# Paternal effects on offspring fitness in a multimale primate society

**M. J. E. Charpentier*[†], R. C. Van Horn[‡], J. Altmann[§][¶][‖], and S. C. Alberts*[¶][‖]**

*Department of Biology, Duke University, P.O. Box 90338, Durham, NC 27708; [‡]Zoological Society of San Diego, Conservation and Research for Endangered Species, P.O. Box 120551, San Diego, CA 92112-0551; [§]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544; [†]Centre d'Écologie Fonctionnelle et Évolutive, Centre National de la Recherche Scientifique, Unité Mixte de Recherche 5175, 1919 Route de Mende, 34293 Montpellier Cedex 5, France ; and [¶]Institute of Primate Research, National Museums of Kenya, Nairobi, Kenya

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**When females mate with multiple males, paternal care is generally expected to be negligible, because it may be difficult or impossible for males to discriminate their own offspring from those of other males, and because engaging in paternal care may reduce male mating opportunities. Consequently, males in multimale societies are not predicted to provide direct benefits to their offspring. We have recently demonstrated, however, that males in a typical multimale primate society (yellow baboons, *Papio cynocephalus*) discriminate their own offspring from those of other males and provide care to them in the form of repeated support during agonistic encounters. This observation raises the question of whether fathers enhance offspring fitness in this species. Here we use 30 years of data on age at maturity for 118 yellow baboons with known fathers. We show that the father's presence in the offspring's social group during the offspring's immature period accelerated the timing of physiological maturation in daughters. Sons also experienced accelerated maturation if their father was present during their immature period, but only if the father was high ranking at the time of their birth. Because age at reproductive maturity has a large impact on lifetime reproductive success, our results indicate a direct effect of paternal presence on offspring fitness. This relationship in turn suggests that the multiple roles that males play in multimale animal societies have not been sufficiently examined or appreciated and that paternal effects may be more pervasive than previously appreciated.**

age at first reproduction | age at maturity | parental care | yellow baboons | paternal care

Paternal care, which typically involves provisioning and/or protecting young, is widespread in birds, fishes, and, to a lesser extent, insects (1–3) and can have significant effects on offspring survival and reproduction (4). By contrast, opportunities to provide care are relatively limited for male mammals because of internal gestation and obligatory postpartum suckling (5–7). In addition, opportunities for males to look for additional mates are greater when fathers do not provide care (5). Consequently, any form of paternal care is unusual in mammals, having been documented in <10% of species (8, 9). Paternal investment, however, should evolve if it improves offspring survival rates, if it does not severely reduce opportunities to mate with other females, and if paternal certainty is high (1, 10). Therefore, paternal care in mammals is generally, but not universally, associated with monogamy (8).

Male care of immature individuals is more common in primates than in most mammals (8), but is often attributed to mating effort, i.e., to an attempt to induce the immature individual's mother to mate, rather than to paternal care (reviewed in ref. 11). This attribution is particularly common in the case of multimale primate societies, in which females mate with several males and males disperse repeatedly among social groups. The difficulties of father–offspring discrimination in such societies would seem to reduce the likelihood that males can target their own offspring for care. Indeed, a good deal of male care in a number of species appears to be directed toward juveniles that the males are not likely to have sired (12). For instance, in baboons, behavioral data indicate that caring males are not always sires (13–16). In Barbary macaques, genetic analyses showed that paternity does not predict the nature of the male–infant relationship (17). In cooperatively polyandrous species such as tamarins, both the subordinate and dominant males care for infants that are probably sired by the dominant individual (18). Furthermore, male care also has been reported as a means to buffer social relationships between males. In Barbary macaques, for example, adult males that show preferred associations with each other often care for the same infant (19).

However, evidence also indicates that in many species males have experienced selection pressure to protect their offspring from infanticide, which may be a considerable risk for some primates and other animals (20–22). Further, males in at least some polygynandrous species can differentiate their own likely offspring from those they are not likely to have sired (23, 24). In Chacma baboons, for instance, male–female friendships appear to depend on the presence of an infant that the male is likely to have sired (23). In Hanuman langurs, Borries *et al.* (24) used genetic paternity analyses to demonstrate that males that protected infants from potentially infanticidal attacks were always confirmed or potential fathers (i.e., had been in the group when the offspring was conceived). Finally, in the well studied Amboseli yellow baboon population (25–27), adult males differentiated their own offspring from the offspring of other males and biased their support in agonistic disputes toward their own offspring, indicating true paternal care (28).

