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IN BABOONS

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REPRODUCTION AND FITNESS IN BABOONS: BEHAVIORAL, ECOLOGICAL, AND LIFE HISTORY PERSPECTIVES

Edited By Larissa Swedell and Steven R. Leigh

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CHAPTER ONE

Perspectives on Reproduction and Life History in Baboons

Larissa Swedell and Steven R. Leigh

INTRODUCTION

This volume explores reproductive behavior, social organization, and life history in baboons of the genera *Papio* and *Theropithecus*, contributing to a nascent discussion of the interrelations among these variables in recognition of their tremendous impacts on fitness (S. A. Altmann, 1998; Alberts and J. Altmann, 2002; Kappeler et al., 2002). Complicated sex- and age-specific strategies and tactics mediate ties among these variables, resulting in considerable diversity depending on ecological conditions, social variables, survivorship, population size, and age structure. The complexity of relations among these variables opens significant opportunities to enhance our understanding of primate adaptation and evolution. Our view is that processes of mating and ways of investing in offspring are related in extremely important, but often neglected, ways. This book aims to address ties between reproduction and life history variation in order to understand the evolution of social, behavioral, genetic, and morphological diversity. We direct our attention primarily to a single genus (*Papio*) that is characterized by remarkable variation in reproduction

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and life history, providing exceptional and perhaps unparalleled opportunities to appraise issues about these aspects of life.

Our exploration of the links between reproductive behavior and life history centers on variables defined as fitness components, or factors directly related to reproductive success (Charlesworth, 1994; Hughes and Burleson, 2000). Fitness components include a wide array of traits, including, among others, mate competition and attraction, offspring growth rates, and age at maturation. While the relationship of fitness to specific fitness components can be straightforward, the relations among these variables and the ways in which they fit into overall courses of life histories remain largely unexamined (but see J. Altmann et al., 1988; Kappeler et al., 2002). This is unfortunate because the behaviors associated with both mating and offspring rearing occupy the most important life history phases in primates, with the greatest impacts on fitness. Moreover, the relationship between these two particular life phases—mating behavior and offspring rearing—remains poorly understood. Certain aspects of social organization, such as dominance rank and ways of maintaining rank or of acquiring mates, may be dynamically interrelated with the attributes of offspring. For example, from the adult perspective, long interbirth intervals (IBIs) may limit opportunities for mating and increase the risk of infanticide. From the offspring's viewpoint, maternal rank and condition affect growth trajectories, body condition, and age at maturation. This kind of complexity, particularly relationships among variables such as rank, morbidity, and age at maturation, requires exploration in various contexts, including analyses of both adults and offspring. Thus, at a broad theoretical level, this volume examines the relations of fitness components to one another at two especially important life history periods. Our major goal in this volume is to evaluate how patterns of behavior associated with rank attainment, mating, and reproduction interdigitate with ecology and life history attributes, particularly those involving allocation of reproductive effort and rearing of offspring.

BABOONS IN PERSPECTIVE

This volume is largely restricted to baboons of the genus *Papio*, although Uddin et al. do consider data from *Theropithecus gelada* and Leigh and Bernstein include data from several papionin genera in their analyses. (In order to streamline the volume, the term “baboon” is used only in reference to *Papio*.) The genus *Papio* is widespread across Africa, being perhaps the

most commonly observed African primate besides humans. *Papio* baboons are taxonomically diverse as well, occurring in at least five main forms recognized to date: hamadryas (*Papio hamadryas hamadryas*), olive (*P. h. anubis*), yellow (*P. h. cynocephalus*), chacma (*P. h. ursinus*), and Guinea (*P. h. papio*). The complexities of biogeography and phenotypic variability among baboons (Jolly, 1993, 2003; Frost et al., 2003), combined with a lack of reproductive isolation at most species/subspecies borders—in particular the well-documented hybrid zone between hamadryas and olive baboons in Ethiopia—suggest that a single-species classification for baboons may be most appropriate (Phillips-Conroy & Jolly, 1986; Williams-Blangero et al., 1990; Jolly, 1993, 2003; Frost et al., 2003; Disotell, 2000; Alberts and Altmann, 2001). Despite their classification as a single species, evolutionarily significant differences characterize baboon subspecies with respect to behavior, adult morphology (Jolly, 1993, 2003; Frost et al., 2003), and some aspects of development (Leigh, in press). As Jolly (1993, 2003) has perceptively recognized, this kind of patterned diversity provides opportunities to study evolutionary dynamics. While baboon taxonomy is still controversial and no one classification is universally accepted, we follow Groves (1993) and Jolly (1993, 2003) in adopting the single-species classification in this volume. Regardless of taxonomic preferences, phylogenetic relationships—both within the genus *Papio* (Newman et al., 2004) and among genera (Disotell, 1994)—are now relatively well understood, facilitating phylogenetically informed comparisons at a variety of taxonomic levels. In part because of their close phylogenetic relations, baboons provide exceptional opportunities to answer questions about life history periods, life history phases, social organization, reproductive behavior, fitness components, and the relations among these variables.

