

# Behavioral Flexibility in Primates: Causes and Consequences

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**BEHAVIORAL FLEXIBILITY IN PRIMATES: CAUSES AND CONSEQUENCES**

By Clara B. Jones

# Behavioral Flexibility in Primates: Causes and Consequences

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# Foreword

Some 50 years ago, researchers started a study on the behavior of Japanese macaques on the islet of Koshima near Japan (Kawai, 1965). To give the monkeys an incentive to emerge from the forest onto the beach they provided sweet potatoes and occasionally some wheat. In 1953, a young female called Imo started washing these sweet potatoes in water before eating them. This novel behavior was soon adopted by other members of the troop and spread through the population. When Imo was four years old, she discovered that by throwing a mix of wheat and sand in the sea she could separate the grains from the unwanted sand. Again, the behavior was imitated by other group members and, after a few years, most monkeys practiced this method of obtaining grains.

This well-known example of innovative behavior and its cultural transmission was one of the first to document primate behavioral flexibility in the field. It is not only in their foraging behavior that monkeys and apes display the most complex arrays of behaviors. For instance, Goodall's work in Gombe (e.g., van Lawick-Goodall, 1968) revealed many examples of behavioral patterns that never failed to surprise field researchers and the interested public alike. Only our own species surpasses other primates in exhibiting such a large repertoire of flexible responses in heterogeneous environments, a factor that certainly contributed to our ability to occupy almost any habitat. This striking similarity in the ability to show flexible behaviors makes primates, including humans, the most fascinating study subjects for students and researchers. Such a perspective is reflected in this book, where Jones outlines the different facets of primate behavior and shows that flexibility is a hallmark of primate behavioral patterns.

The concept of behavioral flexibility basically refers to the capacity to modify behavior in an adaptive way; or, as Jones defines it: behavioral flexibility represents a "toolbox of potential responses over time and space" (Chapter 9) allowing primates to adapt to heterogeneous biotic (including social) and physical environments. Because flexibility is a characteristic of different behaviors (such as foraging, mate choice, and dispersal) and may arise through a number of underlying mechanisms, it is crucial for any study of behavioral flexibility to clearly identify the specific behavior and to define how it is measured.

In this book, Jones considers several detailed examples of how this could be achieved in primates. For instance in Chapter 3, male and female dispersal strategies in mantled howlers (i.e., different thresholds of when to disperse) are discussed as a response to changing habitat conditions. Long-term data showed that deforestation led to a rise in female but not male dispersal rates because female fitness is seen to be more influenced by resource availability than male fitness (females as “energy maximizers”). Another example of how to quantify behavioral flexibility is the “branch-break” behavior exhibited by male mantled howlers in Costa Rica (Chapter 6). This behavior is part of a compound display serving multiple purposes in mate choice and intrasexual competition depending on conditions of local competition. These examples suggest that future studies on behavioral flexibility should focus on situations in which the capacity for switching from one action to another is favored.

In other taxa such as birds and fish, research on behavioral flexibility has focused on different parameters such as the rate at which novel behavioral patterns occur (for a paper in primatology see, for example, Kummer and Goodall’s 1985 article on “conditions of innovative behaviour in primates”). In Chapter 4 of Jones’ book, this perspective is extended by discussing consequences of social cognition [referred to as the ability to perceive conspecifics as intentional agents—reflecting Kummer’s (1971) definition of “social tool use”] as a generator for behavioral flexibility in the context of damaging and nondamaging behavioral tactics.

The history of research in primatology shows that studies have often benefited from applying concepts pioneered in other disciplines such as anthropology, psychology, and behavioral ecology. For instance, Crook and Gartlan’s seminal paper in 1966 related differences in social organization of primate groups to differences in habitat and diet. Some ten years later, Clutton-Brock (1977) showed that within group differences are much more pronounced than differences between groups by analyzing the separate effects of several ecological variables on the same trait and using multivariate statistics. Another example is the use of experimental manipulation in the field to test hypotheses [e.g., Cheney and Seyfarth’s (Seyfarth *et al.*, 1980; Cheney and Seyfarth, 1982) work on vervet communication], generally illustrating how research in primatology was advanced by shifting the predominant paradigm from rather descriptive to more analytical studies.

