

Sex Ratio Bias in Managed Populations of Hylobatids

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Key Words

Gibbon · Siamang · Sex ratio · Hylobatidae · *Nomascus* · *Hylobates* · *Symphalangus*

Abstract

A number of explanations have been proposed for the occurrence of sex ratio bias in primates, including the Trivers-Willard hypothesis on differential investment, local resource competition or enhancement as a result of sex-biased dispersal, dominance-related advantages conferred on one sex but not the other, and the fragile male hypothesis. However, none of these theories was thought to be applicable to monogamous primate species. Here, we examine data on zoo-housed populations of three hylobatid species to test the null hypothesis of equal sex ratio. We analyzed over 40 years of demographic data on *Nomascus leucogenys*, *Hylobates lar* and *Symphalangus syndactylus*. We identified a strong male-biased birth sex ratio in *N. leucogenys*. Male infant mortality was consistently higher than female infant mortality for *N. leucogenys*, but this difference was not significant. We found that prime-age *N. leucogenys* females (aged 13–20) produced significantly more male offspring than female offspring, and young *S. syndactylus* females (<13 years) produced significantly more female offspring. Recent field evidence of more flexible mating systems in *H. lar* and *S. syndactylus* may also be occurring in *N. leucogenys*. However, *N. leucogenys* has not been well studied in the wild. Ecological differences among species may further contribute to these observed patterns.

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Introduction

The idea that animals may gain an advantage by biasing the sex of their offspring has been widely debated. Darwin [1871] first suggested that individuals who are capable of biasing the sex of their offspring towards the sex with greater reproductive potential may leave more descendants and therefore this trait may be select-

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ed for. Building on this idea, Fisher [1930] suggested that a female should produce the sex that gives her the greatest fitness benefit. If the costs and benefits for each sex are equal, the sex ratio may vary over time, but ultimately will return to an equilibrium of 50:50. However, Trivers and Willard [1973] noted that in polygynous species, male and female offspring might differ in the costs of production, as well as in the potential differential fitness gains that a mother may accrue via the production of one sex over another. Specifically, they suggest that females in good condition should produce more males, because male offspring would benefit most from the additional resources that a fit mother could provide. Females in poor condition, on the other hand, would, in theory, produce more female offspring. These female offspring would likely reproduce despite limited maternal investment.

The idea that sex ratios may deviate from equality in adaptive ways has led to a plethora of research, much of it in ungulates [Kojola, 1998; Cote and Festa-Bianchet, 2001; Sheldon and West, 2004] and primates [Nevison et al., 1996; Packer et al., 2000; Brown and Silk, 2002; Rosenfeld and Roberts, 2004; also see Faust and Thompson, 2000, for both ungulates and primates]. Nevertheless, sex ratio bias in non-human primates has posed a particular challenge to researchers, largely due to the complexity and diversity of primate social and mating systems. For example, among female-philopatric primates in which dominance rank is inherited, the Trivers-Willard hypothesis would predict that dominant females would tend to produce female offspring, who in turn will inherit their mother's high rank [Silk, 1983; Berman, 1988; van Schaik and Hrdy, 1991; Brown and Silk, 2002]. However, in other primate species, dominance is associated with male bias (given that males are more likely to benefit from the added resources that their high-ranking mothers may be able to accrue [van Schaik and Hrdy, 1991]), and thus the male bias as originally outlined by Trivers and Willard is the anticipated outcome. In addition, it has been theorized that females may be more likely to produce the sex that disperses from the natal area, given that dispersing young will not be in direct competition with their mothers. This concept has been termed 'local resource competition' [Clark, 1978; Silk, 1984; Perret, 1990; van Schaik and Hrdy, 1991]. On the other hand, females may be more likely to produce the philopatric sex if one sex is more likely to help with future infant care and/or defense; this has been termed 'local resource enhancement' [Silk and Brown, 2008; Zhao et al., 2009].

Alternatively, older females, whose future reproductive potential is low, may be more likely to produce the costlier sex and invest heavily in this presumed final offspring [Rawlins and Kessler, 1986]. Still another theory holds that bias towards the production of the sex that exhibits higher infant mortality may facilitate maintenance of an equal sex ratio at maturity [Nunes and Chapman, 1997]. The fragile male hypothesis suggests that males may be more vulnerable than females prior to adulthood due to more rapid growth and susceptibility to nutritional stress [van Schaik and de Visser, 1990; Fedigan and Zohar, 1997] and would suggest that a male bias at birth would be expected.