Beyond phylogenetic issues, several other desirable characteristics define baboons as excellent candidates for this kind of investigation. First, recent analyses have provided compelling evidence that the attributes and capabilities of extraordinarily young baboons significantly impact lifetime reproductive success (S. A. Altmann, 1998). The juvenile phase thus requires analytical weight equal to that of adult studies in understanding evolutionary dynamics. Second, the genus *Papio* shows a surprising array of variation in social structure (size and composition of groups) and social organization (patterns of social and sexual interactions within groups). For example, we see a range from the strict, male-driven multilevel social structure characteristic of hamadryas baboons (*P. h. hamadryas*) to the looser, multimale/

multifemale groups with female philopatry and matrilineal dominance hierarchies that typify olive and yellow baboons. Significant variability occurs even within subspecies, most notably among chacma baboons. Third, hybrid baboons—particularly between the two extremes of hamadryas on the one hand and olives and yellows on the other—commonly express intermediate characteristics. As several of our contributors discuss, the presence of these intermediates provides excellent opportunities to explore the genetics and evolution of social behavior, setting the foundation for investigations of how variables such as behavior, social organization, and life histories evolve at a genetic level. Fourth, the genus occupies an impressive range of habitats, providing ideal opportunities for “natural experiments” on the relations between ecological variables, reproduction, and life history. At the same time, the presence of hybrid zones and areas of geographic overlap among subspecies facilitates analyses that effectively control for large-scale habitat differences. Finally, understanding the relations between reproduction and life history mandates multigenerational, longitudinal data. Baboons are ideal subjects for such analyses because several field studies have spanned decades.

REPRODUCTIVE BEHAVIOR AND LIFE HISTORIES

Fundamental tenets of parental investment and sexual selection, as defined in classic theoretical contributions (Darwin, 1871; Fisher, 1930; Trivers, 1972), anticipate sex differences in reproductive behavior, investment in offspring, and the course of life histories. These tenets predict that, when parental investment is asymmetrical, the sex that invests more in offspring is effectively a limiting resource. As a consequence, the sex that invests less should compete to gain access to members of the sex that invests more. Life history considerations have a prominent role to play in this framework. In mammals, females produce a tiny fraction of the number of gametes produced by males, release them at long intervals, expend extra energy on pregnancy and lactation, and usually invest more in offspring postpartum than males. Female mammals are thus limited to relatively few potential offspring and, from the outset, invest much more than males in each individual offspring. Factors that impact life histories, such as the length of the infant and juvenile periods, also influence female energy allocation (Altmann et al., 1978). Moreover, energy investment may vary with time, such that mothers experience peak periods of energy investment in offspring while males may expend

variable amounts of energy on reproduction, varying their investments by season or with changes in group composition.

Given these principles, we generally expect males to focus on gaining access to females so as to increase offspring *quantity*, while females prioritize investments that maximize the *quality* of each offspring. At a more refined level, we expect sex differences in energy investments to covary with ecological conditions, group size, and composition. In terms of life histories, bimaturism should characterize baboons, with sexual selection favoring a long male developmental period culminating in large body size, significant canine weaponry, and perhaps the social skills needed to gain reproductive opportunities (Wiley, 1974; Jarman, 1983; Leigh, 1995; Leigh et al., 2005). Once adult, investment in mating opportunities should comprise the largest proportion of male reproductive energy allocation, because the greatest factor contributing to his fitness is his access to female mates and number of successful fertilizations. A male's fitness is also affected by the survival of his offspring, a function of both developmental rates and maternal investment.

Male baboons present a fascinating array of variation in terms of how these general goals are met. For example, a primary concern with access to mates may translate into an exclusion strategy, as seen in hamadryas baboons, whereby a male defends a group of females from all other males and gains exclusive reproductive access to those females for the length of his tenure. More commonly, though, male baboons cannot defend a group of females exclusively and instead tolerate other males in a group and compete for access to females only when they are in estrus. In any case, the allocation of male effort over the lifetime, shaped by immediate ecological and social considerations, is inherently a life history problem. This problem centers on classic tradeoffs between current and future reproduction (Fisher, 1930; Williams, 1966; Roff, 2002) as well as tradeoffs between reproduction and somatic maintenance (van Noordwijk and de Jong, 1986). Tradeoffs occur both in the direct process of insemination and in terms of social bonds to maintain access to females. Baboons are particularly interesting in this regard because of the sheer number of ways in which males seem to cope with such tradeoffs. Several contributors to this volume consider the implications of differences in male reproductive strategies for behavior, physiology, and the evolution of reproduction and life history in baboon males (notably, Bergman in Chapter 4 and Jolly & Phillips-Conroy in Chapter 11).