This book introduces several topics that have recently found widespread interest in behavioral ecology, for instance, the notion of inter- and intragenomic conflict. In Chapter 7, Jones sets out to explore the consequences of inter- and intragenomic conflict and their implications for primate behavior. It will be of particular interest to evaluate the significance of findings in behavioral genetics in other mammalian species with complex social systems for research conducted in primatology. Work on mice on the effects of so-called imprinted genes (genes that are expressed depending on the sex of the parent from which they were inherited) showed that these genes mediate a conflict

between the sexes over maternal investment and have coevolved in an antagonistic way. For example, genes that are expressed only when inherited from the father serve to exploit maternal resource allocation during pregnancy and lactation by favoring higher maternal investment and positively influencing maternal behavior [i.e., females that carried a mutated gene showed impaired maternal behavior (see, for example, Li *et al.*, 1999)]. Studies on human mental disorders suggest that over and above their effects on provisioning behavior, imprinted genes significantly influence more complex social behavioral patterns in mammals (Isles and Wilkinson, 2000). To date, no one has assessed the potential implications of these results for research in primate behavior, despite their clear influence on mammalian parental behavior.

Given that these mechanisms operate in most mammalian species, would it be possible to interpret specific behaviors such as antagonistic male and female strategies as the result of intragenomic or intergenomic conflict? At present it appears that these findings may offer an explanation for a source of behavioral flexibility and underlying mechanisms. However, it will prove rather difficult to design experimental studies in primates that investigate such questions. A first step is taken in this book, where Jones outlines the implications for the antagonistic coevolution of primate male and female strategies such as coercive matings by males or female dominance and homosexuality. While the concept of antagonistic male and female strategies has been discussed in primatology for more than 20 years [e.g., Hrdy's work on infanticide (1979)], recent studies on other mammals suggest that there is clear evidence for such a process not only on the basis of behavioral observations but also as strategies of specific genes [e.g., *Igf2* and *Igf2R*, (Haig and Graham, 1991)] favoring different optima of maternal investment for males and females. These remarkable findings may help to advance some of our previous interpretations of primate social behavior and view them in a new light of antagonistic genetic strategies.

Further, behavioral flexibility touches on other current hot topics in primatology. Flexibility in social behavior may play an important role in the evolution of cooperation in primates as demonstrated by recent studies in capuchin monkeys on inequity aversion. Brosnan and de Waal (2003) found that individuals will reject a reward for a task if they see a conspecific receiving a higher value reward for the same task. If increased behavioral flexibility results in higher sociality, as pointed out in Chapter 4, the ability to exhibit flexible behavior will have profound consequences for an individual's fitness. Work on baboons by Joan Silk and colleagues (2003) recently demonstrated that infants had a higher chance of survival if their mothers exhibited higher levels of sociality. These two examples illustrate that, on a larger scale, the study of behavioral flexibility in primates may improve our understanding of cooperation in nonhuman primates and humans.

While the advantages of behavioral flexibility seem intuitively obvious, it is more difficult to quantify and analyze the costs associated with increased

flexibility. It is clear that greater flexibility will be selected for where it ultimately confers a fitness advantage to the individual. The difficulty arises because several behaviors might interact to create an overall more flexible phenotype, thus confounding a clear assignment of cost to a specific behavior. In addition, costs of increased behavioral flexibility might be incurred indirectly via a third parameter. For instance, costs associated with a higher dispersal rate in Japanese macaques may illustrate this point (Fukuda, 2004). Here, females (which are normally philopatric) had a lower threshold of dispersal in response to decreased food supply. This, in turn, caused increased male dispersal. As a result, not only was individual fitness negatively affected, but the species as a whole was put at a much higher risk of vulnerability because group sizes generally declined.

Other costs of increased flexibility are a higher predation risk, reduced rate of foraging (e.g., when trying novel food), time investment or energy required to exploit new resources. The identification and quantification of such costs, then, allows us to test the hypotheses about the adaptive value of behavioral flexibility. It may be argued that under conditions of limited food availability, individuals should be less willing to experiment and concentrate on food resources that will maintain the necessary rate of food intake.

