

COMMENTARY

“Monogamy” in Primates: Variability, Trends, and Synthesis

Introduction to Special Issue on Primate Monogamy

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This paper is the introduction to a special issue on “Monogamy’ in Primates: Variability, Trends, and Synthesis.” The term “monogamy” has undergone redefinition over the years, and is now generally understood to refer to certain social characteristics rather than to genetic monogamy. However, even the term “social monogamy” is used loosely to refer to species which exhibit a spectrum of social structures, mating patterns, and breeding systems. Papers in this volume address key issues including whether or not our definitions of monogamy should change in order to better represent the social and mating behaviors that characterize wild primates; whether or not primate groups traditionally considered monogamous are actually so (by any definition); ways in which captive studies can contribute to our understanding of monogamy; and what selective pressures might have driven the evolution of monogamous and non-monogamous single female breeding systems. *Am. J. Primatol.* 9999:XX–XX, 2015. © 2015 Wiley Periodicals, Inc.

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INTRODUCTION

The term monogamy has long been applied by scientists to animal species which appeared to live, mate, and reproduce as male-female pairs [Wundt, 1894]. These monogamous species have been compelling to many scientists as models to understand human behavior and its evolutionary origins [Fuentes, 1998; Reichard, 2003; Reno et al., 2003; Wundt, 1894]. This has been especially true for primates, which as a group, have had a higher proportion of species traditionally characterized as monogamous (ca. 15%), compared with other mammals (ca. 3–5%) [Kleiman, 1977; Munshi-South, 2007].

This usage of the term monogamy became controversial in the early 1990’s, when many bird species, of which ~90% were presumed to be monogamous [Lack, 1968], were shown to have generated offspring with individuals other than the pair-mate [Bray et al., 1975; Lifjeld et al., 1993; Quinn et al., 1987]. The same has been true of primate species presumed to be monogamous, many of which were also found to have offspring conceived outside of the pair [Reichard, 1995; Fietz et al., 2000]. These findings prompted a re-evaluation of the concept of monogamy, and other mating systems, that led to the separation of the concept into “social monogamy” and “genetic monogamy” [Gowaty, 1996;

Reichard, 2003]. Social monogamy was defined as a social structure consisting at its most basic of the same male and female living as pairs or pairs with their offspring over some extended period of time (e. g., several breeding seasons). Additional characteristics (not every characteristic being displayed by every species) attributed to social monogamy have included joint territorial defense, highly coordinated behaviors between a male–female pair, male parenting, low sexual dimorphism, and other signs of a pair-bond such as distress upon separation and preference for the partner over a stranger [Mendoza & Mason, 1986]. This redefinition aided in reconciling some of

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the empirical observations, for example, of multiple adult males and/or multiple adult females including a second breeding female in some species, that contrasted with the conceptual notion of monogamy. Expectations concerning the characteristics of monogamous social and breeding systems have undergone periodic reevaluation with various modifications proposed [Fuentes, 1998; 2013]. Is the concept of social monogamy even still useful today, or should we be breaking these social systems down into smaller component parts [see Díaz-Muñoz, this issue]?

The evolutionary pressures that have led to social monogamy in primates and other mammals continue to be a topic of substantial interest and debate in the literature, focusing most recently on the role of male infanticide in the development of social monogamy [de Waal & Gavrilets, 2013; Dixson, 2013; Lukas & Clutton-Brock, 2013, 2014; Opie et al., 2013a,b, 2014]. The evolution of social monogamy also has been considered in concert with the evolution of the genes for oxytocin, vasopressin, and their receptors [Ren et al., 2014, 2015; Vargas-Pinilla et al., 2015]. These recent articles, however, have relied on a very broad interpretation of social monogamy which includes many species for which debate on their social structure still exists, for example, the callitrichid primates (marmosets and tamarins) [Caine, 1993; Goldizen, 1988]. One question that we address in this special issue is the current state of our knowledge regarding the monogamous, or non-monogamous, social structure of species traditionally classified as “monogamous,” particularly relying on new data from wild monkeys and apes.