Female baboons also express a variety of reproductive options related to classic life history tradeoffs, so that no uniform pattern holds across all taxa. For females, life history theory has an especially vital role to play in defining these options by providing “an elaborate answer to the simple question of why having more offspring is not always selected for” (van Noordwijk and de Jong, 1986, p. 137; see also Williams, 1966). Kappeler et al. (2002) have identified a number of links between life histories and social behavior in primates, emphasizing life history variables that are likely to impact social organization. For example, female investment in the form of gestation and lactation, rates of infant development, and lifespan duration all influence how males and females allocate reproductive effort. As noted above, the general expectation is that the most important factor contributing to female fitness is the degree to which the survival and overall “quality” of each offspring can be maximized. This means ensuring that each infant is as healthy as possible (through adequate nutritional intake by the mother and/or the infant) and survives to reproductive age and beyond. The optimal allocation of reproductive effort for a female may include conceiving, giving birth, and/or weaning at the most appropriate time (with regard to maximizing food resources for herself or her offspring at critical periods); choosing the “best” mates (either to maximize offspring quality or to promote offspring survival); increasing access to high-quality mates by inciting male–male competition (either agonistic or sperm competition); and competing effectively against other females (so as to increase resources available for her own offspring). This array of reproductive considerations results in the expression of significant variation among baboon female reproductive and life history strategies and tactics. Several contributors to this volume illustrate variation in “optimal” reproductive strategies and offspring investment by female baboons. Notably, Barrett et al. offer an “elaborate answer” to a seemingly simple question about allocation of investment in offspring, defining significant correlates between life history and reproductive behavior. Leigh and Bernstein argue that baboon females make exceptional allocations to offspring during the early growth. Swedell and Saunders suggest that the mating strategies of female baboons are shaped primarily by the importance of ensuring the survival of their young infants, but that hamadryas and savanna baboons approach this problem in fundamentally different ways.

Infant mortality, through either predation or infanticide by males, has emerged recently as a major factor influencing the reproductive behavior and

life history of baboons. As discussed by Palombit et al. (1997, 2000; see also Palombit, 2003) and Cheney and colleagues in Chapter 7, both infanticide and predation pose clear risks for infant baboons, with sexually selected infanticide by males impacting the evolution and maintenance of social and reproductive strategies of baboon females and infants as a result. For females, this may select for a motivation to mate with multiple males or to form associations with protective males. For infants, this may result in a life history pattern that reflects their greater vulnerability at certain stages of development. The links among infant mortality and morbidity, reproductive and social strategies of both females and males, and aspects of life history such as juvenile development are crucial to a full understanding of the evolution of behavior and social organization in baboons and other primates.

CHAPTER OVERVIEWS

The scope of a project that considers multiple life history phases is broad, but, as noted, we have chosen to focus on only two major life history periods. Specifically, Part I examines what it takes for adults to reproduce, concentrating on mating behavior and general mating strategies and tactics. The chapters in this section investigate links between social organization, mating behavior, and various measures of fitness. Part II broadly considers what it takes for offspring to reach adulthood. Contributors to this section dissect the consequences of social interactions among adults on offspring-weaning behaviors, condition, and mortality. Still other chapters consider how morphologies relate to social variables, exploring the relationship between morphologies and the scheduling of reproduction. Coupling a focus on reproductive parameters and life history provides a more complete view of fitness in baboons (and primates more generally) than could be attained by concentrating on either in isolation. In effect, we evaluate how baboons go about the process of reproducing as a lifetime commitment. Our contributors ask how it is that male and female baboons go about finding mates, scheduling reproductive events, allocating reproductive investment, and successfully raising offspring.

In Chapter 2, Larissa Swedell and Julian Saunders use a comparative perspective to elucidate the relationship between female mating behavior and fitness in hamadryas baboons. Unique among *Papio* baboons, hamadryas have a rigid, multilayered social system in which mating occurs mainly within

one-male units and female behavior is largely controlled by males. Female mating strategies and tactics are difficult to even detect in such a system. Swedell and Saunders argue that hamadryas female behavior, though tempered by highly structured relationships with males, is nevertheless similar to that of other baboon females in that it is closely tied to infanticide avoidance. In hamadryas society, the amount of protection females receive from their leader males—both for themselves and their offspring—appears to be a direct determinant of their own fitness. From this point of view, the one-male unit social structure characteristic of hamadryas baboons is advantageous with regard to female fitness.