Researching behavioral flexibility not only yields highly interesting results that help to elucidate the complexity of primate behavior but also has immediate applications in the conservation of primates and their habitats (Chapter 9). For example, analyzing the behavioral flexibility that is typical of different species in response to habitat change (which in turn affects food or territory availability) would help to better classify the vulnerability of a species to changing environments and, thus, to prioritize conservation efforts. A new additional approach in primate conservation seems particularly important because, as an example, the current classification of species into generalists (more flexible, thus, less vulnerable) vs. specialists has shortcomings as some specialist species may behave opportunistically if required. Thus, measures of the ability to exhibit flexibility in different behaviors (e.g., foraging, dispersal) will facilitate the estimation of how a given species will react to habitat disturbances such that a decrease in dispersal rates may be taken as an indicator for increased vulnerability.

Another reason to consider measures of behavioral flexibility in studies of primate biodiversity is the effect on rates of evolution in a species' genotype. Behavioral flexibility can be a major driving force for evolution because a high rate of novel behaviors may lead to increased evolutionary rates even if the variation in behavior is initially not due to underlying genetic variation but due to facultative responses that are culturally transmitted. The reason is that individuals who show high levels of behavioral flexibility will then be subject to different selection pressures. In turn, this will also affect whether newly arising genetic mutations will be selected for or against in a new context and may even lead to speciation.

The breadth of approaches to studying behavioral flexibility combined with examples of how to measure it in different behaviors make this book a valuable source for students and researchers alike. Jones shows that the knowledge of behavioral flexibility and the underlying mechanisms can significantly improve our understanding of primate social behavior and will help to unravel the complexity involved by identifying individual behaviors that, combined, result in phenotypic plasticity. Moreover, the study of behavioral flexibility holds particular importance for the conservation of primates and their habitats in directing the focus on behaviors that can be used as a measure for the adaptability to changing environments and the likelihood of a species' vulnerability.

Above all, this book is exciting to read for anyone who is interested in the scientific study of primate behavior. Jones introduces novel ideas into the field of primatology whose implications we only begin to grasp. I am looking forward to see future theoretical and empirical studies stimulated by the topics discussed here.

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# Preface

In a sense, I have never progressed beyond the age of six when children appear to be obsessed with the question, “Why?” Until very recently, “How?” questions failed to interest me very much, and they only captivate my imagination presently because I now see clearly in what ways the two sorts of questions are necessarily related (see Dixson, 1998, Glimcher, 2003, or West-Eberhard, 2003, if you are still unconvinced). I recall reciting a “book” to my maternal grandmother when I was three or four years old. She was ironing, and I was talking incessantly, as was my custom during my formative years. Even then, I was aware that I was privileged to have a caretaker who made me feel (and think!) that I was the center of her existence—more important than ironing, more important than cooking, more important than having an independent life of her own. This context, this privilege, afforded me the freedom to imagine a life beyond ironing and cooking, beyond the role of caring for others’ dreams to become the reservoir of others’ memories.

Wilson’s (1971), *The Insect Societies*, influenced me during my years as a graduate student even more than Crook’s (1964) monograph on weaverbirds, the seminal work in behavioral ecology. I believe that Wilson’s book (especially Chapter 11) had a greater impact upon me because the comparisons between insects and vertebrates seemed so counterintuitive while the correlations described by Crook seemed, once demonstrated, self-evident. Wilson’s 1971 volume and his *Sociobiology: The New Synthesis* (1975) helped me to see the study of social behavior as *aunified* enterprise, although recent work by Crespi and Choe (1997a; B.J. Crespi, personal communication) has helped me to understand the constraints on this approach.

Perhaps because of my own psychic particularities (e.g., temperament) combined with other factors (e.g., personal experience, education), Crook’s (1970, p. xxvix) assertion that “co-operation . . . seems often to be a subterfuge whereby an individual is enabled to gain or maintain that degree of social control of others at which his or her own behaviour is relatively unconstrained” influenced me in a manner that virtually insured my specializing in aspects of extreme selfishness, including spite, rather than, say, cooperation or altruism. As a result I have, possibly to a fault, studied topics such as interindividual

conflicts of interest (e.g., power, homicide) and intraspecific social parasitism, including phenotypic manipulation. Early in my graduate training I formed a passionate interest in studying social behavior at the whole organism level. I was induced to study questions for their significance to ultimate causation primarily as a result of the excitement of seminars conducted by Jack Bradbury and Steve Emlen.