In the case of monogamous primates (monogamy being defined as the social system in which one male and one female form a long-term pair bond, and generally exhibit mating exclusivity [Fuentes, 1999]), no reasonable theory holds about why a female may benefit from biasing the sex ratio of her offspring. The reproductive success of males and females in monogamous mammalian species tends to be equal, and males and females also tend to lack substantial sexual size dimorphism.

Thus, it can be assumed that neither the probable costs nor benefits of producing males and females is likely to differ substantially [Krackow et al., 2003].

Given the apparent absence of a suitable theory for sex ratio bias in monogamous species, one would not expect to observe such a bias in species that exhibit this mating system. Evidence is inconclusive, with some data supporting and some failing to support, this notion. Rothe et al. [1992] examined secondary sex ratios in common marmoset (*Callithrix jacchus*) populations and found that they were skewed slightly, but not significantly, towards females. In contrast, Poole and Evans [1982] found the opposite pattern, with *C. jacchus* secondary sex ratio skewed slightly towards males, with the difference largely disappearing by maturity due to higher mortality of males. Kleiman [1979] reported a male-biased secondary sex ratio in captive golden lion tamarins (*Leontopithecus rosalia*), and suggested that this related to greater intrasexual aggression among females. However, French et al. [1996] found no such bias in *L. rosalia*, but found a male bias in *L. chrysopygus* and a female bias in *L. chrysomelas*.

Given the paucity of studies on sex ratio bias in monogamous species, it is not surprising that no published studies have examined patterns of sex ratio bias in the hylobatids. Here, we describe the results of an investigation of sex ratio bias in zoo-housed populations of three species of hylobatids representing three genera: white-cheeked gibbons (*Nomascus leucogenys*), white-handed gibbons (*Hylobates lar*) and siamangs (*Symphalangus syndactylus*). As part of routine master planning for the zoo population of *N. leucogenys*, during which demographic parameters for the population are assessed, we noticed a possible pattern of male bias in the zoo population both at birth and at maturity. Thus, we sought to confirm the validity of this observation and to explore whether similar patterns were found in zoo populations of related hylobatids. Given the prevailing theories of sex ratio bias in primate species, we had no a priori expectations for detecting sex ratio bias in any of these presumed monogamous taxa. Thus, our null hypothesis was that there would be no biased sex ratio in hylobatids. This would be expected if the costs of producing males and females, as well as the fitness benefits of males and females, are equal. Recent field work has provided support to the idea that hylobatids may not be as strictly monogamous as previously thought (*H. lar* [Reichard, 1995, 2009; Savini et al., 2009]; *S. syndactylus* [Morino, 2011]; *H. lar* and *S. syndactylus* [Palombit, 1994]). If that is the case, the possibility arises that males may in fact have greater reproductive potential and as a result females would stand to benefit by producing more male offspring, or investing more in male offspring. If our data support the alternative hypothesis, this would be consistent with recent field evidence suggesting that gibbon social and mating systems may be more variable than previously thought.

Methods

The Association of Zoos and Aquariums (AZA) maintains managed populations of three hylobatid species: white-cheeked gibbon (*N. leucogenys*), white-handed gibbon (*H. lar*) and siamang (*S. syndactylus*). For all three species, animals are managed as monogamous pairs, and offspring remain in their natal groups until or beyond sexual maturity (determined by population needs and family-specific dynamics). The AZA studbooks for each of the three species were examined using Poplink 2.1 [Faust et al., 2009], a software program that manages and analyzes studbook data. We applied several filter options to the database prior to analysis in order to re-

strict our analysis to captive-born animals in North America. We omitted any births for which sex was not entered into the studbook.