Jacinta Beehner and Thore Bergman further clarify the role of female reproductive strategies in baboon social organization with their analysis of female social and mating strategies among hamadryas–olive hybrid baboons in the Awash hybrid zone. A comparison of females of varying phenotypes reveals that females exhibit mating strategies consistent with their phenotype, suggesting a correlation between genetics and patterns of association and mating behavior among female baboons. Beehner and Bergman’s results complement Swedell and Saunders’ contribution by providing more evidence supporting the notion that female baboons derive fitness benefits from a one-male unit social structure. Both contributions suggest that infants may be more likely to survive to adulthood in one-male units than in the looser, multimale multifemale aggregations typical of olive, yellow, and chacma baboons. It should be emphasized that these two studies effectively hold macroenvironmental variables constant by conducting their investigations in the same geographic region.

Thore Bergman’s contribution helps complete this picture by providing a male perspective on baboon reproductive strategies. His study of hamadryas–olive hybrid baboons in the Awash hybrid zone capitalizes on behavioral variation among hybrid males to shed light on the evolutionary origins of the inflexible, stereotypical behavior of hamadryas males. Bergman proposes several evolutionary “precursors” for hamadryas male behavior and then tests for the presence of these precursors in the hybrid population. Bergman concludes that it is the temporary consortships of nonhamadryas baboons that are most likely to have led to the suite of male traits that shape hamadryas society today.

Guinea baboons may have a multilayered social structure similar to that of hamadryas, but this inference is based on sketchy data that derive mainly from

captive populations (Boese, 1975). Anh Galat-Luong, Gerard Galat, and Suzanne Hagell address this issue with their contribution, but data on wild Guinea baboons remain frustratingly difficult to acquire. These authors suggest that Guinea social organization is only superficially similar to that of hamadryas: Subgroupings seem to be looser and less consistent in composition, males do not herd females in the same manner, and females do not appear to be as constrained in their behavior nor as monandrous. Galat-Luong et al. argue that the social flexibility of Guinea baboons provides adaptive benefits in that groups are able to adjust in size and composition as a response to what may be fairly significant swings in food availability. Selection in the highly seasonal and unpredictable West African environment may favor this kind of social flexibility, with important implications for understanding the social organization of both Guinea and hamadryas baboons.

The contribution by Monica Uddin, Clifford Jolly, and Jane Phillips-Conroy provides further insight into the relationship between behavior and fitness, but this time within the context of the evolution and maintenance of baboon endogenous virus (BaEV). Specifically, Uddin et al. test the hypothesis that differing patterns of reproductive behavior in various baboon populations influence BaEV diversity and patterning. Their results show that populations that reproduce within smaller, more closed breeding units—resulting in higher levels of inbreeding and relatedness among individuals—maintain higher copy numbers of BaEV than populations with more open reproductive units and lower levels of relatedness among individuals. Uddin et al. argue that, under the conditions of an increased BaEV copy number, inbreeding confers a selective advantage by decreasing the likelihood of ectopic exchange, which may lead to deleterious gene rearrangements. In this context, inbreeding in itself can be viewed as a reproductive tactic that leads to higher fitness under certain conditions. Uddin et al.'s analysis provides a clear starting point for future discussions of social and genetic evolution in primates, and shows how genetic data may be used to track social parameters.

Contributors to Part II explore a range of questions relating to life history in baboons. Life history adaptations condition opportunities for mating and the allocation of reproductive effort. The contribution by Dorothy Cheney and colleagues provides a fine-grained perspective on the dynamics of life history and reproduction in Botswana's Moremi chacma baboon population. Their study, when coupled with Johnson's analysis (Chapter 8), clearly reveals articulations among variables such as social behavior (notably rank acquisition

and maintenance), demography, life history, and fitness. In so doing, they provide a necessary complement to Barrett et al.'s (Chapter 9) exposition of ecological dimensions of reproduction, life history, and fitness. More specifically, long-term research in Botswana's Okavango Delta offers extensive longitudinal data enabling studies of demography, life history, and behavior. Cheney et al. investigate an entire decade of demographic data, focusing on the reproductive consequences of mortality and rank in this population. Predominant sources of mortality include predation and infanticide, which operate on a strongly seasonal cycle. Slight reproductive advantages accrue from rank when sources of mortality that relate to resource acquisition are considered. On the other hand, "mediocrity" pays off because cessation of reproductive investment through infanticide affects both higher- and lower-ranking females more than middle-ranking individuals. However, predation affects reproductive success independent of rank.