In this context, a symposium entitled “Monogamy” in *Primates: Variability, Trends and Synthesis* was held at the *American Society of Primatologists* meeting in San Juan, Puerto Rico on June 19, 2013. This special issue on Primate Monogamy arises from the proceedings of this symposium and outlines the major advances and challenges remaining in the study of monogamy.

VARIABILITY

The extent of intraspecific variability or phenotypic plasticity in these species, traditionally defined as monogamous, has emerged as a key issue [Diaz-Munoz, 2015; 2015; Thompson, 2015] in the study of monogamy. A prominent example has been variability in callitrichid (marmoset and tamarin) groups in the wild, which have been described as monogamous [Baker et al., 1993; Kleiman, 1977, 1979; Leutenegger, 1980], polyandrous [Goldizen 1987; Sussman & Garber, 1987], and “flexible” [Caine, 1993; Goldizen, 1988]. This variability affects, and is effected by, our underlying definition of monogamy and therefore, our inferences of the evolutionary pressures leading

to social monogamy [de Waal & Gavrilets, 2013]. A major focus of the symposium was updating field data from putatively monogamous species. This included field studies of siamangs [Morino, this issue] and tamarins [2015].

Morino [2015] studied seven wild siamang (*Symphalangus syndactylus*) groups in Sumatra over a period of nearly 2 years. He documented stable socially polyandrous associations, all of which had two males and a single female sharing a territory over an extended period of time. Although agonistic interactions were rare, there was a clear dominance hierarchy among the males, suggesting this was a mechanism stabilizing the socially polyandrous association. Along with other studies of hylobatids [Lappan, 2007], the results suggest that pair-living may not be the only, or even the most common, arrangement in this primate group traditionally considered to be socially monogamous.

Garber et al.’s [2015] contribution uses field and genetic data to dissect the social organization of 12 groups of wild saddleback tamarins (*Saguinus weddelli*) in Northern Bolivia. Garber and co-workers highlight the contrasting social organizations observed in field and lab studies of callitrichines, again providing convincing evidence that in the wild, tamarin social organization should not be characterized as monogamous, despite the long-standing status of callitrichines as models for the study of monogamy. Garber and co-worker’s results underline the variability in callitrichine social organization and the failure of traditional labels to describe adequately their social and mating system. Thus, an important conceptual contribution from this paper is the suggestion to describe complex primate groups using separate terms to identify the social, mating, and breeding (e.g., genetic) systems of a given species [also see 2015].

TRENDS

While the study of putatively monogamous primates in captivity is not new, in recent years there have been new directions in the study of monogamous species in the lab. Large colony databases, spanning decades of study and generations of animals, are now available to examine life history parameters in different species [1986]. Controlled laboratory conditions and standardized tests have allowed us to ask probing questions, especially regarding the socioemotional aspects of monogamy [Mendoza & Mason, 1986]. Carp, Rothwell, and co-workers [2002] validate an operational measure for pair-bonding and use it to examine different types of relationships in titi monkeys (*Callicebus cupreus*) with relevance to monogamous societies. As a whole, we continue to use captive primate behavior and demography to make inferences about the social structure of wild primates.

Larson and co-workers [this issue] compare life history parameters in populations of Azara's owl monkeys (*Aotus azarae*) from the Argentinian chaco and the Keeling Center for Comparative Medicine and Research in Bastrop, TX. In both populations, males and females lived for similar lengths of time, although captive lifespans were longer; and in captivity, females in particular had a reduced risk of dying prematurely. Quantitative data on life history aids us in understanding the proximate pressures affecting survival and reproduction. For instance, the relative lack of divergence in life history patterns of male and female owl monkeys stands in contrast to the dimorphism in reproductive strategies demonstrated in saddle-back tamarins by Garber and co-workers [this issue] and previously in golden lion tamarins (*Leontopithecus rosalia*) by Dietz, Baker, and co-workers [Baker et al., 2002; Dietz & Baker, 1993].