To calculate birth sex ratio, we analyzed the data in 10-year increments as well as for each studbook in its entirety. Our data set included data from 1970 to 2009 for *N. leucogenys*, 1960 to 2009 for *H. lar*, and 1960 to 1999 for *S. syndactylus*. We did not analyze individual decades with fewer than 10 births, but these decades were included in the overall population analysis. We used a binomial test [<http://www.graphpad.com/quickcalcs/binomial1.cfm>, 2005] to detect deviations from an equal sex ratio. We then calculated sex ratios at birth (secondary sex ratio), at 1 year of age, and at sexual maturity (tertiary sex ratio) for each species. Sexual maturity was estimated at 5 years of age based on studbook data on youngest females to conceive. We conducted a survival analysis using the procedure LIFETEST for SAS [SAS version 9.3]. We included all individuals born during the designated date ranges for each species and for whom we could confirm status (living or dead) at 5 years of age. We included as censored data any animals that were alive but less than 5 years of age at the end of the interval. All animals that were at least 5 years of age were considered to have survived to sexual maturity; their exact ages were not included in the analyses. We also conducted a Fisher's exact test [<http://www.graphpad.com/quickcalcs/contingency1.cfm>, 2005] to compare survival to 1 and 5 years for males and females for each species. Finally, we examined the sex ratio of infants born to 'young' mothers (12 years and younger), mothers in their 'prime' (13–20 years of age), and 'old' mothers (≥ 21 years of age) using a binomial test. Alpha was set at 0.05 for all analyses.

Results

Our data set comprised 105 *N. leucogenys* births that occurred between 1970 and 2009, 490 *H. lar* births between 1960 and 2009, and 264 *S. syndactylus* births between 1960 and 1999. *N. leucogenys* was found to have a male-biased secondary sex ratio over the whole date range of 1970–2009 (62% male, binomial test, $p = 0.019$). No statistically significant sex ratio bias was found in any single decade. However, the bias approached significance between 2000 and 2009 (67% male, binomial test, $p = 0.08$), and showed a consistent trend towards male births in all decades with an adequate sample size (table 1).

No significant differences in sex ratio were found for the *H. lar* and *S. syndactylus* populations for any single decade or overall. The *H. lar* population was found to have an approximately equal secondary sex ratio for the whole date range of 1960–2009, with 52% of births being males. Similarly, the sex ratio for the *S. syndactylus* population did not deviate significantly from equality (49% male). From decade to decade, the *H. lar* population sex ratio fluctuated between 50 and 56% male births, while the *S. syndactylus* population fluctuated more widely between 38 and 64% male births.

The proportion of infants that survived to 1 year of age was noticeably (though not significantly) higher for females in *N. leucogenys*, with 88.6% female survival compared to 75.9% male survival (fig. 1). Significantly more *H. lar* females survived to maturity than did males, with 54.1% male survival and 64.5% female survival (Fisher's exact test, $p = 0.04$); for *N. leucogenys*, there was a non-significant trend, with 85.7% female survival compared to 68.5% for males (Fisher's exact test, $p = 0.08$; table 2). A survival analysis indicated a similar non-significant trend towards higher survival to maturity in females than males in *N. leucogenys* (log rank test, $\chi^2 = 2.65$, d.f. = 1, $p = 0.10$) but not for *H. lar* or *S. syndactylus* (log rank test, $\chi^2 = 2.26$, d.f. = 1, $p = 0.13$ for *H. lar*; $\chi^2 = 0.24$, d.f. = 1, $p = 0.88$ for *S. syndactylus*).

Table 1. Sex ratio at birth for white-cheeked gibbon (*N. leucogenys*), white-handed gibbon (*H. lar*) and siamang (*S. syndactylus*)

Decade	Number of births	Proportion of males	p (binomial test)
White-cheeked gibbon (<i>N. leucogenys</i>)			
70–79	6	0.500	
80–89	24	0.625	0.308
90–99	42	0.595	0.280
00–09	33	0.667	0.080
Total	105	0.619	<i>0.019</i>
White-handed gibbon (<i>H. lar</i>)			
60–69	33	0.545	0.728
70–79	144	0.500	1.066
80–89	220	0.509	0.840
90–99	72	0.556	0.410
00–09	21	0.524	1.000
Total	490	0.516	0.498
Siamang (<i>S. syndactylus</i>)			
60–69	16	0.375	0.455
70–79	47	0.638	0.079
80–89	135	0.437	0.168
90–99	66	0.515	0.902
Total	264	0.489	0.758

The p values represent the result of a 2-tailed binomial test on the proportion of male births. The p value in italics is significant.

Given these results, we also sought to examine the relationship between the sex ratio bias of offspring and maternal age at birth. We analyzed the ratios of males and females born among ‘young’ mothers (12 years of age and under), ‘prime age’ mothers (13–20 years of age) and ‘old’ mothers (21 years of age and older). Among *N. leucogenys*, we found significantly more males born to ‘prime age’ mothers (binomial test, $p = 0.003$), as compared to ‘young’ and ‘old’ mothers, where the birth sex ratio was approximately equal. There was a trend for ‘old’ *H. lar* to produce more males (binomial test, $p = 0.06$), and ‘young’ *S. syndactylus* mothers produced significantly more female offspring (binomial test, $p = 0.007$).

