

## Anchoring the Clade: Primate-Wide Comparative Analysis Supports the Relationship between Juvenile Interest in Infants and Adult Patterns of Infant Care

Stephanie L. Meredith

Harvard University, Cambridge, Mass., USA

### Key Words

Male care · Learning to mother · By-product · Sex differences

### Abstract

Female-biased juvenile interest in infants is common in primates. Proposed hypotheses to explain juvenile infant interest are that it helps immature individuals learn to parent, is a by-product of selection on adult infant care behavior, is kin-selected cooperative rearing, or is a form of harassment. If juvenile infant interest is associated with adult infant care, either functionally or as a by-product, sex-biased patterns of juvenile infant interest and adult infant care should show correlated evolution; if juvenile infant interest functions as cooperative rearing or harassment, they should not. Comparisons of nested bayesian Markov chain Monte Carlo models of independent and dependent evolution of juvenile infant interest and adult infant care indicate strong support for co-evolution of juvenile infant interest and adult infant care. Expanding comparative analysis to include available data from lemurs strengthens this support, suggesting that the function of juvenile infant interest does not differ between strepsirrhines and haplorhines. As such, strepsirrhine taxa currently maintained in captivity will be particularly useful in future work aiming to test between the learning to parent and by-product hypotheses for juvenile infant interest.

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### Introduction

Juvenile female primates often exhibit greater interest in infants than juvenile males [Silk, 1999], which has been hypothesized to facilitate experience with infants that will increase their competence as primiparous mothers [Lancaster, 1971]. This hypothesis is difficult to test because primiparous females lacking prior exposure to

infants are uncommon in natural populations [Hrdy, 1976], and direct tests have produced mixed results. Vervet monkeys [Fairbanks, 1990], common marmosets [Tardif et al., 1984], and cotton-top [Tardif et al., 1984], golden lion [Hoage, 1978] and saddleback tamarins [Epple, 1975] have lower primiparous infant mortality if they have had prior experience with infants, but Barbary macaques [Paul and Kuester, 1996] and mantled howling monkeys [Clarke et al., 1998] do not seem to benefit from it. Alternative hypotheses to explain juvenile interest in infants [reviewed in Paul and Kuester, 1996] are that it is a by-product of selection for competent adult infant care behaviors, is a form of kin-selected cooperative rearing, or functions as harassment of unrelated individuals. If juvenile infant interest is selected to help juveniles ‘learn to parent’, or if it is a by-product of selection for behaviors that facilitate appropriate offspring care in adulthood, sex bias in juvenile infant interest should show correlated evolution with sex bias in adult infant care across primates. In contrast, if juvenile infant interest serves as kin-selected cooperative rearing or harassment, it should be uncorrelated with adult infant care (hereafter, adult care), because under both of these hypotheses, juvenile males and females should be equally motivated to interact with infants irrespective of eventual adult care patterns.

Comparative investigation of juvenile infant interest has not previously been attempted, but comparative studies of allocare indicate that allocare is associated with higher maternal reproductive output in haplorhines [Mitani and Watts, 1997; Ross and MacLarnon, 2000], but not in strepsirrhines [Tecot et al., 2012, 2013]. This disparity may call into question ultimate explanations of primate infant-directed behavior that depend on indirect rather than direct fitness (e.g. kin selection). Or, it may indicate fundamental differences in the function of infant-directed behavior in strepsirrhines and haplorhines. No investigations of the function of juvenile infant interest have included strepsirrhines, but juveniles of some species, particularly lemurs, exhibit marked interest in infants [Meredith, unpubl. data; reviewed in Tecot et al., 2013]. Here, I test the comparative support for the correlated evolution of sex bias in juvenile infant interest and adult care in haplorhines. Then, I explore whether adding data from lemurs strengthens or weakens this support and discuss whether this suggests fundamental similarities or differences in the function of juvenile infant interest between the suborders.

## Methods

Tests of correlated evolution of sex-bias in juvenile infant interest and adult care were performed by computing log Bayes factors that compare the harmonic means of the posterior probability distributions of Bayesian Markov chain Monte Carlo models of independent and dependent evolution of juvenile infant interest and adult care integrated over a 100-tree block using discrete analysis in BayesTraits V2.0 Beta (downloaded from <http://www.evolution.reading.ac.uk/>) [Pagel et al., 2004]. log Bayes factors of  $>10$  are considered strong evidence for correlated evolution. The tree block was constructed using the Gen Bank taxonomy of 10kTrees version 3 (<http://10ktrees.fas.harvard.edu/>). Prior probabilities on trees, branch lengths and parameters of the model of sequence evolution were set to uniform, reflecting an assumption that all values of the parameters are equally likely [Pagel et al., 2004]. The chain was run for 10 million iterations with a burn-in of 1 million iterations and was thinned to every 1,000th sample. Tracer v1.6 (downloaded from <http://tree.bio.ed.ac.uk>) was used to check that the likelihoods had stabilized by the end of the burn-in period. Analyses were run in triplicate using independent seeds for each run. These methods appropriately account both for phylogenetic signal in the data and uncer-