Carp, Rothwell, and co-workers [this issue], standardize a partner preference test for coppery titi monkeys. A standardized partner preference test is widely used in the study of rodent monogamy, which has allowed comparisons across laboratories, across time, and across species [Williams et al., 1992, 1994; Millan & Bales, 2013], and this test uses similar parameters. Titi monkeys, like owl monkeys, have been used as a model species to demonstrate the classic characteristics associated with social monogamy, including joint defense of a territory, coordinated behavior, intrasexual aggression or "jealousy," male parenting, and a socioemotional pair-bond [Mendoza et al., 2003]. This in some ways makes their behavior a benchmark for other putatively monogamous species. While many tests of partner preference have been performed in titi and other New World monkeys, they have been far from standardized. This contribution provides a tool for this primate group and, hopefully other primates, to quantify one of the important elements of social monogamy.

SYNTHESIS

Tecot and co-workers [this issue] propose a new schema of definitions for monogamy, in an attempt to disentangle the often-confused terms *pair-living*, *pair-bonding*, and *monogamous*. They propose the definition of "pair-living" as two adults and their non-reproductive offspring sharing a home range; "pair-bonding" as a long-term social relationship between two individuals of the opposite sex, and "monogamy" as a mating and breeding system with sexual exclusivity. A species could demonstrate none, some, or all of the above. After reviewing these terms as applied to the Lemuroidea, they then examine red-bellied lemurs (*Eulemur rubriventer*), classified as pair-living and pair-bonding, with regard to hypotheses focused on the ecological and social variables

that contribute to these social systems. They conclude that the resource defense hypothesis best explains the social structure of this species.

Fernandez-Duque's [this issue] contribution examines a rich long-term data set on wild owl monkeys (*Aotus azarae*), which are largely agreed to be monogamous based on both social and genetic criteria [Fuentes 1998; Huck et al., 2014]. This contribution examines the hypothesis that the spatial and temporal distribution of resources (and females) are predictors of social monogamy in *Aotus*. While availability of food resources during the dry season may be of importance for social monogamy in owl monkeys, in this study predictions based on food resources did not offer strong support for the hypothesis. Fernandez-Duque highlights the challenges in using a single hypothesis to explain the evolution of social monogamy in primates and calls for a move beyond qualitative patterns to quantitative predictions to focus on the causal drivers of social organization.

Díaz-Muñoz's contribution [this issue] proposes a framework to describe and examine inter- and intra-specific variability in social organization in callitrichids. This contribution proposes that measures of infant care costs (based on infant:adult body weight ratios and home range sizes) can be used to understand variability in social organization (ex. number of adult males and females per group), across the callitrichine tree. Díaz-Muñoz, along with Garber and co-workers, call for a more nuanced and precise description of the social organization of primates and other animals to better understand the forces shaping different group-living arrangements. Once again, marmosets and tamarins present an opportunity to examine pressures that affect traits relevant to monogamous and non-monogamous social and breeding systems in short time-frames.

CONCLUSIONS

This special issue in Primate Monogamy has highlighted several key issues. Primate species that have been classified as monogamous in the past, and some that continue to be described as monogamous, actually show large amounts of variability in social organization in nature and in the lab. Concomitantly, these contributions highlight the need for more nuanced and precise descriptors of primate social behavior and the evolutionary outcomes of these behaviors. Regardless of the amount of social variability, simple explanations for the appearance and maintenance of monogamy are not supported by the empirical data [Fernandez-Duque, this issue]; and increasingly quantitative approaches [Fernandez-Duque, this issue; Carp et al., this issue] that focus on the drivers of social organization will provide the next breakthroughs in our understanding of primate mating and breeding strategies. The

papers collected herein give clear routes for future research on: more extensive field studies, more attention to the role of phenotypic plasticity in understanding the evolution of monogamy, more quantification and predictive models, and the importance of integrating lab and field studies. This special issue provides a roadmap for the study of monogamy, and other mating systems, that bypasses simple terminological debates and correlational observations, towards the predictive, quantitative, and integrative study of the primary drivers of primate social and reproductive systems.