Discussion

Sex ratio bias remains a complex topic, and identifying supporting evolutionary explanations is often problematic. In the case of monogamous primates, there is no strong prediction regarding the direction or extent of sex ratio bias. However, recent field work suggests that species generally reported to be monogamous may in fact exhibit greater flexibility in mating system than previously thought. If this is the case, then ‘monogamous’ species may be expected to follow patterns more typically

Fig. 1. Proportion of males (■) and females (□) surviving to 1 year of age (a) and to sexual maturity, estimated at 5 years (b). * $p < 0.08$; ** $p < 0.04$. WCG = White-cheeked gibbon; WHG = white-handed gibbon; SIA = siamang.

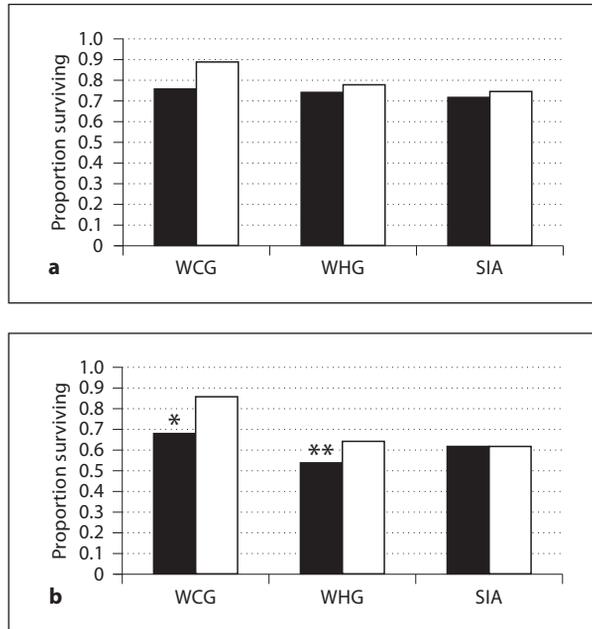


Table 2. Percent survival to 1 year and to sexual maturity (estimated at 5 years) for *N. leucogenys*, *H. lar*, and *S. syndactylus*

Species	Number of births	Proportion of males	Males survive to 1 year, %	Females survive to 1 year, %	p (Fisher's exact test)	Males survive to 5 years, %	Females survive to 5 years, %	p (Fisher's exact test)
<i>N. leucogenys</i>	90	0.6	75.9	88.6	0.17	68.5	85.7	0.08
<i>H. lar</i>	390	0.53	74.4	77.6	0.48	54.1	64.5	<i>0.04</i>
<i>S. syndactylus</i>	247	0.49	71.9	74.6	0.67	62.0	61.9	1.0

The p value in italics is significant.

attributed to polygynous species: more variable and potentially greater reproductive success for males leading to a fitness advantage for pairs that produce male offspring. Our study has demonstrated a sex ratio bias in a captive population of *N. leucogenys*, but not in comparable populations of other hylobatids (*H. lar* and *S. syndactylus*). We offer several possible explanations for these findings.

Given the small sample size ($n = 105$ *N. leucogenys* births) it is possible that these findings are nothing more than chance variation in birth sex ratio. Similar patterns have been found in other zoo populations of primates and other mammals [Faust and Thompson, 2000]. However in their study, Faust and Thompson found that the direction of bias tended to fluctuate over time from male biased to female biased. Our

Table 3. Relationship between maternal age and sex of offspring for *N. leucogenys*, *H. lar* and *S. syndactylus*

Species	Age group	Number of births	Proportion of males	p (binomial test)
<i>N. leucogenys</i>	≤12 ('young')	33	0.515	1.000
	13–20 ('prime')	47	0.723	<i>0.003</i>
	≥21 ('old')	24	0.625	0.308
<i>H. lar</i>	≤12 ('young')	206	0.515	0.728
	13–20 ('prime')	162	0.494	0.937
	≥21 ('old')	64	0.625	0.060
<i>S. syndactylus</i>	≤12 ('young')	139	0.266	<i>0.007</i>
	13–20 ('prime')	113	0.513	0.661
	≥21 ('old')	43	0.395	0.311

p values represent the result of a 2-tailed binomial test on the proportion of male births.
p values in italics are significant.

finding of a consistent trend of male bias in every decade examined suggests that this may represent a real biological phenomenon rather than just random chance.