Cheney et al. illustrate subtle but important relations between behavior, life history, and reproduction. For example, interactions among adults (rank maintenance and competitive interactions), maternal behaviors, and day-to-day decisions such as travel paths have important consequences for whether or not offspring can be brought to adulthood. One major result is that rank has comparatively small effects on offspring mortality in this population, raising important theoretical questions about the evolvability of social systems. This result should stimulate considerable discussion on the evolutionary significance of female dominance hierarchies.

Further analyses of the Moremi population by Sara Johnson nicely complement Cheney et al.'s study. Johnson moves beyond the "life or death" binary to explore relations between maternal attributes and offspring condition. At first pass, the effects of rank on offspring condition seem to be minimal. However, Johnson shows readily evident, but complicated, consequences of rank on offspring growth parameters. For example, female offspring of low-ranking females are much more likely to be smaller than comparably aged offspring of high-ranking females, but males appear to present a more complicated picture. Unfortunately, the effects of small size-for-age on offspring fitness are presently unknown, in part because of uncertainty regarding the consequences of small size-for-age at first reproduction. Similarly, maternal age independently affects offspring condition, with age regressive effects. Thus, while Cheney and colleagues illustrate few, if any, consistent effects of rank on mortality, Johnson shows that rank matters, at least in terms of the

condition of infant and juvenile females. The consequences of offspring condition may be especially important during times of resource shortfalls.

One of the most important determinants of reproductive allocation and fitness is interbirth interval (IBI) length. Louise Barrett, Peter Henzi, and John Lycett address this issue with their intriguing analysis of factors that affect IBI in two baboon populations. Their study offers a strong and convincing critique of models based on direct links between habitat “quality” and reproductive or life history parameters (ideas generally compatible with a traditional r–K-selection continuum). Specifically, Barrett and coauthors compare reproductive parameters, particularly IBI, in a population occupying what might be considered a marginal habitat (the Drakensberg) with a population occupying what might be seen as a highly productive habitat (De Hoop). Drakensberg baboons have strongly seasonal births and a comparatively lengthy average IBI, while the De Hoop population distributes births more evenly across seasons. Paradoxically, infant mortality and other life history parameters fail to meet key predictions of traditional life history theories. In addition to addressing this interesting pattern, the chapter provides new insights into genetic conflicts of interests, a key issue in discussions of fitness. Thus, the scheduling of reproduction, patterns of infant care, behaviors surrounding weaning, and ultimately, reproductive success, can be seen as highly responsive to particular sources of mortality (intrinsic versus extrinsic). Traditional life history perspectives account poorly for different sources of mortality and thus do not adequately explain the key aspects of reproduction and life history in these populations. Barrett et al. note that sources of mortality result from complex interrelations among variables such as infant growth rates, conditions animals face at weaning, habitat quality and predictability, providing a complex picture of life history consequences of ecological variation.

Steven Leigh and Robin Bernstein position baboon life history within a larger context established by comparisons among several papionin primate species. Their comparisons suggest that baboons manifest an unusual and perhaps derived suite of life history characteristics in comparison to closely related species. Most notably, heavy investments in brain growth during pre- and early postnatal periods distinguish baboons from other papionins. These expenditures have important consequences for how papionins reach maturity and for the scheduling of reproductive events. In comparison to other papionins, *Papio* baboons invest heavily and early in each offspring, possibly

reflecting a tradeoff between offspring quality and lifetime fecundity. Analyses of ontogenetic patterning in baboons offer strong critiques of traditional life history perspectives that rely on concepts of r- and K-selection. Leigh and Bernstein argue that the concept of a “life history mode” offers insight into questions about life histories that cannot be extracted from a traditional viewpoint. This critique aligns closely with that of Barrett et al. (Chapter 9), despite major differences in taxonomic levels of analysis.

Clifford Jolly and Jane Phillips-Conroy emphasize male life histories and reproductive attributes by analyzing relative testicular ontogeny across baboon subspecies. Their research reveals morphological and developmental dimensions of problems considered in Chapters 3 and 4 by Beehner and Bergman, bringing reproduction and life history together in very direct ways. More generally, males often receive short shrift in life history studies, so Jolly and Phillips-Conroy redress a palpable lack of literature on males. Testicular relative growth trajectories vary considerably, particularly in the phase immediately prior to attainment of adulthood. Of special interest are comparisons between hamadryas baboons and other subspecies, where differences in testicular developmental trajectories are interpreted in social terms. Specifically, the importance of sperm competition varies in tandem with social organization. For example, previous research by these authors comparing testicular growth trajectories between hamadryas and olive baboons indicates that sperm competition appears to be much less important for hamadryas than for olives. In the present contribution, they broaden this comparison to other subspecies, revealing unexpected patterns for yellow baboons. Importantly, Guinea baboons closely resemble hamadryas in their testicular proportions, a result that complements Galat-Luong et al.’s exposition of this understudied subspecies. In general, analyses of testicular growth trajectories reveal links among such diverse variables as male reproductive behavior, social organization, morphology, and life history.