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REFERENCES

- Baker AJ, Bales KL, Dietz JM. 2002. Mating system and group dynamics in lion tamarins. In: Kleiman DG, Rylands AB, editors. *Lion Tamarins: biology and conservation*. Washington, DC: Smithsonian Institution Press. p 188–212.
- Baker AJ, Dietz JM, Kleiman DG. 1993. Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Animal Behaviour* 46:1091–1103.
- Bray OE, Kennelly JJ, Guarino JL. 1975. Fertility of eggs produced on territories of vasectomized red-winged blackbirds. *The Wilson Bulletin* 87:187–195.
- Caine NG. 1993. Flexibility and cooperation as unifying themes in *Saguinus* social organization and behaviour: the role of predation pressures. In: Rylands AB, editor. *Marmosets and tamarins: systematics, behaviour, and ecology*. Oxford: Oxford University Press. p 200–219.
- Carp SB, Rothwell ES, Bourdon A, Freeman SM, Ferrer E, Bales KL. 2015. Development of a partner preference test that differentiates between established pair bonds and other relationships in socially monogamous titi monkeys (*Calli- cebus cupreus*). *Am J Primatol*.
- de Waal FBM, Gavrilets S. 2013. Monogamy with a purpose. *Proceedings of the National Academy of Sciences, U.S.A.* 110:15167–15168.
- Diaz-Munoz, S. 2015. Complex cooperative breeders: using infant care costs to explain variability in callitrichine social and reproductive behavior. *American Journal of Primatology* this volume.
- Dietz JM, Baker AJ. 1993. Polygyny and female reproductive success in golden lion tamarins, *Leontopithecus rosalia*. *Animal Behaviour* 46:1067–1078.
- Dixson AF. 2013. Male infanticide and primate monogamy. *Proceedings of the National Academy of Sciences, U.S.A.* 110:E4937–E4937.
- Fietz J, Zischler H, Schwiegk C, Tomiuk J. 2000. High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behavioral Ecology and Sociobiology* 49:8–17.
- Fuentes A. 1998. Re-evaluating primate monogamy. *American Anthropologist* 100:890–907.
- Garber PA, Porter LM, Spross J, Fiore AD. 2015. Tamarins: insights into monogamous and non-monogamous single female social and breeding systems. *American Journal of Primatology* this volume.
- Goldizen AW. 1987. Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology* 20:99–109.
- Goldizen AW. 1988. Tamarin and marmoset mating systems: unusual flexibility. *Trends in Ecology and Evolution* 3:36–40.
- Gowaty PA. 1996. Battles of the sexes and origins of monogamy. In: Black Jeffrey M, editor. *partnerships in birds: the study of monogamy*. Oxford University Press. p 21–52.
- Huck M, Fernandez-Duque E, Babb P, Schurr T. 2014. Correlates of genetic monogamy in socially monogamous mammals: insights from Azara’s owl monkeys. *Proceedings of the Royal Society B* 281:20140195.
- Kleiman DG. 1977. Monogamy in mammals. *Quarterly Review of Biology* 52:39–69.
- Kleiman DG. 1979. Parent-offspring conflict and sibling competition in a monogamous primate. *American Naturalist* 114:525–531.
- Lack DL. 1968. *Ecological adaptations for breeding in birds*. Chapman and Hall.
- Lappan S. 2007. Social relationships among males in multi-male siamang groups. *International Journal of Primatology* 28:369–387.
- Larson SM, Colchero F, Jones OR, Williams L, Fernandez-Duque E. 2015. Age and sex-specific mortality of wild and captive populations of a monogamous pair-bonded primate (*Aotus azarae*). *American Journal of Primatology* this issue.
- Leutenegger W. 1980. Monogamy in callitrichids: a consequence of phyletic dwarfism. *International Journal of Primatology* 1:95–98.
- Liffield JT, Dunn PO, Robertson RJ, Boag PT. 1993. Extra-pair paternity in monogamous tree swallows. *Animal Behaviour* 45:213–229.
- Lukas D, Clutton-Brock T. 2014. Evolution of social monogamy in primates is not consistently associated with male infanticide. *Proceedings of the National Academy of Sciences, U.S.A.* 111:E1674–E1674.
- Lukas D, Clutton-Brock TH. 2013. The evolution of social monogamy in mammals. *Science* 341:526–530.
- Mendoza SP, Mason WA. 1986. Attachment relationships in New World primates. *Annals of the New York Academy of Sciences* 807:203–209.
- Mendoza SP, Reeder DM, Mason WA. 2003. Nature of proximate mechanisms underlying primate social systems: simplicity and redundancy. *Evolutionary Anthropology* 11:112–116.
- Millan MJ, Bales KL. 2013. Towards improved animal models for evaluating social cognition and its disruption in schizophrenia: the CNTRICS initiative. *Neuroscience and Biobehavioral Reviews* 37:2166–2180.
- Morino L. 2015. Dominance relationships among siamang males living in multimale groups. *American Journal of Primatology* this volume.