The occurrence of paternal care in our study population motivated us to examine whether males influenced components of their offspring's fitness. Specifically, we examined the effects of the father's presence on age at maturity. In this species, males are the dispersing sex and may disperse repeatedly during their lifetime. Therefore, juveniles vary in whether their father resides in their social group and in the time spent in coresidency with their father. Consequently, juveniles vary in their exposure to paternal care (28), as well as in the effects of that care. We also assessed whether the consequences of father–offspring coresidency differed with the father's dominance rank by considering the effects of the male's rank and of the interaction between rank and the extent of coresidency on age at maturity. We chose age at maturity as a potential target of paternal effects for three reasons. First, it can have a large impact on lifetime fitness in a wide range of environmental conditions and social systems (reviewed in refs. 29 and 30). Second, age at maturity in female baboons in Amboseli is an important source of variance in

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[‖]To whom correspondence may be addressed. E-mail: altj@princeton.edu or alberts@duke.edu.

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**Table 1. Effects of the extent of father–offspring coresidency on age at maturity in sons and daughters and on age at first live birth in daughters**

| Response variables | N | Covariables | F | P |
|---|---|---|---|---|
| Menarche in daughters | 71 | Father's coresidency | $F_{(1,69)} = 4.40$ | 0.04 |
| | | Father's dominance rank | $F_{(1,69)} = 2.06$ | 0.16 |
| | | Interactive term | $F_{(1,69)} = 0.80$ | 0.38 |
| First live birth in daughters* | 52 | Father's coresidency | $F_{(1,50)} = 1.39$ | 0.25 |
| | | Father's dominance rank | $F_{(1,50)} = 3.06$ | 0.09 |
| | | Interactive term | $F_{(1,50)} = 1.10$ | 0.30 |
| Testicular enlargement in sons | 40 | Father's coresidency | $F_{(1,38)} = 18.14$ | 0.0002 |
| | | Father's dominance rank | $F_{(1,38)} = 1.58$ | 0.22 |
| | | Interactive term | $F_{(1,38)} = 6.81$ | 0.01 |

*This response variable represents residuals from a model that included age at menarche as well as other predictors (see text). For all three models, the *F* and *P* values displayed represent values after applying a backward model-selection procedure (56).

lifetime reproductive success, such that early maturing females have an average reproductive advantage of ≈1/2 an infant over the lifetime relative to late-maturing females (31); this effect is substantial for a long-lived mammal with a slow life history. Third, previous work on this population has identified several sources of variance in age at maturity in both sexes, but has left considerable variance unexplained (31–33).

## Results

We examined three maturational milestones. The first two were age at menarche in females and age at testicular enlargement in males; these milestones represent the attainment of sexual maturity (puberty) for each sex (31, 32, 34). The third was age at first live birth in females, another important life history milestone. Specifically, the three response variables in these analyses were the residuals of the unexplained variance of age at maturity obtained from a generalized linear model that incorporated other known sources of variance, including maternal, genetic, demographic, and environmental effects (see *Material and Methods*; refs. 31–33, 35). Together these other sources of variance explained 22% of the variance in age at menarche and 19% of the variance in age at testicular enlargement. Age at menarche is an additional strong predictor of age at first birth in females and, with the other variables, accounted for 58% of the variance in age at first live birth.

As a first predictor variable, for each offspring and each maturational milestone, we measured the extent of father–offspring coresidency during the juvenile period, defined as the proportion of time from birth to age $A_{EX}$ that the father was a coresident with the offspring in its social group. $A_{EX}$ was the earliest age at which any individual among the studied animals achieved a given maturational milestone, $X$ (see *Material and Methods*). Specifically, $A_{EM}$ and $A_{EB}$ were the earliest observed age at menarche and age at first live birth among the studied females (3.48 and 4.94 years, respectively), and $A_{ET}$ was the earliest observed age at testicular enlargement among the studied males (4.43 years). We considered two additional predictor variables: the father's dominance rank at the birth of the offspring, and the interaction between this paternal dominance rank and the extent of father–offspring coresidency (see *Materials and Methods*).