It is possible that captivity may influence birth sex ratio in a number of ways. Females used for breeding in zoo populations are expected to be in 'good' physical condition and thus may be expected to produce more of the costlier sex. In most polygynous species, males are the costlier sex, but also have the greatest variability in reproductive success. This explanation does not hold for the hylobatids, in which little sexual size dimorphism is demonstrated and in which reproductive success is considered to be approximately equal for males and females. However, this assumes a monogamous mating system.

Studies on other monogamous primates may provide insights into the observed patterns in hylobatids. For example, findings on the generally monogamous golden lion tamarin (*L. rosalia*), in the field and in captivity, suggest that breeding females may be more aggressive towards mature same-sex offspring than they are towards mature opposite-sex offspring, suggesting a role for local resource competition [Kleiman, 1979; Baker et al., 1993]. Furthermore, sex ratio has been reported to be male biased in *L. rosalia*, and females tend to disperse from the natal area at a younger age than do males. The group structure of this species has been found to vary, with some groups possessing a single breeding male and others comprising multiple breeding males [Bales et al., 2006]. Although we do not have data to address all these factors in the managed populations of hylobatids under investigation here, similarities in ecology and social structure between the generally monogamous lion tamarins and the hylobatids suggest that similar patterns of sex ratio bias may be likely. Brockelman et al. [1998] found that both sexes disperse in his study population of *H. lar*, and parents were known to display tolerance of mature young on their territories, suggesting that delayed dispersal may be common. A study of agile gibbons (*Hylobates agilis*) by Mitani [1990] found that approximately equal numbers of subadult males

and females disappeared from their natal groups after becoming peripheralized, indicating that both sexes disperse and that tolerance of maturing offspring may be more limited in this species. Recent findings by Lappan [2007] suggest that siamang females may disperse further from their natal groups than do males, and as a result may suffer higher mortality during this vulnerable dispersal period. *H. lar* appears to exhibit a higher level of social tolerance of maturing young than is seen in other species studied to date.

In the zoo environment, hylobatids are managed as nuclear family groups. Efforts to integrate multiple adult males (or multiple adult females) have been problematic and unstable [J. Petersen, pers. commun.]. Offspring typically remain in their natal group beyond sexual maturity; however, aggression by parents towards offspring has sometimes required separation of mature young. In addition, mature young may attempt incestuous matings, also necessitating separation of group members or contraception of adults. The zoo environment may therefore impose limitations on normal patterns of dispersal which in turn may influence relative costs and benefits of the sexes.

Although we cannot offer any conclusive explanation for our findings, we suggest some possible management implications, and offer a potential explanation for the observed pattern. From a management standpoint, the male bias in *N. leucogenys* has had negative impacts on the demographic and genetic structure of the population; a similar male bias of *N. leucogenys* has been found in the European Association of Zoos and Aquariums population as well [Lefaux, 2010]. The male bias, combined with the apparent age effect on offspring sex, suggests the importance of potentially breeding 'young' *N. leucogenys* females (12 years of age and under), as these females tend to produce offspring with an unbiased sex ratio. Breeding 'prime age' females (aged 13–20) appears to be the driving force behind the male bias in the population and yet may be unavoidable. This should be taken into account when making breeding recommendations, in the hopes of moving the *N. leucogenys* population back to an equal sex ratio.

Recently, and primarily as a result of the relative shortage of females in the population, females under the age of 13 have received breeding recommendations [Petersen et al., 2010]. This decision is based on the current demographics of the population; however, this strategy is not without risks. It is not unusual for young, primiparous females to be unsuccessful with their offspring. In addition, as a consequence of the small population size, every effort is made to place all females, regardless of age, in potential breeding situations (provided a genetically and socially compatible partner can be found). The male bias in offspring produced by prime age females may reflect the presumed better condition and greater likelihood of breeding success for females in this age range. While we can continue to monitor reproductive success and sex ratio among current breeding pairs, we may not be able to target specific age ranges as breeding priorities due to the small population size and limited genetic diversity.