**Table 1.** Sex bias in juvenile interest in infants and adult infant care by primate species

Taxon	JII	AC	C/W	References
<b>Haplorhines</b>				
<i>Alouatta palliata</i>	F	F	W	1, 2
<i>Aotus trivirgatus</i>	B	B	C + W	3, 4
<i>Callicebus moloch</i>	B	B	W	4
<i>Callimico goeldii</i>	B	B	C	5
<i>Callithrix jacchus</i>	B	B	C	6–8
<i>Callithrix pygmaea</i>	B	B	C	9, 10
<i>Cebus apella</i>	B	F	C + W	11–13
<i>Cebus olivaceus</i>	B	F	W	14–16
<i>Cercopithecus mitis</i>	F	F	W	17
<i>Chlorocebus aethiops</i>	F	F	C + W	18, 19
<i>Erythrocebus patas</i>	F	F	C + W	20, 21
<i>Leontopithecus rosalia</i>	B	B	C	8, 22
<i>Macaca fuscata</i>	F	F	C + W	23, 24
<i>Macaca mulatta</i>	F	F	C + W	25, 26
<i>Macaca nemestrina</i>	F	F	C	27, 28 cited in 29
<i>Macaca radiata</i>	F	F	C	27, 30
<i>Macaca silenus</i>	F	F	W	31
<i>Macaca sylvanus</i>	B	B	C + W	32–34
<i>Papio anubis</i>	F	F	W	35, 36
<i>Papio cynocephalus</i>	F	F	W	13, 37, 38
<i>Papio ursinus</i>	F	F	W	39, 40
<i>Saguinus fuscicollis</i>	B	B	C	8, 41
<i>Saguinus labiatus</i> <sup>1</sup>	B	B	C	42, 43
<i>Saguinus oedipus</i>	B	B	C	7, 44
<i>Saimiri boliviensis</i>	F	F	C	45
<i>Saimiri sciureus</i>	F	F	C	46–48
<i>Semnopithecus entellus</i>	F	F	W	49, 50
<i>Tarsius spectrum</i> <sup>1</sup>	F	F	W	51
<i>Theropithecus gelada</i>	F	F	W	13
<i>Trachypithecus pileatus</i>	F	F	W	13, 52
<b>Strepsirrhines</b>				
<i>Eulemur flavifrons</i>	B	B	W	53
<i>Eulemur mongoz</i>	F	B	C + W	54, 55
<i>Eulemur rubriventer</i>	B	B	W	56, 57
<i>Lemur catta</i>	F	F	W	58, 59

JII = Juvenile infant interest; AC = adult care; C/W = captive/wild; F = female; B = both.

<sup>1</sup> Not represented in 10Ktrees and not included in the analysis.

tainty in the topology and branch lengths of the phylogeny, all of which can bias estimates of character evolution [Pagel et al., 2004; Pagel and Meade, 2006].

Available tests of correlated evolution use either binary or continuous traits. Continuous measures of juvenile infant interest were not available for most species in the literature. Therefore, juvenile infant interest and adult care were dichotomized as in recent analyses of allocare [Mitani and Watts, 1997; Ross and MacLarnon, 2000; Tecot et al., 2013]. Juvenile infant interest

**Table 2.** Data for model comparisons and calculated Bayes factors

	Harmonic means		log BF	Average log BF
	dependent	independent		
Haplorhine JII only				
Run 1	-29.299	-36.779	14.960	15.321
Run 2	-29.372	-37.187	15.630	
Run 3	-29.051	-36.737	15.372	
All JII				
Run 1	-36.092	-43.526	14.868	16.289
Run 2	-35.051	-43.303	16.504	
Run 3	-34.992	-43.740	17.496	

JII = Juvenile infant interest; BF = Bayes factors.

was scored as 'female-biased' if qualitatively or quantitatively described as such in the literature or if juvenile females but not juvenile males were reported to provide direct care to infants. Juvenile infant interest was scored as 'both' if juvenile female rates of infant-directed behavior were not greater than those of juvenile males, or if both male and female juveniles were reported to provide allocare to infants. As per the thresholds used for dichotomizing allocare used in Ross and MacLarnon [2000], adult care was scored as 'female care' if species were reported to have a negligible male care of infants ( $\leq 5\%$ ), and all species with non-negligible levels of male care ( $> 5\%$ ) were categorized as 'both care'. Behaviors that were considered male care were limited to direct care such as carrying, food sharing, guarding in the absence of the infant's mother, and grooming [Mitani and Watts, 1997; Huck et al., 2004; Tecot et al., 2013]. Analysis was limited to taxa for which information about both adult care and juvenile infant interest was available in the literature (table 1). Whether species designation was derived from data from captive and/or wild populations is indicated. Citations used are enumerated and listed in the online supplementary material (for all online suppl. material, see [www.karger.com/doi/10.1159/000368356](http://www.karger.com/doi/10.1159/000368356)).