The extent of father–daughter coresidency from birth to $A_{EM}$ significantly predicted age at the daughter's menarche; the greater the extent of father–daughter coresidency, the earlier the daughters reached menarche (Table 1 and Fig. 1). This effect was independent of the father's dominance rank, which had no significant effect (Table 1). The extent of father–daughter coresidency before $A_{EB}$ did not predict the age at which daughters first gave birth (Table 1). However, 53% of the variance in age at first live birth for females was accounted for by age at menarche, which was included as a predictor variable in the model whose residuals we tested here (33). The fact that we did not detect an additional paternal effect on age at first birth indicates that the father's presence accelerated age at first live birth of his daughters only through its impact on age at menarche.

The extent of father–son coresidency from son's birth to $A_{ET}$ significantly impacted age at testicular enlargement; the longer fathers and sons were coresident, the earlier sons reached testicular enlargement (Table 1). However, this effect occurred only for sons born to high-ranking males (alpha and beta males; 28% and 48% of variance explained, respectively) (Fig. 2). Our sample size for male milestones other than testicular enlargement is more limited (see *Materials and Methods*), but our sample to date indicates that age at testicular enlargement predicts other maturational milestones for males, including age at first consortship (refs. 32 and 33 and S.C.A. and J.A., unpublished data). Consequently, the presence of a high-ranking father during the son's juvenile period has the potential to accelerate age at first reproduction in sons through its impact on age at testicular enlargement.

## Discussion

Our findings represent evidence that paternal presence impacts offspring fitness components in multimale primate societies and

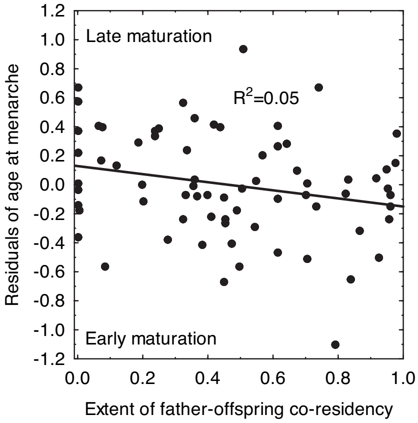

**Fig. 1.** Age at menarche in female baboons as a function of the extent of father–daughter coresidency. The *y* axis represents the residuals obtained from a regression that included the other known predictors of this milestone (33). Negative residuals represent individuals that matured earlier than expected from this equation, and positive residuals represent individuals that matured later than expected.

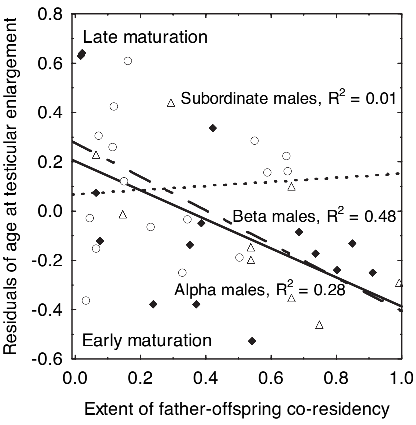

**Fig. 2.** Age at testicular enlargement in male baboons as a function of the extent of father–son coresidency and the father's dominance rank. The *y* axis represents the residuals obtained from a regression that included the other known predictors of this milestone (33). Negative residuals represent individuals that matured earlier than expected from this equation, and positive residuals represent individuals that matured later than expected. In this figure, we divided the father's rank into three classes: alpha males (rank = 1, *n* = 15; filled diamonds), beta males (rank = 2, *n* = 9; open triangles), and lower ranking males (rank = 3–7, *n* = 16; open circles). This subdivision was chosen to equilibrate the samples sizes. However, whatever subdivision was chosen, the pattern remained constant: Coresidency with low-ranking fathers did not influence sons' age at testicular enlargement.