The final “capstone” chapter, contributed by Susan Alberts and Jeanne Altmann, evaluates baboons in a broad evolutionary sense. Their investigation, tempered by the kinds of intimate details that can only be obtained from a commitment to long-term research, positions baboon adaptive flexibility in relation to climatic variation. Alberts and Altmann’s analysis, couched in a theoretical context developed in paleoanthropology (Potts, 1996), defines and interprets responses of baboons to both short- and long-term climatic variability. Among their conclusions are that certain species, including

baboons and humans, have evolved under circumstances of environmental variability and unpredictability and that key aspects of baboon life history and social organization were shaped by these processes.

PROSPECTIVE

In our view, these contributions go far toward establishing goals for future studies of the ties between reproductive behaviors and life histories in primates. We have prioritized contributions from newly established scholars, partly in the hopes of encouraging further research into these areas. In any case, seeking to understand these links necessitates expertise in numerous fields, suggesting the potential for fruitful collaborations among behaviorists, geneticists, and morphologists. Intensive study of reproductive behavior, life history, and fitness in baboons provides a strong foundation for comparable studies at higher taxonomic levels. Addressing questions about reproduction and life history may yield especially valuable insights when posed in interspecific studies, particularly in cases in which social organization differs radically among taxa (see Garber and Leigh, 1997). This approach melds a number of specialties, offering unique insights into the evolution of social organization, morphology, and life history. We anticipate that such research will reveal a fundamentally important role for life histories and reproduction in driving variation in social organization among primates.

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PART I

Reproductive Behavior and Mating Strategies

CHAPTER TWO

Infant Mortality, Paternity Certainty, and Female Reproductive Strategies in Hamadryas Baboons

Larissa Swedell and Julian Saunders

CHAPTER SUMMARY

Hamadryas differ from other *Papio* baboons in that their social organization centers around reproductively exclusive one-male units. Infanticide and aggression toward infants are risks for hamadryas and other baboons and, as has been suggested for other primates, these risks may have played a role in shaping female baboon reproductive strategies. One way that females may reduce aggression toward (and promote protection of) infants is by increasing paternity uncertainty through promiscuity and the incitement of male contest and sperm competition. Presentations to multiple males, postcopulation darts, and copulation calling in particular have been suggested as mechanisms whereby females may incite male competition at both the pre- and postcopulatory levels. Accordingly, a coupling of infanticide risk and multiple mating by females (and the associated male competition)

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characterizes many baboon societies. Another, alternate route to ensure protection against infanticide and other forms of infant mortality is association and exclusive copulation with a single protective male. Paternity certainty is probably quite high among hamadryas leader males, and protective behavior toward infants has likely been selected for. Correspondingly, compared to other baboons, female hamadryas are less promiscuous, do not frequently initiate copulation, and rarely behave in ways that might incite male–male competition. We suggest that, while all baboon females use a combination of paternity concentration and confusion to varying degrees, hamadryas baboon females in particular focus on paternity concentration rather than confusion and that this can be explained by changes in male and female reproductive strategies during the evolution of hamadryas social organization.

1. INTRODUCTION

While olive (*Papio hamadryas anubis*), yellow (*P. h. cynocephalus*), and most populations of chacma (*P. h. ursinus*) baboons are characterized by a multi-male, multifemale social system in which there is little consistent substructuring, hamadryas baboon (*P. h. hamadryas*) social groups split regularly and consistently into progressively smaller subsets (Kummer, 1968; Swedell, 2006). The smallest stable social unit in hamadryas society is the one-male unit (OMU), consisting of a single “leader male” and several females. OMUs are often accompanied by *follower males*, which socialize with, but do not usually have sexual access to, the unit’s females. Several OMUs comprise a *clan*, whose male members are thought to be related (Abegglen, 1984; Swedell, 2006), and two or more clans comprise large aggregations called *bands*, analogous to the “groups” or “troops” of other baboons. Finally, two or more bands may assemble at sleeping cliffs for the night, forming *troops*.