The primary goal of the present volume is to incorporate the extensive literature on behavioral flexibility in evolutionary biology and behavioral ecology into the canon of primatology in order to advance the Hamiltonian unification program within the Primate Order. My own conceptual framework, however, emphasizes the importance not only of optimization of genetic benefits but also of benefits to the phenotype, reflecting West-Eberhard's (2003) notion of the phenotype as a "bridge" between genotype and environment. This perspective appreciates that even where an individual's genotype is not directly favored by condition-dependent responses, promotion of the success of one's phenotype has the potential to enhance fitness over the long-term (see West-Eberhard, 1989, 2002).

West-Eberhard's (2003) subtle insights indicate that genotype and phenotype may be induced by different factors and may have different effects, often in interaction with each other and with the environment, suggesting that interests of the genotype and phenotype may be in conflict. In future, it will not be sufficient to think of responses simply in terms of their consequences for inclusive fitness. It will be necessary to consider individuals' "decisions" in terms of their effects on both genotype and phenotype. West-Eberhard's (2003) concept of the "bridging" phenotype and my extension of it in this book assume that the individual behaves in a manner that is fundamentally self-interested, thus, not to be confused with Wilson's (1980) discussion of "trait groups."

It is my hope that this project will promote the conceptual, theoretical, and empirical unification of primatology and the other (Darwinian) natural sciences. While most primatologists investigate behavior in relation to proximate (immediate) rather than ultimate (evolutionary) causation, and most primatologists have been trained to appreciate the significance of intraindividual variations in response, several recent publications have emphasized the need to integrate the proximate and ultimate perspectives (e.g., Dixon, 1998; Abbott *et al.*, 1998; Jones and Agoramorthy, 2003). The present volume places a primary emphasis upon ultimate causation since this conceptual, theoretical, and empirical canon has been effectively absent from the canon of the social sciences (compared to that of biology) until relatively recently. If, as Charnov (2002) puts it, organisms "live to reproduce," it may be a helpful exercise to explore how primate behavior and social organization are shaped when limited by the energetic and temporal constraints of reproductive effort.

It is also a goal of this volume to promote the experimental investigation of intraindividual phenotypic variation in primate behavior. Such a project

would extend the success of experimental studies in behavioral ecology (see Piersma and Drent, 2003) and advance primatology as a truly hypothetico-deductive science with the potential to contribute to attempts to describe general principles of behavior. For example, the findings of Widdig *et al.* (2004), studying Rhesus macaques (*Macaca mulatta*), support recent attempts to develop a unifying theory of social interactions by lending support to the view that modified “tug of war” models of reproductive skew operate relative to taxon, environmental conditions, and other factors (see Hager, 2003).

Another example from the primate literature contributes to our understanding of “the mechanisms and processes that shape the expression of genetic variation in phenotypes” (Stearns, 2002, p. 10229). Through experiment, Maestripieri (2003) has recently demonstrated an apparent example of conserved traits between cross-fostered infant female Rhesus macaques and their biological mothers. In this study, infants raised by foster mothers demonstrated social and aggressive characters more similar to their biological than their adoptive mothers. This study raises the important point that plasticity may vary as a function of the target trait and that the relative advantages and disadvantages of developmental plasticity may differ as a function of age, sex and, possibly, other factors (e.g., nutritional status, kinship, or dominance rank). Maestripieri’s research supports the view that intraindividual variation in response is induced by a genetic “switch” sensitive to the ecological and demographic environment (West-Eberhard, 1979; Gross, 1996; Jones and Agoramoorthy, 2003).

On the other hand, Weaver *et al.* (2004, p. 847) report that maternal behavior in rats “altered the offspring epigenome at a glucocorticoid receptor . . . gene promoter in the hippocampus.” These results, which were reversed by cross-fostering, “show that an epigenomic state of a gene can be established through behavioral programming, and it is potentially reversible.” These remarkable findings on “maternal effects” elucidate mechanisms of maternal behavior, in particular, “the nongenomic transmission of individual differences in stress reactivity across generations” (Weaver *et al.*, 2004, p. 847) and appear to contradict Maestripieri’s (2003) study in which cross-fostered Rhesus macaques demonstrated affiliative and aggressive traits more similar to their biological than their adoptive mothers. If Maestripieri’s results are confident, the contrast may indicate that some primates and, possibly, other taxa, demonstrate less plasticity in response to exogenously induced maternal stimuli (and, possibly, other exogenous stimuli).