- Munshi-South J. 2007. Extra-pair paternity and the evolution of testis size in a behaviorally monogamous tropical mammal, the large treeshrew (*Tupaia tana*). *Behavioral Ecology and Sociobiology* 62:201–212.
- Opie C, Atkinson QD, Dunbar RIM, Shultz S. 2013a. Male infanticide leads to social monogamy in primates. *Proceedings of the National Academy of Sciences, U.S.A.* 110:13328–13332.
- Opie C, Atkinson QD, Dunbar RIM, Shultz S. 2013b. Reply to Lukas and Clutton-Brock: infanticide still drives primate monogamy. *Proceedings of the National Academy of Sciences, U.S.A.* 110:E4938–E4938.
- Opie C, Atkinson QD, Dunbar RIM, Shultz S. 2014. Reply to Lukas and Clutton-Brock: infanticide still drives primate monogamy. *Proceedings of the National Academy of Sciences, U.S.A.* 111:E1675–E1675.
- Quinn TW, Quinn JS, Cooke F, White BN. 1987. DNA marker analysis detects multiple maternity and paternity in single broods of the lesser snow goose. *Nature* 326:392–394.
- Reichard U. 1995. Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). *Ethology* 100:99–112.
- Reichard UH. 2003. Monogamy: past and present. In: *Monogamy: mating strategies and partnerships in birds, humans, and other mammals*. Cambridge, England: Cambridge University Press. p 3–25.
- Ren D, Lu G, Moriyama H, Mustoe AC, Harrison EB, French JA. 2015. Genetic diversity in oxytocin ligand and receptors in New World monkeys. *PLoS ONE* 10:e0125775.
- Ren D, Chin KR, French JA. 2014. Molecular variation in AVP and AVPR1a in New World monkeys (Primates, Platyrrhini): evolution and implications for social monogamy. *PLoS ONE* 9:e111638.
- Reno PL, Meindl RS, McCollum MA, Lovejoy CO. 2003. Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. *Proceedings of the National Academy of Sciences* 100:9404–9409.
- Sussman RW, Garber PA. 1987. A new interpretation of the social organization and mating system of the Callitrichidae. *International Journal of Primatology* 8:73–92.
- Tecot SR, Singletary B, Eadie E. 2015. Why “monogamy” isn’t good enough. *American Journal of Primatology* this volume.
- Thompson CL. 2015. To pair or not to pair: Sources of social variability with white-faced saki monkeys (*Pithecia pithecia*) as a case study. *American Journal of Primatology*.
- Vargas-Pinilla P, Paixão-Côrtes VR, Paré P, Tovo-Rodrigues L, Vieira CM, Xavier A, Comas D, Pissinatti A, Sinigaglia M, Rigo MM, Vieira GF, Lucion AB, Salzano FM, Bortolini MC. 2015. Evolutionary pattern in the OXT-OXTR system in primates: coevolution and positive selection footprints. *Proceedings of the National Academy of Sciences* 112:88–93.
- Wundt W. 1894. *Lectures on human and animal psychology*. New York: Swan Sonnenschein & Co.
- Williams JR, Carter CS, Insel T. 1992. Partner preference development in prairie voles is facilitated by mating or the central administration of oxytocin. *Annals of the New York Academy of Sciences* 652:487–489.
- Williams JR, Insel TR, Harbaugh CR, Carter CS. 1994. Oxytocin administered centrally facilitates formation of a partner preference in female prairie voles (*Microtus ochrogaster*). *Journal of Neuroendocrinology* 6:247–250.