Hamadryas female behavior is different from that of other female baboons in that it is, on the surface at least, largely controlled by males. Male herding—through visual threats, chasing, and neckbiting—is the cohesive force holding OMUs together, and each female is conditioned by her leader male to remain near him, copulate only with him, and avoid interaction with individuals outside the unit. Within such a society, it is hard to imagine that females have social or reproductive strategies of their own, or that they are able to exert such strategies.

As with other females, however, we expect female hamadryas to act in ways that maximize individual reproductive success. From a female's point of view, enhancing the "quality" of each of her offspring (e.g., through better nutrition, socialization, or protection) is one of the most important ways in which she can do so. Ultimately, the fitness of a female baboon is determined by the survival and eventual reproductive success of her infants.

As shown by Cheney and colleagues for the Moremi chacma baboon population (Cheney et al., this volume), infant survival may be impacted by ecological factors such as seasonality and predation as well as social factors such as infanticide by males. In many primates and other mammals, immigrant or newly dominant males sometimes kill dependent infants that are present at the time of the immigration or takeover (Hrdy, 1974, 1977; Brooks, 1984; Packer and Pusey, 1984; Vogel and Loch, 1984; Sommer, 1994; Blumstein, 2000; van Schaik, 2000a,c). In most of these taxa, such behavior appears to be a male competitive strategy that has evolved via sexual selection (Hrdy, 1979; Hausfater and Hrdy, 1984; van Schaik, 2000a). Infanticide and attempted infanticide by males—either directly observed or strongly inferred—has been reported for most populations of baboons that have been studied to date (summarized in Palombit, 2003). While there is wide variation among baboon populations in its occurrence, the prevalence of infanticide in the genus *Papio* as a whole would suggest that it is a behavioral predisposition shared by all baboon males (Palombit, 2003). Palombit (2003) argues that variation in infanticide rate across baboon populations can be best explained by looking at specific demographic and reproductive characteristics of each population. He explains the high rate of infanticide among chacma baboons of the Drakensberg of South Africa as resulting from a combination of long interbirth intervals, low infant mortality (from sources other than infanticide), and high reproductive skew (see Barrett et al., this volume for further discussion of this population). At least the latter two of these factors—high reproductive skew and low infant mortality—are shared by hamadryas as well, suggesting that hamadryas females should, in theory, confront at least as high a risk of infanticide as females in other baboon populations.

But what evidence is there for infanticide in hamadryas baboons? Reports of infanticide in hamadryas derive mainly from captive populations, in some of which an exceptionally high rate of infanticide occurs (Angst and Thommen, 1977; Rijksen, 1981; Gomendio and Colmenares, 1989; Kaumanns et al., 1989; Chalyan and Meishvili, 1990; Zinner et al., 1993).

Infanticide also takes place in the wild (Kummer et al., 1974; Swedell, 2000, 2006; Swedell and Tesfaye, 2003), but at a far lower frequency. The first incidence of infanticide among wild hamadryas occurred during the field experiments reported by Kummer et al. (1974): Two mothers with infants were moved into new OMUs, after which one infant disappeared and the other was found dead with large canine-inflicted wounds on its skull and thighs. Although the evidence was only circumstantial, these infants may well have been killed by their mothers' new leader males. More recent evidence of infanticide in wild hamadryas derives from the Filoha population: After four takeovers of known females, the only black infant (aged less than 6 months) associated with each takeover either (a) disappeared (in two cases), (b) was the victim of prolonged kidnapping with no protective behavior on the part of its mother's new leader male (in one case), or (c) was attacked and killed by its mother's new leader male (in one case; Swedell, 2000; Swedell and Tesfaye, 2003). The first two cases were initially conservatively interpreted as accidental infant death by prolonged kidnapping resulting from a lack of protection by the females' new leader males (Swedell, 2000, 2006). Hamadryas leader males normally defend infants from harassment and kidnapping by extra-unit individuals, and the absence of such protection is unusual within the context of hamadryas society (Swedell, 2006). The more recent observation of direct infanticide in the same wild population, however, suggests the possibility that the first two infants may have been killed, rather than just neglected, by their mothers' new leader males (Swedell and Tesfaye, 2003; Swedell, 2006).