are consistent with previous observations that males in these societies provide paternal care (23, 24, 28). How might this paternal effect be achieved? First, one form of paternal care documented in this and other species is protection during the first years of life in the form of behavioral interventions in agonistic disputes or, for neonates, protection from infanticidal attacks (23, 24, 28). If protection persists during the entire juvenile period, it could create a buffered social environment for offspring development, reducing the stress associated with agonistic disputes as well as providing an additional link in the offspring's social network (see ref. 36 for the potential benefits of social integration). Second, fathers may help offspring attain a higher quality and/or quantity of food; in Rhesus macaques, juveniles with persistent relationships with adult males (whose paternal status was unknown) gained greater access to food resources (37). This form of paternal care may be beneficial if offspring forage near their fathers and are thereby protected from feeding interruptions or if proximity to fathers helps them gain access to better food sources through observational learning of food types or foraging skills (38–40). Food acquisition influences both growth rates and age at maturity in a number of primate species (41, 42), including baboons (35, 43), and could be a major mediator of the paternal effects documented here. A long-term analysis of father–offspring behavioral relationships from birth to maturation will help to elucidate the different forms that paternal care may take in baboons.

The effect of the father's coresidency could potentially be indirect, rather than directly mediated by paternal behavior. That is, it could reflect the fact that fathers with "good genes" are (*i*) high ranking, (*ii*) remain in groups longer (and hence have longer coresidency with their offspring), and (*iii*) have offspring that mature earlier because they inherited their father's good genes. This set of conditions would produce the relationship that we observed even in the complete absence of any direct paternal care. Two pieces of evidence argue against this hypothesis. First, the father's dominance rank had no effect on age at maturity in females, and coresidency appears to be more, rather than less, important for sons of high-ranking males. Second, we performed a within-male analysis of the effect of coresidency by comparing, for each male that had more than one offspring, the offspring with whom he had the longest period of coresidency and the offspring with whom he had the shortest. That is, we asked whether the same father produced a relatively early maturing offspring if he was present for a larger proportion of their juvenile period and a relatively late-maturing offspring if he was present for a smaller proportion of their juvenile period. We restricted the comparisons to pairs of offspring of the same sex because males and females mature on different schedules (i.e., if the father's shortest coresidency was with a daughter and his longest was with a son, we excluded that father from the analysis). We found that within fathers, offspring of the same sex generally matured earlier if the father was coresident for a longer period and later if he was present for a shorter period ($n = 16$ fathers; Wilcoxon signed rank test; $Z = 47$, $P = 0.013$; specifically, in 13 of 16 cases, the offspring with the shorter coresidency with its father matured later). This result strongly suggests that the male's presence *per se*, rather than an individual characteristic of the father, such as good genes, is responsible for the coresidency effect that we have documented.

The fact that sons only benefited from coresidency with high-ranking fathers, whereas daughters benefited from coresidency with fathers of all ranks, is a puzzle. Juvenile baboons experience social conflicts with adults and juveniles of all ages (44). If a primary form of paternal care is intervention by the father into his offspring's social conflicts, it may be that fathers of all ranks are effective allies for daughters, whose most relevant opponents are adult and juvenile females (all of whom rank below all adult males). If, in contrast, the most relevant interactions for maturing males are those with adult males, then only high-ranking fathers would be consistently helpful to their maturing sons against many of these adult male opponents. Testing this hypothesis will require a detailed understanding of the nature and consequences of agonistic interactions involving juveniles as well as the nature of the paternal support they receive.

The acceleration of age at maturity that we have documented in yellow baboons contrasts with results from humans and several other mammals, especially cooperative breeders. In these species, parental presence delays maturation in the offspring, and this delay has been interpreted as a mechanism to avoid either incest or parent–offspring competition (45–47). However, both father–daughter mating opportunities and father–son mating competition are probably more rare in multimale societies with male dispersal than in cooperative breeders because (*i*) multimale societies will typically have a larger number of reproductive individuals of both sexes than cooperative breeders (reducing both the intensity of competition and the probability of mating between any particular pair), and (*ii*) fathers will frequently have dispersed from their offspring's group or died by the time the offspring has begun to reproduce (81% of daughters and 88% of sons in our sample). These conditions will result in different selection pressures across mating systems and a potential fitness advantage to fathers in multimale societies that are able to accelerate their offspring's reproductive careers.

Parental effects are a topic of great current interest in evolutionary biology, but the majority of work has focused on maternal effects; few researchers have examined the direct effects of fathers on their offspring. Our result that males in a multimale animal society with presumed low paternity confidence engage in paternal care and have direct effects on their offspring's fitness suggests that paternal effects are more important than has previously been recognized.