A different pattern emerges for *S. syndactylus*. Significantly more females are born to young mothers (under the age of 13). In the zoo environment, this may be offset by actively delaying age of first breeding. However, the sex ratio evens out by maturity, and no overall sex bias was observed in this species. Sex differences in dispersal and competition over preferred resources in the larger-bodied siamangs may be one possible explanation for this maternal age effect.

It is important to note that infant and subadult mortality tend to be higher for male *N. leucogenys*, and subadult male mortality is significantly higher for *H. lar*. These findings seem to support the fragile male hypothesis [van Schaik and de Visser, 1990; Fedigan and Zohar, 1997] and following from this, one might predict that a male-biased secondary sex ratio, coupled with higher male infant mortality, might lead to an equal tertiary sex ratio as the number of males is reduced to a greater extent than the number of females. That is not the case in the *N. leucogenys* population; the tertiary sex ratio remains male biased. The stability of the captive environment may ameliorate (to some extent) high male infant mortality, and thus the sex ratio remains male biased. Because hylobatids are managed as monogamous pairs, an equal sex ratio is critical in order to maximize the potential number of breeding pairs and facilitate social housing for all animals.

The results of our captive study, combined with new insights into gibbon social structure from field studies, allow us to speculate on some possible explanations for the observed pattern in sex ratio bias described here. Recent field data support the notion that hylobatids may exhibit a more flexible mating system than previously assumed [Palombit, 1994; Reichard, 1995, 2009; Savini et al., 2009; Morino, 2011]. Polygyny and polyandrous groups are known to occur, and extrapair copulations have been documented [Reichard, 1995, 2003]. The higher male mortality that we report here in zoo-housed *N. leucogenys* and *H. lar* is similar to prior findings on other monogamous primates, including species of callitrichids [Kleiman, 1979], and suggests that a male-biased sex ratio at birth may approach equality by sexual maturity. In the zoo setting however, the availability of resources and lack of ecological stressors may offset higher male mortality, thus leading to a continued male bias even after maturity. This was the case for our *N. leucogenys* population, but not for the larger *H. lar* population.

Generalizing from zoo-based investigations to natural populations must be done speculatively at best, particularly in light of the limited data available. Growing evidence points towards hylobatids being less strictly monogamous than previously believed, and as a result, explanations usually applied to polygynous species may hold. In addition, reports of greater aggression directed towards same-sex individuals in hylobatids and other socially monogamous primates suggest a role for local resource competition and therefore male bias, since females are more resource limited.

Why this pattern is seen in *N. leucogenys* but not in *H. lar* or *S. syndactylus* remains puzzling. *Hylobates* and *Symphalangus* are better studied, and their ecology and life histories are better understood than those of *Nomascus* (for an overview, see Malone and Fuentes [2009]). It is possible that lack of data on *Nomascus* may limit our ability to draw appropriate conclusions regarding patterns of sex ratio bias and its implications.

Ecological differences may offer some additional insights. Siamangs have been reported to be more folivorous than gibbons [Palombit, 1997]; however, Elder [2009] found no significant differences in dietary composition between gibbons and siamangs in a large meta-analysis comprising 21 studies at 15 sites and spanning all four genera of Hylobatidae. Due to their larger body size, siamangs are expected to out-compete the smaller-bodied gibbons in areas of sympatry; however, locomotor costs associated with interspecific competition are likely to be greater as well. Competition over preferred resources may also influence patterns of sex-biased dispersal and ultimately sex ratio.

Crested gibbons, which comprise the genus *Nomascus*, are capable of inhabiting somewhat higher elevations than other species of gibbons [Malone and Fuentes, 2009]. As a consequence of these habitat differences, crested gibbons may need to depend on less rich food resources at times, with leaves comprising a seasonally important component of their diet [Bleisch and Chen, 1991]. In such cases, competition over more preferred food resources (limited sources of fruit for example) may lead to greater intraspecific competition, and could lead to local resource competition. Collectively, these differences in ecology may impose different suites of selective pressures on *Nomascus*, *Hylobates* and *Symphalangus*. These differences may have led to adaptive advantages of biasing the sex ratio so as to reduce feeding competition via local resource competition.

Although our data from managed populations must be interpreted with some degree of caution, we believe that patterns observed in provisioned zoo populations may serve to highlight or intensify patterns that may be found in natural populations. As more field data accumulate and our understanding of *N. leucogenys* and other species of crested gibbons expands, we may be able to confirm the validity of this intriguing pattern of sex ratio bias and its implications for hylobatid mating systems.

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