## Results

Harmonic means and Bayes factors of dependent and independent models of coevolution of juvenile infant interest and adult care from repeated runs including and excluding lemur data are shown in table 2. Repeated runs yielded similar results, and all show strong support for correlated evolution of juvenile infant interest and adult care. Adding lemurs to the data set slightly increased this support on average.

## Discussion

Strong support for correlated evolution of sex-biased juvenile infant interest and adult care is not consistent with juvenile infant interest as kin-selected cooperative rearing or harassment and is consistent with both the hypothesis that juvenile infant interest is selected to facilitate learning to care for infants and the hypothesis that juvenile infant interest is a by-product of selection for adult infant care behavior. Add-

**Table 3.** Lemur species available for study at the Duke Lemur Center

Taxon	JII	AC	C/W	References
<i>Cheirogaleus medius</i>	–	F	W	60, 61
<i>Eulemur collaris</i>	–	F	W	62
<i>Eulemur flavifrons</i>	B	B	W	53
<i>Eulemur mongoz</i>	F	B	C + W	54, 55
<i>Eulemur rubriventer</i>	B	B	W	56, 57
<i>Haplemur griseus</i>	–	B	W	54, 63
<i>Lemur catta</i>	F	F	W	58, 59
<i>Microcebus murinus</i>	–	F	W	64, 65
<i>Propithecus coquereli</i>	–	F	W	66
<i>Varecia rubra</i>	–	B	W	67
<i>Varecia variegata</i>	–	B	W	63, 68

Abbreviations follow conventions in table 1.

ing currently available data on lemur juvenile infant interest to comparative analysis of haplorhines further strengthened the already strong support for correlated evolution of juvenile infant interest and adult care, suggesting that strepsirrhines do not differ fundamentally from haplorhines in the causes of juvenile infant interest. These results cannot distinguish between the learning to parent and by-product hypotheses, but strong coevolution of juvenile infant interest and adult care implies that if juvenile infant interest is a by-product of selection on adult care, juvenile infant interest must be mechanistically linked to adult care behavior in both males and females that provide it.

Some studies on individual species have rejected the ‘learning to parent’ hypothesis for juvenile infant interest because experienced females also exhibit interest in infants [Manson, 1999; Silk, 1999] or because mothers whose infants recently died often exhibit the most interest in infants of any age/sex class [Paul and Kuester, 1996]. However, interest in infants may reflect different proximate motivations and ultimate causes in different types of individuals. For example, maternal behavior in adult macaques [Maestripieri and Wallen, 1995] and callitrichines [Fite and French, 2000] and paternal behavior in callitrichines [Nunes et al., 2001] and humans [Gettler et al., 2011] are correlated with circulating gonadal steroid hormones. Additionally, in macaques [Maestripieri and Zehr, 1998] and callitrichines [Pryce et al., 1993], maternal behavior can be induced in nonpregnant adult females by experimental administration of estrogens and/or progestogens. However, in contrast to adults, gonadal hormones of juveniles are not active [Wallen, 2005], and juvenile infant interest in macaque females is resistant to prenatal hormone manipulation [Herman et al., 2003]. Differences in the proximate mechanisms underlying infant-directed behavior by juveniles and adults may suggest that they have different ultimate causes. Minimally, it suggests that selection could act separately on infant-directed behavior in different parts of the life span. If so, studies treating infant-directed behavior (i.e. *allocare* or infant interest) as a unitary entity, irrespective of sex and life stage, may conflate behaviors that serve different functions.

In order to distinguish between the learning to parent and by-product hypotheses for juvenile infant interest, future work will need either to identify more fitness

benefits of experience with infants to juveniles who go on to provide adult infant care or to identify mechanistic linkages between juvenile infant interest and adult care. Several lemur species (table 3) would be especially useful for further investigation of either hypothesis. Due to their relatively rapid maturation, high reproductive rates, and availability for research in captivity [Zehr et al., 2014], the lemurs have great potential to further elucidate the ultimate function of juvenile infant interest.

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