## Materials and Methods

**Subjects and Studied Variables.** Study subjects (40 maturing males and 78 maturing females) were members of eight well habituated, wild-feeding baboon social groups that occupied overlapping home ranges in the Amboseli basin at the foot of Mount Kilimanjaro (e.g., refs. 25–27). The Amboseli baboons are a wild population primarily comprised of yellow baboons (*Papio cynocephalus*), which occasionally hybridize with immigrant anubis baboons [*P. anubis* (33, 48, 49)]. This study population has been under continuous observation since 1971. All individuals born into the study groups were individually known; demographic events, behavioral data, and extensive life history, including births, maturation events, immigrations, deaths, and emigrations, were recorded on a routine basis as part of daily monitoring. The study groups included $\approx$150 reproductive individuals of both sexes and a similar number of maturing individuals of all ages, and they exhibited a typical baboon social organization. In Amboseli baboons as in other baboon populations, males disperse as they approach maturity and females remain in their natal group throughout their life (50, 51). These groups were relatively stable in size over the entire study period, except in the 1960s, when the population size experienced a dramatic decline (52).

We first analyzed age at physical maturation in males and females, i.e., testicular enlargement and menarche. Testicular enlargement was assessed by monthly visual inspection of the scrotum (see ref. 32 for details), and menarche was assessed by daily visual inspection of the sexual skin for evidence of the first sexual swelling (see refs. 31 and 53 for details). These life history milestones signal puberty and were attained at a median ages of 5.30 years in the studied males ($n = 40$) and of 4.56 years in the studied females ($n = 71$). For females, we further analyzed variation in the age at first reproduction, measured as the age at which females gave birth for the first time to a live offspring (median age: 5.84 years; $n = 52$). Ideally, we also would have examined age at first reproduction in males, but this milestone was more difficult to obtain because males dispersed into and out of study groups repeatedly and because our noninvasive methods precluded the possibility of paternity assignments for some live births (i.e., we could not assign paternity to infants that died before we obtained fecal samples for them). Both of these things meant that we may have missed the first reproductive event for many males.

**Paternity Analysis.** Genetic samples (primarily fecal samples) were available for 118 studied subjects born between 1982 and 2002, their mothers, and their potential sires. The QIAamp DNA Stool Mini Kit (Qiagen) was used to extract DNA from feces, with modifications as described in ref. 28. We genotyped the studied individuals by using 12 tetranucleotide and 2 dinucleotide microsatellite loci amplified with human primers (as in ref. 25). No reactions were multiplexed. With the exception of two loci, we used microsatellites located on different chromosomes to avoid potential linkage problems. We used quantitative PCR to measure DNA concentrations in baboon fecal extracts before genotyping began. We used the multitubes approach to increase the reliability of genotyping (25). We then assigned paternity by using simple exclusion and a likelihood-based approach using the program Cervus version 2.0 (54). Both methods showed a high level of agreement. The 118 offspring (from 42 fathers) represented all genotyped offspring that survived to maturity (see below). We assume that this sample of offspring was random with respect to the father's identity.

**Father–Offspring Coresidency.** We considered the extent of father–offspring coresidency for the three maturational markers studied. We measured coresidency from offspring birth to $A_{EX}$, rather than the offspring's age at maturity, because the probability that a father was still in his offspring's group decreased with time because of male mortality and male dispersal (50, 51). Consequently, offspring that matured later were inevitably less likely to have their fathers still present in their natal group at the time that they reached maturity. Therefore, to eliminate this spurious correlation between paternal presence and the actual attainment of maturity (because they were both functions of passing time), we constrained our analyses to the study of the father's presence from birth to $A_{EX}$. Specifically, we did not consider offspring whose fathers left the group after $A_{EX}$; that is, we only considered offspring for whom the proportion of time from birth to $A_{EX}$ that the father coresided was $<$1.0 (there were no cases in which the father left on the day equivalent to $A_{EX}$; all cases where the proportion was equal to 1.0 were cases where the father also coresided after $A_{EX}$, representing 56 father–offspring dyads that were excluded from our sample). This second restriction resulted in an analysis only of individuals whose fathers left sometime before $A_{EX}$ and therefore avoided the potentially confounding effects on maturation of the father's presence after $A_{EX}$.