The relatively few observations of infanticide in hamadryas baboons compared to other taxa, including those on other baboons and other mammals living in one-male groups, might suggest that infanticide in hamadryas is a relatively rare occurrence and not much of a risk for females. This apparent rarity is misleading, however, for two reasons. The first is that the number of observation hours spent on individually identified wild hamadryas baboons is a tiny fraction of that spent on groups of other monkeys in which infanticide has been reported. For example, the Hanuman langurs of Ramnagar, Nepal (e.g., Borries et al., 1999) and the baboons of the Moremi Game Reserve in Botswana (e.g., Palombit et al., 1997, 2000; Cheney et al., this volume; Johnson, this volume) have each been observed for tens of thousands of hours over several decades, compared to less than 1,500 hr of observation for the hamadryas baboons at the Filoha site in Ethiopia. The second reason

behind the apparent rarity of infanticide in hamadryas is that its occurrence appears to be closely tied to OMU takeovers, which are in themselves rare occurrences, having been observed only a handful of times (see Swedell 2000; Swedell and Tesfaye 2003). When takeovers do occur, typically only 1–4 females are involved, most of which may not have a black infant at the time. Thus, the circumstances under which infanticide would be expected to occur—male takeovers of females with young infants—do not arise very often. Overall, therefore, the actual rate of infanticide in hamadryas populations is probably quite low, but it is still undoubtedly a risk for females after takeovers. This can be described in terms of chronic versus acute risk: In savanna baboon populations such as that at Moremi (e.g., Palombit et al., 2000; Cheney et al., this volume; Johnson, this volume), where adult males are commonly in contact with infants they likely did not sire, there is a *chronic* risk of infanticide. In hamadryas populations, however, the chronic risk of infanticide is quite low but the *acute* risk after takeovers is high. In fact, the normally high rate of infant survival in hamadryas baboons (Sigg et al., 1982; Swedell, 2006) coupled with the observed and inferred infant mortality after takeovers (Swedell 2000; Swedell and Tesfaye 2003) suggests that infanticide may be the primary cause of death for hamadryas baboon infants.

Regardless of the actual number of successful infanticides that occur, infanticide is clearly a selective factor affecting hamadryas and other baboon females. Even if infanticide occurs, on average, only once in a female's lifetime, it reduces her lifetime reproductive success by negating a period of maternal investment and should therefore have an impact on the evolution of female behavior (van Schaik et al., 1999; van Schaik, 2000b). In female baboons, adaptive responses to male infanticide may include minimizing one's losses through abortion, premature birth or weaning, or an otherwise earlier return to reproductive condition following immigration or takeovers (Pereira, 1983; Colmenares and Gomendio, 1988; Alberts et al., 1992; Swedell, 2000, 2006); the manipulation of paternity assessment through "pseudoestrus" (Zinner and Deschner, 2000) or mating with multiple males (Hausfater, 1975; Smuts, 1985; Bercovitch, 1987b; Swedell, 2006); and social bonding with a protective male to obtain protection for one's infants (Smuts, 1985; Palombit et al., 1997; Weingrill, 2000; Swedell 2006). van Schaik et al. (1999) emphasize the duality of female counterstrategies to infanticide, hypothesizing that "female sexuality in species vulnerable to male infanticide has been molded by the dual need for paternity

concentration and confusion: concentration in order to elicit infant protection from the likely father, confusion in order to prevent infanticide from non-likely fathers” (p. 207).

In this chapter, we compare four components of female sexual behavior across baboons as a preliminary examination of the qualitative and quantitative differences between the reproductive strategies of hamadryas females and females of other baboon subspecies. We regard our interpretations as hypotheses for further testing rather than empirically supported conclusions. We begin with the assumption that baboon infants are at a risk of mortality from infanticide or other sources and that female baboons may employ one of the two general strategies—paternity concentration and paternity confusion—to counteract this risk. We focus on four components of behavior in particular: female exclusivity of mating, female initiation of mating, postcopulatory darts, and copulation calls. We have chosen these behavioral elements because they are largely female initiated and thus indicative of sexual motivation and underlying strategies of females rather than behavioral compromises between females and males (which would be reflected by measures such as copulation frequency and grooming rates). Each of these variables is used for heuristic purposes only and is simply meant to give us an indication of whether females are using a general strategy of paternity confusion or paternity concentration (cf. van Schaik et al., 1999). We use female *exclusivity of mating* as a direct measure of the number of males that each female mates with during an estrus period. We acknowledge that the number of males with whom a female ultimately copulates is, in part, a result of male as well as female strategies. Nevertheless, we expect this number to increase with a general strategy of paternity confusion and decrease with a strategy of paternity concentration. We use the variable *female initiation of mating* as a second measure of female promiscuity. We assume that females that are using a paternity confusion strategy would be more likely to initiate copulations with multiple males than females using a paternity concentration strategy. On the other hand, females using a paternity concentration strategy have little need to expend energy in either initiating copulations or even maintaining this behavioral element in their repertoire. We acknowledge, however, that a behavioral pattern whereby a female repeatedly initiates copulations with only one male would not be indicative of a general strategy of paternity confusion. Finally, we use female *postcopulatory darts* (the postcopulation withdrawal response, in which females run away from a male at the end of a copulation) and