosnan extends this evidence to say that IA evolved from archaic social functions (2006), albeit in incremental steps, such as: (I) the ability to recognize rewards and payoffs of others; (2) the ability to respond to perceived differences; and (3) the evolution of more IA-specific structures, like second-order IA (i.e. the willingness to sacrifice to lower the payoffs for distribution deemed unequal) (Brosnan and Bshary 2016). These steps unpack the possible psychological underpinnings of IA, meaning that IA did not appear in humans de novo. While this conclusion is probably true, Brosnan and others' social explanation may be too assumptive (given NHP variation in theory of mind), and too specific to the social-domain of NHPs (of which modern researchers can only predict).

Chen and Santos (2006) give an alternative to Brosnan's hypothesis that IA evolved as a domain-specific social mechanism; instead, they propose that IA evolved from more general reward mechanisms across multiple domains, influenced specifically by *loss-aversion* and *reference-dependence*. Several experiments demonstrate the former in capuchin monkeys (*Cebus apella*) (e.g. Brosnan and de Waal 2003; de Waal and Davis 2003), and chimpanzees (*Pan troglodytes*; Melis *et al.* 2009), wherein subjects sacrifice material rewards to minimize their perceived losses. Additionally, Chen *et al.* (2006) used a similar token-exchange method to the original experiment (Brosnan and de Waal 2003) to demonstrate that capuchins weigh payoffs based on a certain reference-point.

In contrast to the original experiment, which tested rate and latency of token-exchange between LPF and PFs (i.e. cucumbers and grapes), Chen *et al.* (2006) used only apple slices (PF), but in varying amounts: At the onset of each trading-task, two human experimenters would show the capuchin subject either one apple slice or two apples slices, respectively, after which the capuchin had a choice to trade tokens with one of the two experimenters. The first experimenter would begin by showing two apple slices, but would only give the capuchin one apple slice when presented a token for food exchange; in contrast, the second experimenter began by showing the capuchin one apple slice and always traded this single apple slice when the subject presented her with a token. After three trials, the capuchins avoided the experimenter who delivered the apple slice that was perceived as a loss. In sum, the experimenters delivered identical payoffs (i.e. *one* apple slice), but their interactions differed in terms of the initial reference-point they established with the capuchin subject—allowing for the researchers to parse out the effect of relative 'expectations' (i.e. mental states based on some pre-established perception of reward as a loss or gain) upon IA.

One could say, too, that the capuchin subject who received a grape (PF) in Brosnan and de Waal's (2003) inequity trial (IT) serves as a reference-point for the partner subject who subsequently receives a LPF (thus perceived as a loss) and becomes upset/rejects the reward (i.e. displays IA) (Chen and Santos 2006). This is analogous to humans basing their happiness off of an initial reference-point (e.g. another person, a certain income bracket, or prior earnings/experience), which could change as the person becomes wealthier or happier—not because of social interactions *per se*, but because their perception of themselves or society around them shifts their reference-point. This intimate, human-to-human 'culture of comparison' is quite complex and emotionally evolved, but this is not to say that NHPs or other animals cannot cultivate a similar culture of relativity.

Chen and Santos (2006:201) argue that NHPs' assessments of relative payoffs (and/or displays of IA, as defined in the current literature) have a "domain-general" evolutionary origin, rather than having evolved as a primarily social adaptation, as Brosnan and Bshary (2012) and others posit. In fact, while Chen et al.'s experiment (2006) gives evidence of IA via loss-aversion and reference-points, they do not insist that such two-player experiments or observed present-day advantages of a particular trait can necessarily prove its ancestral benefits or evolutionary function. This is especially true of cognitive traits, which are more developmentally plastic and do not fossilize or remain visibly vestigial. Although the scenarios in which Brosnan and Bshary (2012) would expect to see IA are justified and logical, it is more likely that primates and other animals naturally developed expectations about rewards in a multitude of different scenarios (not just social interactions; e.g. solitary foraging) and thus developed mechanisms to distinguish when these expectations have been violated; hence forming preferences that may manifest in IA.