The majority of father–offspring pairs that coresided before offspring maturity showed continuous coresidency; that is, the father was present at the offspring's birth and remained in its social group with no interruption until his final departure from it. In a few cases, however, the father was present discontinuously ($n = 7$ sons and 5 daughters born to 7 fathers); that is, the father left the offspring's social group at some point while it was immature, but subsequently returned to its group at least once. We excluded these cases of discontinuous coresidence from the analysis because they were heterogeneous with respect to the patterns of continuity. Including these cases did not qualitatively change our results, but the $P$ values for the effect of fathers' coresidency on both sons' and daughters' maturation changed (to $P = 0.003$ and $P = 0.23$, respectively).

**Paternal Dominance Rank.** Male dominance ranks were determined by assigning wins and losses in dyadic agonistic encounters between males. Males won agonistic encounters when they showed only aggressive or neutral (nonsubmissive) gestures while their opponent showed only submissive gestures toward them. After assigning wins and losses, we assigned ranks inferred from a square matrix of interactions in which entries below the diagonal (which would represent wins by the lower ranking animal) were few or zero (26, 55).

In most cases, we used the father's rank at the offspring's birth as our measure of paternal dominance rank (for $n = 102$ offspring). In cases in which the father left the group before the birth of his offspring ($n = 16$ offspring), we considered the last rank that the father attained in his offspring's group before his departure. The father's rank at birth was highly correlated with the father's rank at the offspring's conception ($n = 102$; $R^2 = 0.73$), and results obtained with this second metric did not change (data not shown).

**Other Sources of Variance in Age at Maturity and Statistical Analyses.** We examined eight other sources of variance in age at maturity (see ref. 33 for details): the social dominance rank of the individual's mother at birth, the presence of female maternal relatives (both the mother and the number of maternal half-sisters), demographic characteristics of the individual's group in the month it matured (i.e., either the number of mature females for age at menarche and age at first live birth or the number of ''excess'' cycling females for age at testicular enlargement), rainfall in the year before the individual's maturity, the individual's hybrid ancestry (i.e., its estimated percent anubis genetic ancestry) (33, 48, 49), and its genetic heterozygosity.

For age at menarche, we found that females matured earlier when born from high-ranking mothers, when the number of mature females decreased in the groups while the number of their maternal half-sisters increased, and when the amount of rain increased the year before menarche. Moreover, hybrid females tended to reach menarche earlier (33). Together, these sources of variance explained 22% of the variance in age at menarche. For age at first live birth, we found another effect of the number of mature females: Females gave birth earlier in small groups. Moreover, the inclusion of age at menarche into the model resulted in greater explanatory power, accounting for 58% of the variance in age at first live birth (33). In males, age at testicular enlargement was attained earlier in sons of high-ranking mothers and when the number of excess females increased. Moreover, hybrid males also matured earlier (33). Altogether, these variables explained 19% of the variance in age at testicular enlargement for males (33).

Our response variables in the analyses presented in this article were the residuals obtained from the regressions of age at menarche, age at first live birth, and age at testicular enlargement and the sources of variance described in the two previous paragraphs. Our explanatory variables were the extent of father–offspring's coresidency, the father's dominance rank at the offspring's birth, and an interaction term between the father's dominance rank and the extent of father–offspring coresidency. When no effect of the interaction term was found, we removed it to select a best-fit set of explanatory variables (backward model-selection procedure) (56). We then removed the variable showing the highest $P$ value (when $P > 0.05$) from the model (the father's coresidency or dominance rank). As a measure of goodness of fit, we used the Akaike information criterion (AIC) (57). Final models showed, in all cases, the best fit to our data in the sense that they had the lowest AIC values of all models we tested. All models were analyzed by using a mixed-model approach (mixed procedure in SAS version 9.0; SAS Institute), where social group membership was treated as a random effect to correct for potential random effects due to the group identity. Because each of the study groups shifted its home ranges from poor to better habitats at a discrete point in time during the three decades of study (58, 59), we considered the quality of the habitat (0, before home range shifts; 1, after home range shifts) as an additional random effect (33).

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