Day *et al.* (2003) have recently published data which may facilitate the understanding of when individuals in populations or species will and when they will not exhibit behavioral flexibility. Seven callitrichid species from three genera (*Saguinus*, *Leontopithecus*, and *Callithrix*) were studied in their study of neophilia, innovation, and social attentiveness. Individuals belonging to species of *Leontopithecus* (lion tamarins) proved more neophobic than species in the other genera, consistent with the view that species dependent upon

less manipulative and explorative foraging are more neophobic. Importantly, the work of these researchers did not support the view that dietary specialization was associated with neophobia. These findings may have broad implications for our understanding of the phenotype and exploitation of the niche.

*Behavioral Flexibility in Primates: Causes and Consequences* highlights similarities (signatures) and differences of primates to demonstrate that events in the world vary—one of the first lessons learned in introductory statistics. Species are subject to varying degrees of environmental heterogeneity, including stochasticity, a set of factors that may favor phenotypic plasticity, including, behavioral flexibility. Primates are among those taxa advanced to display an uncommon degree of behavioral flexibility (e.g., Boesch *et al.*, 2002), responses which, within the constraints of social parasitism, are presumed to optimize inclusive fitness for selfish (genetic and/or phenotypic) gain. Although many responses may be “the best of a bad job,” the individual is expected to perform in his/her interests given the options available—all other things being equal.

The present book’s discussion of behavioral flexibility in relation to evolutionary causes and consequences is advanced with full understanding that behavioral flexibility can only be demonstrated to be adaptive if evidence, preferably experimental, is presented showing that the relevant features have been shaped by evolution to enhance lifetime reproductive success (fitness, Hamilton, 1964; West *et al.*, 2001; Reeve, 2002). Stressing the importance of the study of behavioral flexibility to this program, Piersma and Drent (2003) state: “Rather than emphasizing that a capacity for phenotypic change is an adaptation (which it might well be: Pigliucci, 2001, p. 231), we argue that intra-individual trait variation itself should be used to evaluate the ‘goodness of design’ criterion for phenotypic adaptation (Williams, 1966).” For example, Garber and Leigh (1997) illustrate how comparisons in patterns of reproduction and infant care among small-bodied Neotropical primates yield strong inferences about function, in particular the energetic costs of reproduction and maturation, factors fundamental to an understanding of life history tactics and strategies.

Time and energy are limiting for organisms, making the allocation of these resources essential to an understanding of life history (e.g., Schoener, 1971; Charnov, 2002). Furthermore, every act performed by an individual will have effects with potentially significant consequences for the fitness of the actor and all individuals influenced by the act(s) (West *et al.*, 2002). For this reason, it is important to describe events before and subsequent to any response(s) of interest (e.g., Jones, 1983).

I am an advocate of the expanded use of mathematical models and other quantitative techniques not often employed in primatology, an inclination reflected in the present bibliography. While this project has received generous encouragement from numerous colleagues within and outside primatology,

many of my peers remain skeptical, resistant, or, even, hostile to theory as defined in Economics, Ecology, and Evolutionary Biology. Numerous primatologists have pointed out that mathematical treatments can help the scientist to frame his/her questions clearly and precisely. However, perhaps the most important utility of mathematical models, simplified as they may be, is to test whether our questions conform to particular assumptions, such as those of Darwinian theory. It seems insufficient to collect data and to ask questions without reference to a conceptual framework that has received theoretical support. Theoretical treatments, then, can provide initial stages in scientific programs in order to constrain our search relative to the questions worth asking and to guard against what Wynne (2004) has called “the perils of anthropomorphism.” Few behavioral and social scientists would object to using a chi-square “goodness-of-fit” test to assess their hypotheses before investing in expensive empirical investigations. Utilizing other “goodness-of-fit,” estimation, and simulation techniques have similar and, in many cases, more powerful utility (see Dunbar, 2002).

