

Adopting adoption

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*(Received 11 June 1997; initial acceptance 23 July 1997;
final acceptance 29 September 1997; MS. number: 5564)*

Abstract. The common occurrence of adoption among birds and mammals presents evolutionary biologists with an explanatory challenge. The benefits to adoptees are self-evident, but the benefits to the adopter(s), the origin of the set of behaviours that constitute 'adoptive' behaviour, and the conditions for its spread in populations are not always clear. Explanations in terms of direct and indirect benefits to adopters and adoptees, and in terms of conflict between them have been suggested to account for the current functions and the evolutionary origin of 'adoptive' behaviour. In this paper we emphasize one aspect of the parenting behaviour associated with adoption that has been neglected: we suggest that adoption in birds and mammals is a route for the transfer of learnt information through social learning of patterns of behaviour, including styles of parenting. By using simple models we show that learning parenting from non-parents may provide additional opportunities for the spread of the 'adoptive' behaviour itself, even when it has no selective advantage. We also offer an additional explanation for the adaptive significance of adoption for both adopters and adoptees. Our 'match-making' hypothesis suggests that in some cases, by adopting foreign young, parents provide their genetic young with future ecologically compatible, but genetically unrelated, mates.

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Until 15 years ago, there were relatively few field and theoretical studies on adoption, although instances of adoption have been reported in over 120 species of mammal, and over 150 species of bird (Riedman 1982; Boness 1990). Because of the seemingly extreme altruistic nature of adoption, it was common to interpret adopting behaviour as a result of reproductive error, that is, of parental mistakes in the recognition of their young (Andersson & Eriksson 1982; Riedman 1982) or, in failed breeders, of the inability of parents to resist adoption because of a non-adaptive residual hormone titre that primes them to care (Riedman 1982; Birkhead & Nettleship 1984). Although reproductive error may be a satisfactory explanation in some instances, parents in some species

adopt young after the development of parent-offspring recognition (e.g. Choudhury *et al.* 1993; Williams 1994) and often successful breeders adopt additional young. Moreover, studies of 'adoptive' behaviour show that it is not a uniform pattern of behaviour. Adoption by a replacement parent, by failed reproducers, by taking over a whole brood (brood amalgamation), and by successful reproducers assuming full responsibility for a single (or few) foreign young, are very different behaviour patterns, which sometimes require distinct adaptive explanations (Riedman 1982; Rohwer 1986; Pierotti 1991). There are also important differences in the significance of adoption for adopters of precocial, semi-precocial and altricial young.

Rohwer (1986) and Pierotti (1991) considered infanticide and adoption as opposite consequences of evolutionary conflicts. Rohwer reviewed adoption and infanticide by replacement-parents (foster parents) in birds with altricial young and biparental care, which he interpreted as manifestations of male–female conflict (Rohwer

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1986; Meek & Robertson 1992; Smith et al. 1996). Pierotti (1991) and Hébert (1988) argued that in semi-precocial colonial birds such as terns and gulls, and wandering young in group-living mammals, the behaviour of adopters and adoptees should be analysed in terms of parent-offspring conflict and adoption viewed as an instance of successful intraspecific parasitism that reduces the short-term fitness of the adopting parents (Carter & Spear 1986; Pierotti & Murphy 1987; Morris et al. 1991; