ORIGINAL ARTICLE

Paola Bressan

# Why babies look like their daddies: paternity uncertainty and the evolution of self-deception in evaluating family resemblance

**Abstract** It has been suggested that in a socially monogamous system where fathers invest in their mate's offspring but paternity is far from certain, it will be adaptive on the part of infants to conceal their father's identity; but the opposite claim has also been made that this is against the genetic interests of the fathers, and a high frequency of adulterine births will select instead for paternal resemblance. In this article, I present a simple theoretical model that suggests that neonatal anonymity benefits fathers, mothers, and children. Once anonymity becomes established, however, all babies start paying the cost of paternity uncertainty, that is, the reduction in paternal care due to fathers not knowing whether they have truly sired their mate's offspring. By diminishing the fitness of babies, such a cost bounces back as lowered fitness for parents as well. We should then expect the evolution of maternal strategies directed to decrease paternity uncertainty, in the form of instinctive and unsolicited comments on babies' resemblance to their putative fathers. In contradiction to the widespread belief that it would be in fathers' interest to be skeptical of these allegations, the model suggests that, under conditions of infant anonymity, fathers will actually promote their own fitness by believing their spouses.

**Keywords** Resemblance · Confidence of paternity · Parental investment · Kin recognition · Evolutionary psychology

One of the most important things to realize about systems of animal communication is that they are not systems for the dissemination of the truth.

Robert Trivers, *Social evolution*

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P. Bressan (✉)
Dipartimento di Psicologia Generale, Università di Padova,
Via Venezia 8, 35131 Padova, Italy
e-mail: paola.bressan@unipd.it
Tel.: +39-049-8276691, Fax: +39-049-8276600

Human babies do not look much like their parents, and it can be argued that, from an evolutionary stance, they have good reason not to. In socially monogamous mating systems such as our own, where paternity is nevertheless far from certain, babies may gain from displaying their father's phenotypic traits, but the putative father and the biological father will not always coincide. On the assumption that fathers have been selected to invest in their genetic progeny only, adulterine babies will suffer a cost, which may range from neglect to extreme forms of abuse, such as infanticide (Daly and Wilson 1984). It has been suggested that, given the severity of this cost, a proportion of extra-pair conceptions larger than 1 in 10 would be enough to favor concealment of paternity (Pagel 1997). More specifically, the fitness of babies with a "badge" or label of paternal identity would be less than the fitness of babies without a badge. Yet, the opposite claim has also been made: according to Johnstone (1997), when the frequency of adulterine births is high the genetic interests of fathers overcome the lower incentive of babies to reveal their identity, selecting *against* concealment of paternity.

It is clear that, in general, the genetic interests of the baby and those of its father partly overlap, but they do not necessarily match. The baby is perfectly related to itself, but related by only one-half to either parent. Both father and child will try to maximize their personal fitness, even at some cost to each other in the event of a conflict of interest. The question, then, is this: it is fine that the baby wants to conceal its father, but does the father want to be concealed? Human babies are anonymous, but how have they managed to become or remain such, if the interests of their fathers call for a "baby-looks-like-father" strategy?

## A model of father–infant resemblance: father's point of view

Investing so little at the time of copulation, males are selected to try to pair with a female whose offspring they

will help to raise, while at the same time attempting to copulate with other females whose young they will not raise [in the quintessential prose of Trivers (1985)]. Such a strategy, however, strikes back by causing males to run the risk of investing in young that are not their own. The implications make for an interesting paradox. On the one hand, fathers who mark their progeny for subsequent identification will recognize adulterine children and neglect them, which will confer an advantage to genes coding for a paternal identifier. On the other hand, fathers who do not mark their progeny will avoid having their "satellite" children recognized as adulterine and neglected, which in turn will confer an advantage to genes coding for phenotypic anonymity.

Pagel (1997) has proposed a simple theoretical model to investigate the evolutionary interests of the baby in matters of paternal resemblance. Adopting the same logic and terminology, we can rewrite his equations to illustrate the evolutionary interest of the father, as follows:

$$
\begin{aligned}
W_B &= m + (1-m)\,[(k + (1-k)(1-s_1) \\
&\quad - (1-k)q(1-s_1) - (1-k)(1-q)(1-s_2)] \\
W_A &= m + (1-m)\,[(k(1-s_2) + (1-k)(1-s_2) \\
&\quad - (1-k)(1-q)(1-s_2) - (1-k)q(1-s_1)]
\end{aligned}
\tag{1}
$$

where $W_B$ is the fitness of fathers producing babies with a badge (hereafter, B-fathers), and $W_A$ is the fitness of fathers producing babies without a badge, that is, anonymous (hereafter, A-fathers).[1] The model's parameters are listed in Table 1.

The general assumption underlying the argument is that the fitness that a parent accrues through each offspring is a function of the amount of investment received by that offspring. In the proportion $m$ of marriages that are strictly monogamous, all fathers have a fitness of 1. In the $1-m$ marriages in which females are promiscuous, $k$ is the proportion of offspring in which the domestic (or putative) father is also the biological father. In these cases, B-fathers will have a fitness of 1, but A-fathers will have fitness $1-s_2$, where $s_2$ is the effect, on the father's fitness, of the reduction in paternal care due to paternity uncertainty. It has been shown, for example, that a father will diminish his investment in the young if he has not had exclusive mating access to the female (see for a brief review Clutton-Brock 1991). Of course, B-fathers will not pay this cost because the phenotypic badge constitutes evidence that they have indeed sired this baby.

On the $1-k$ occasions in which domestic father and biological father do not coincide, we ought to consider separately the repercussions on the fitness of males in either role. If we limit our attention to paired individuals, each male is at the same time a domestic father and a biological father: $m$ times in monogamous marriages and $k$ times in promiscuous marriages, both roles having as re-

**Table 1** The model's parameters

| Parameter | Description |
| --- | --- |
| $m$ | Proportion of strictly monogamous marriages |
| $k$ | Proportion of offspring whose domestic and biological fathers coincide |
| $q$ | Proportion of fathers who mark their children |
| $s_1$ | Repercussion, on parental fitness, of the reduction in baby's fitness associated with its carrying the wrong badge, and being thus recognized as adulterine |
| $s_2$ | Repercussion, on parental fitness, of the reduction in baby's fitness associated with its being phenotypically anonymous, and thus engendering paternity uncertainty |
| $a$ | Ratio between the reduction in parental care given to anonymous babies ($s_2$) and paternity uncertainty ($1-k$) |

cipient the same offspring. In the $1-k$ cases in which a male is a biological (but not domestic) father, B-fathers have fitness $1-s_1$, where $s_1$ is the effect on the father's fitness of the cost suffered by a "satellite" baby who (by virtue of its carrying a badge) is recognized as adulterine. In the same $1-k$ cases, the "satellite" babies of A-fathers (because of their phenotypic anonymity) will not be recognized as adulterine and will be spared $s_1$. However, their anonymity will constitute grounds for the disinvestment linked to the paternity uncertainty of their domestic fathers: therefore, in these circumstances A-fathers have fitness $1-s_2$.

In the cases considered so far, the portions of fitness deriving from the various situations are added together in the appropriate proportions. In the $1-k$ cases in which a male is a domestic (but not biological) father, however, his fitness is not augmented but decreased. If each parent has a fixed total parental investment, which is allocated between offspring (e.g., Maynard Smith 1980), it is reasonable to posit that the amount given to an unrelated child is ideally subtracted from the amount that should have been given to a related child. The adulterine child who is successfully raised to reproductive maturity takes the place of a biological child, thus robbing the domestic father of the same amount of fitness that the latter would have donated. Now, such an adulterine baby can either carry some other man's badge and be thus recognizable (in the $q$ cases in which it has been conceived with a B-father, where $q$ is the proportion of B-fathers in the population) or be anonymous (in the $1-q$ cases in which it has been conceived with an A-father), and this will affect its destiny identically whether it happens to be born in an A- or a B-household. On the $1-k$ occasions in which a male's spouse presents him with an adulterine baby, the fitness of *all* fathers is decreased by $1-s_1$ in $q$ cases, and by $1-s_2$ in $1-q$ cases; Eq. 1 thus becomes

$$
W_B = m + (1-m)\,[k + (1-k)(1-s_1)]
$$
$$
W_A = m + (1-m)(1-s_2)
\tag{2}
$$

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[1] Pagel (1997) presents two basic variants of his "baby's viewpoint" model, which differ as to whether a very small metabolic or other physiological cost is paid by the baby either in producing the badge, or in producing anonymity. For simplicity, the model presented here introduces neither cost; this does not affect the conclusions.

We seek the values of $k$ for which $W_B > W_A$ (i.e., the fitness of fathers who mark their offspring is larger than the fitness of fathers who produce anonymous offspring). These are

$$k \succ (s_1 - s_2)/s_1 \qquad (3)$$

Whether marking one's baby is advantageous, then, depends on three parameters: how much the baby pays if it looks like some other man; how much the baby pays if it looks like no one in particular; and how often babies are conceived with males other than one's spouse. The proportion $m$ of monogamous families and the proportion $q$ of B-fathers in the population are immaterial. Equation 3 is essentially identical to the core of that representing the fitness of babies (Pagel 1997); indeed, if the costs are taken to refer directly to babies' fitness rather than to its repercussion on fathers' fitness, Eq. 2 expresses the fitness of babies as well as that of fathers. From a population perspective, the genetic interests of fathers and children coincide.

Equation 3 shows that the cost of anonymity $s_2$ is crucial. If this is zero, badges will not evolve. The higher $s_2$ is, the more likely the evolution of badges becomes. In the simplest and not unrealistic case in which $s_1=1$ (none of the babies carrying the wrong badge reaches reproductive maturity), Eq. 3 becomes

$$k \succ 1 - s_2 \text{ or } s_2 \succ 1 - k. \qquad (4)$$

When $k=0.8$, for example, $s_2$ must be larger than 0.2 for badges to be beneficial. That is, if two out of ten children are a product of extra-pair mating, a father stands to gain from marking his children only when more than two out of ten anonymous-looking children die as a result of paternal disinvestment. In general, when the probability of conceiving an adulterine baby is higher than the probability of having one's own baby die because of paternity uncertainty, a father will do best to produce anonymous offspring.

The equations above show that the smaller $k$ becomes (more adulterine offspring), the less beneficial it is for fathers to mark their children. The greater reluctance to carry a paternal badge when this is often the wrong one is obvious from the babies' standpoint, but not at all obvious when fathers' interests are considered. It has actually been proposed (Johnstone 1997) that a high frequency of adulterine births will select *against* concealment of paternity. This conclusion rests on an evolutionary-game approach to the issue, in which the interests of both the signaler (the baby) and the receiver (the father) are simultaneously considered. In such a model, when signalers often prove undesirable (i.e., babies are often adulterine), the greater fastidiousness of receivers forces signalers to reveal their identity (i.e., to carry a badge) despite the signalers' lower incentive to do so. In other words, advertisement of identity is more likely when $k$ decreases.

In the model presented here, on the contrary, the interests of signalers and receivers when it comes to parentage advertisement turn out to be the same. This discrepancy between predictions is due, I believe, to an inappropriate application of Johnstone's model. In the model, the level of identity information that the signaler will provide is a direct function of the ratio between the costs of acceptance and rejection errors for the receiver. Consider the case of kin discrimination in colonies of paper wasps for purposes of admission of visitors to the nest. An acceptance error (allowing into the nest an unrelated wasp, coming to steal eggs) has a higher cost to the receiver than a rejection error (refusing admittance to a homeless relative that may become a helper). A high probability of encounters with undesirable signalers (visits by intruding wasps), therefore, will favor the evolution of kin discrimination, no matter how strong the disadvantage to the signalers is.

In the context of progeny identification by males, however, an increasing probability of encounters with undesirable signalers (adulterine offspring) will increase the cost of rejection errors relative to acceptance errors, working *against* the evolution of discrimination. Mistakenly rejecting one's own youngster is more costly when one's spouse produces relatively fewer of them, whereas the costs of acceptance errors cancel out. It is true that each father does not want to take care of $(1-k)$ of his alleged offspring, but it is also true that he wants his own $(1-k)$ out-of-wedlock offspring to be taken care of by their putative fathers. Thus, the evolutionary benefit accrued to fathers by their fastidiousness is counterbalanced by the inconvenience caused to them by the fastidiousness of the males who are presented with their satellite offspring.

There is ample evidence that parental expenditure depends on the probability of relatedness. Males may attack the young when replacing previous territory holders, as in tropical house wrens (Freed 1987), or they may assist in rearing only if they have had mating access to the female, as in dunnocks (Davies 1992). These data, however, are not in contradiction with our conclusions. The point is not that males benefit from raising foreign young (they of course do not), but that they benefit from producing anonymous offspring. Thus, forms of progeny identification based on indirect cues, such as breeding access to the female, will be advantageous to the individuals that adopt them, whereas, paradoxically, forms based on a direct cue such as offspring marking will turn out to be deleterious.

## A model of father–infant resemblance: mother's point of view

Will a mother want her baby to resemble its father? It has been posited (Christenfeld and Hill 1995) that she will, and that it may be to her advantage for the transmission of her own genes that they express themselves as late as possible, so as to give free rein to paternal genes in determining the newborn's traits (thereby increasing paternal confidence and investment). But again, the opposite claim has also been made (McLain et al.

2000): for a mother who is not strictly monogamous the payoff of maximizing her baby's similarity to its father appears dubious, in that children conceived with other males will also resemble their fathers, and these children would have fewer chances of transmitting mom's genes.

I suggest that for mothers we distinguish two separate cases, depending on whether we assume that women *can* actively affect paternal resemblance (as in the phenomenon of genomic imprinting, where the mother can switch off her own genes). If marking children is an exclusively male affair, what we may ask is whether women would do better to choose as a long-term partner and caretaker an A- or a B-father. In this case the evolutionary interests of mothers can be expressed as follows:

$$W_{WB} = m + (1-m)[k + (1-k)q(1-s_1)$$
$$\quad + (1-k)(1-q)(1-s_2)]$$
$$W_{WA} = m + (1-m)[k(1-s_2) + (1-k)q(1-s_1)$$
$$\quad + (1-k)(1-q)(1-s_2)] \tag{5}$$

where $W_{WB}$ is the fitness of mothers whose spouse produces babies with a badge (hereafter, B-wives), and $W_{WA}$ is the fitness of mothers whose spouse produces anonymous babies (hereafter, A-wives). In the $k$ cases where the baby was sired by their spouse, B-wives will have a fitness of 1 and A-wives will have fitness $1-s_2$, where $s_2$ is the effect on their own fitness of the reduction in baby's fitness due to paternity uncertainty (and consequent paternal disinvestment). In the $1-k$ cases in which the baby was sired by some other male, all mothers will have fitness $1-s_2$ in the $1-q$ births in which this male is an A-father; or fitness $1-s_1$ in the $q$ births in which this male is a B-father, where $s_1$ is the repercussion on the mothers' fitness of the cost suffered by a baby who (because of its identifier) is recognized as adulterine.

The values of $k$ for which $W_{WB}>W_{WA}$ are

$$ks_2(1-m) \succ 0. \tag{6}$$

Whenever $m<1$ and $s_2>0$, $W_{WB}>W_{WA}$ is true for any $k$. Associating with a partner who marks his children is always advantageous to mothers, regardless of the frequency of adultery in a society and of the actual likelihood of conceiving an adulterine child. Women who marry B-fathers will enjoy better reproductive success than women who marry A-fathers. This conclusion may seem counterintuitive, but becomes less so when one appreciates that the single difference between the wives of A- and B-fathers emerges in the instance in which they present their husband with his own baby. In this case, only the wives of A-fathers will pay a cost.

Let's now turn to the alternative assumption. If women do have a choice between concealing or not concealing paternal resemblance in their babies, which course of action will maximize their fitness? In this case their evolutionary interests would be

$$W_{MB} = m + (1-m)[q(k) + (1-q)k(1-s_2)$$
$$\quad + q(1-k)(1-s_1) + (1-q)(1-k)(1-s_2)] \tag{7}$$
$$W_{MA} = m + (1-m)[k(1-s_2) + (1-k)(1-s_2)]$$

where $W_{MB}$ is the fitness of mothers who produce babies with a badge (hereafter, B-mothers), and $W_{MA}$ is the fitness of mothers who produces anonymous babies (hereafter, A-mothers). In the $k$ cases where the baby was sired by their spouse, B-mothers will have fitness 1 in the $q$ births in which this is a B-father, and fitness $1-s_2$ in the $1-q$ births in which this is an A-father. In the $1-k$ cases in which the baby was sired by some other male, B-mothers will have fitness $1-s_1$ in the $q$ births in which this male is a B-father, $1-s_2$ in the $1-q$ births in which this male is an A-father. The A-mothers, because of their giving birth to anonymous babies, will have fitness $1-s_2$ in all cases. Thus, $W_{MB}>W_{MA}$ is true when

$$qs_1(k-1) + qs_2 \succ 0$$

or, simplifying (since $q \succ 0$),

$$s_1(k-1) + s_2 \succ 0. \tag{8}$$

Given that $s_1>s_2$ (this is true by definition), B-mothers enjoy an adaptive edge over A-mothers whenever $s_2>1-k$, which is exactly what obtains in the case of fathers (see Eq. 4).

## Genetic strategies: concealing father–infant resemblance

Taken together, these equations indicate that all parties will want babies to advertise paternal identity only when the babies' probability of being allowed to die because of their phenotypic indistinctiveness is larger than their probability of being adulterine. My model, like Pagel's, treats $s_2$ as fixed, rather than dependent on $k$. However, as we have seen, there is evidence that parental care actually varies according to the probability of relatedness, not only in birds and rodents (see Clutton-Brock 1991), but also in humans (Gaulin and Schlegel 1980). Thus, we may assume that $s_2$ is proportional to the paternity uncertainty expressed by $1-k$, that is, $s_2=a(1-k)$. In this case, Eq. 3 becomes $k>(s_1-a(1-k))/s_1$, which yields $k>1$. Since $k<1$ by definition, $W_B>W_A$ is false for any $k$. If parental expenditure increases in relation to the probability of relatedness (proportion of children sired by their domestic father in a population), badges will *never* evolve.

For babies, this is not the best of possible worlds: by being anonymous, they all pay the cost of uncertainty $s_2$.

## Psychological strategies: remarking on father–infant resemblance

The cost of uncertainty basically means that, given promiscuous females and anonymous offspring, the amount of paternal care that males are willing to offer will be less than that they can potentially provide. A mother cannot physically force her mate to invest in her baby more resources than he is disposed to give. However, she can try to reduce the primary source of disinvestment, paternal uncertainty, via psychological tactics. Besides

that of playing faithful wife, and more to the point, the most exemplary of such tactics will be that of remarking on baby's resemblance to her mate.

The expected reaction of fathers is interesting. One could think that they would be selected to resist their spouse's manipulation. However, as long as their progeny are not identifiable, they will enjoy larger reproductive success when led to believe that the domestic offspring are their own. This is because, as shown by Eq. 2, the fitness of A-fathers increases when the cost of uncertainty $s_2$ decreases. If the whole argument holds, then, we should predict no consistent strategy of skepticism by fathers in the face of allegations of paternal resemblance. If it is in women's genetic interest to increase paternity confidence by emphasizing baby's resemblance to their mate, it is in men's genetic interest to believe such claims.

We should then expect that, across cultures, mothers should be inclined to claim that babies look just like their daddies (because in our evolutionary history, those who did so enjoyed a larger fitness than those who did not); and fathers should be happy to go along (because in our evolutionary history, those who believed such claims increased their fitness more than those who did not).

The available empirical evidence supports both points. In a mail survey by Daly and Wilson (1982), Canadian new mothers and fathers showed an "overwhelming consensus of paternal similarity." Fathers' relatives did not allege paternal resemblance significantly less often than mothers' relatives, either. Regalski and Gaulin (1993) found that Mexican fathers were less likely to claim paternal resemblance than mothers; yet, both parents agreed in their resemblance allegations much more often than would be expected by chance, and the most common response was that the baby resembled the father. Both mothers and fathers are more likely to claim paternal, versus maternal, resemblance than unrelated judges (P. Bressan and S. Dal Pos, in preparation); and this happens even when neutral observers match these just-like-father babies to their mothers more easily than to their fathers (McLain et al. 2000).

The often-repeated notion that it would be in fathers' evolutionary interests to be skeptical of mothers' claims, then, is not backed up by the facts. Regalski and Gaulin (1993) tried to account for this puzzling lack of skepticism by arguing that perhaps mothers are persuasive to the point that they "actively shape paternal views." If the model I have presented in this article is correct, the propensity of fathers to let their views be actively shaped comes as no surprise in evolutionary terms.

## Conclusions

Many organisms can identify their relatives (see Pfennig and Sherman 1995). Interestingly, however, kin recognition based on direct phenotypic cues (as opposed to cues related to time or place, such as considering as offspring all the young in the nest) has not been reported in the context of progeny identification. For example, male dunnocks are unable to discriminate their own eggs or chicks from those of other fathers (Davies 1992); and male red-winged blackbirds feed all the chicks in their nest, even though about one in four is not their offspring (Westneat et al. 1995).

Humans are no exception. The success rate in matching newborns to their true fathers is only slightly higher than chance (1.1 times the chance expectation: McLain et al. 2000). Of course, the absence of paternal markers in newborns (it is well known that nearly all Caucasian babies, for instance, are born with eyes and hair of a temporary color, which may take several months before becoming set) represents no direct evidence that babies have been selected to *conceal* such markers. However, the provision of cues of paternal identity is, in principle, certainly possible, and it makes good sense to ask whether it would be beneficial.[2] The model presented here suggests that, contrary to previous proposals (Christenfeld and Hill 1995; Johnstone 1997), the evolutionary interests of fathers, mothers, and babies coincide. It is advantageous for babies to abstain from showing paternal marks. It is advantageous for parents to produce offspring lacking distinctive signature cues. It is advantageous for all parties to decrease paternity uncertainty, which, by harming babies through paternal disinvestment, decreases the fitness of both mothers and fathers. Allegations of paternal resemblance, thus, may be interpreted as mechanisms of deception and self-deception (see Trivers 1985) – or, in more palatable psychological parlance, as self-serving cognitive biases. From the genes' viewpoint, as in other kinds of manipulation, the deception might be more effective if the deceiving component is unconscious on both sides. We may then expect evolution to render mothers unaware of their deceiving, and fathers unaware of their being deceived. To the eyes of mothers and fathers, babies do indeed look like their daddies.

Of course, what matters is the ultimate effect on the interested parties' fitness of the beliefs they entertain, not their validity. Whether babies do genuinely resemble their fathers is beside the point: as long as clear identification of their sire is impossible, it is likely that they somewhat do, to differing extents. If the model is correct, indeed, a little resemblance might be better than none at all: a resemblance not large enough that a baby can be reliably matched to its true father, but large enough that, whenever putative and biological father coincide, there are some grounds (however tiny) on which allegations of father–infant resemblance can be based and then enlarged upon. Not a signal bell (which would have a way of turning into a warning bell), then, but a faint whistle.

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[2] In the context of kin (but not offspring) recognition, phenotypic information on the paternal line can indeed be used: honeybees can distinguish between full siblings and paternal half-siblings (see Pfennig and Sherman 1995), and pigtail macaques raised in isolation spend more time with paternal half-siblings than with nonrelatives (Wu et al. 1980).

In general, psychological tactics that prove repeatedly adaptive are liable to give rise to stable cultural traits. It has been observed that, across cultures, there seems to be a norm prescribing allegations of paternal resemblance (Daly and Wilson 1982). If a "baby-looks-like-daddy" bias is evolutionarily advantageous to all parties, and to all those other individuals who with such parties share some genetic interest, we might predict it to become quite general, perhaps to the point of coming automatically into action every time we evaluate the resemblance between a parent and a child, whether or not they are relatives of ours. After all, we spent most of our evolutionary history living in groups in which everybody was to some degree related to everybody else. An inclination to find (and communicate to others) a resemblance between children and their presumed fathers, then, could have been generally beneficial. Indeed, it has been experimentally shown that the mere belief that two people are parent and child significantly increases the perceived resemblance between them, a cognitive bias that works exactly to this effect (Bressan and Dal Martello, in press). Apparently, family likeness is too delicate a matter to be left to the genes.

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