The present volume proposes that genetic conflicts of interest are ubiquitous in primates who may employ force, coercion, persuasion, persistence, scrambles, cooperation, altruism, exploitation, manipulation, social parasitism, dispersal, or spite to resolve or to manage them. Where one individual or group imposes severe costs to inclusive fitness upon a conspecific, the latter may adopt a counterstrategy in an attempt to minimize its costs. This counterstrategy may, in turn, impose costs upon the original actor(s), and so on, possibly yielding an evolutionary “chase” (“interlocus contest evolution”, Rice, 2000; Nunn, 2003). The evolution of phenotypic plasticity and/or behavioral flexibility in primates may often pertain to attempts to mitigate genetic conflicts of interest, and, consistent with Trivers’ (1972) treatment of parental investment, Schoener’s (1971) classic paper leads to the conclusion that for females (“energy-maximizers”), conflict will pertain primarily to competition for food (that can be converted to gametes and/or offspring) while, for males (“time-minimizers”), conflict will pertain primarily to competition for mates, *ceteris paribus*. Recent empirical work on primates supports Schoener’s theoretical formulations (e.g., male *Pan troglodytes*, Newton-Fisher, 2002; male and female *Alouatta palliata*, Clarke and Glander, 2004).

While mutation or other intragenomic effects may be a source of intraindividual and interindividual variation in the behavior of primates, most behavioral flexibility in social taxa of this order probably arises via trial and error, associative, or cognitive processes as novel, facultative responses to heterogeneity in physical and/or biotic, including social, regimes. The present volume explores the contexts, ecology, development, and evolution of condition-dependent responses in primates. These responses will sometimes be manifestations of tactics and strategies to optimize survival, lifetime reproductive, and/or phenotypic success, and/or may be counteradaptations to intraspecific social parasitism and intergenomic conflict.

It is my hope that students, specialists, and the general public interested in the diverse manifestations of environmental heterogeneity upon primate behavior and social organization will find this book a “good read” and a rich source of ideas for discussion as well as theoretical and empirical investigation. Environments are often unpredictable and the outcomes of individual decisions often uncertain, costly, and, possibly, risky—conditions that will limit the ability of individuals to behave optimally. A broader understanding of these states and their outcomes than is currently reflected in the primate literature has the potential to generate a revised view of the landscapes upon which primates behave and evolve and the ways that preadaptations, adaptations, and (genetically autocorrelated) responses to these regimes (see Miller, 1956; Lewontin, 1957; Slobodkin and Rapoport, 1974; West-Eberhard, 2003) may have favored the characteristics commonly associated with human beings (see, for example, Miller, 1997).

# Acknowledgments

In nonhuman primate societies, acknowledgments would take the form of rear-present postures, kissing, lip-smacking, G-G rubbing, grooming, or, possibly, greeting ceremonies. Despite differences, for most primates, including humans, signs of appreciation are, in part, a reflection of our inherent social natures and the extent to which the expression of our individuality is dependent upon the acts of others. The spirit of gratitude with which I write these acknowledgments, then, is informed by the motivating principle of the book as a whole—the biotic (including social) and abiotic constraints giving rise to homologies, convergences, and conservative effects within and between populations and species in their expressions of interindividual behavior and socio-reproductive organization.

My career can be described as the outcome of a multitude of combinatorial effects—abiotic (class, marital satisfaction) and biotic (gender, race). Numerous persons have contributed to the production of this book, some directly, many others indirectly. My interest in the evolution of social behavior would not have matured without the patience, wisdom, and knowledge of numerous professors, colleagues, and fellow students and post-docs. I am grateful, in particular, to Jack Bradbury, Bill Dilger, Steve Emlen, Dick Lewontin, Bob Trivers, Mary Jane West-Eberhard, and the late Jasper Loftus-Hills who have served to model the very best practices of ethology, sociobiology, and behavioral ecology. Irwin Bernstein, Ruth Buskirk, Irenäus Eibl-Eibesfeldt, Sarah Hrdy, the late Grif Ewer, and many others have also provided helpful input and constructive criticism. My participation in the course, *Tropical Ecology 73-2*, sponsored by the Organization of Tropical Studies, was a critical personal and professional influence, and I am especially devoted to the training provided by Don Wilson, Norm Scott, Dan Janzen, Dick Root, Mary Willson, Jeff Graham, Gordon Frankie, and José Sarukhán. In some ways, the most important early influences were Bill Dilger, Bob Johnston, and Fred Stollnitz, biopsychologists responsible for introducing me to the discipline of Psychology (the science of behavior, brain processes, and emotions) and the specialization of Primatology in a manner that was inclusive of several paradigms and research programs for the conceptualization and investigation of behavior,

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