It is easy to imagine that, over evolutionary time, paying attention to others' rewards would be useful—not only to compare relative value of one's own rewards to others' or their prior payoffs, but to see how the effect of a changing environment (Chen *et al.* 2006) may depreciate or enhance these payoffs. In gregarious social groups, weighing payoffs and IA would seem to give more cues—environmental or otherwise—than simply focusing on one's own rewards in a vacuum. Moreover, if this kind of IA evolved from domain-general, referential loss aversion, then solitary primates who are perceptive, self-reflecting, or expectant (in a non-anthropomorphized sense) would gain this selective advantage even in the absence of social interactions. Put simply, perfectly equal payoffs rarely occur in nature.

Neiworth et al.'s (2009) study on cotton top-tamarins

and the narrow scenarios in which tamarins display IA (i.e. limited resources, limited effort) supports the incremental, domain-general evolution of IA. This could certainly be reinforced by social emotions—such as the envy effect displayed in Roma *et al.*'s (2006) experiment, the penchant to observe others' payoffs in a biological market, or the desire for third-party reciprocity (Brosnan and Bshary 2016).

This reference-setting hypothesis also helps to explain the overwhelming individual variation of IA based on the stability of a given social group-a significant independent variable in Brosnan, de Waal, and Schiff (2005). More specifically, Chen and Santos (2006) predict that IA is a better function of environmental stability, after which social stability follows. For instance, comparing one's own payoffs to stable members of a social group (rather than more transitory members) may convey more about the fixed environment than of social dynamics (Chen and Santos 2006). Prompted by environmental factors, it follows that NHPs would seek information (i.e. reference point formation) via social exploration, for example, that directly correlates with the payoffs he or she seeks (e.g. observing the best hunters to stabilize IA and reap better food-rewards). Additionally, competitive strategies or leveling mechanisms may have been used by early hominins (Chen and Santos 2006); these fundamentally environmental adaptations could have selected for social advantages, such as hierarchy, dominance, and cooperation, insofar that IA may have served as a counterbalance to keep hierarchy or cooperation in check. Chen et al.'s new prediction-that IA should be greatest in uncertain environments where optimal strategies are highly variable-should be further tested across primate species and social organizations, perhaps outside of a captive setting (2006). This connection also underscores the importance of the experimental environments within IA tests, and potentially highlights flaws in the popular token-exchange for food reward paradigm-wherein the importance of food, cooperation, and social interaction may be more species-specific than previously assumed.

# CONCLUSION

The overwhelming attention to inequity aversion (IA) in non-human primates (NHPs) speaks to its present-day importance as a social emotion and an evolutionary precursor to fairness, though this is not necessarily why or how it evolved. The scientific literature has mixed conclusions about the factors that influence IA (namely social group stability, dominance, and work effort) and those factors that do not (e.g. sex and kinship). While Brosnan, de Waal and others have introduced complex social theories of IA, there may be far more parsimonious explanations to the phenomena witnessed in their numerous experiments, replications, and methodologies-such as the influence of contrast, audience, and/or frustration effects. Nevertheless, ruling out IA in a certain captive experiments or models (i.e. token-exchange) should not rule out IA altogether, and vice-versa for affirmative data. It is plausibly adaptive for animals to not only consider relative gains versus absolute gains vis-à-vis recognizing the benefits of others, but also for NHPs to evaluate personal benefits purely in terms of what is available or preferable. This matches the intuitive notion that NHPs should understand inequity in order to guide cooperative decision-making, yet the jury is still out whether this recognition depends on social psychology or other factors related to resource scarcity. More often than not, domain-general theories are more convincing because they can incorporate, rather than preclude, certain hypotheses.

# ACRONYMS/KEY TERMS

IA = Inequity Aversion PF = Preferred Food LPF = Lesser Preferred Food NHP = Non-Human Primate NT = No Token exchanged RR = Reject Reward / Reward Refusal "Original experiment" = Brosnan and de Waal 2003

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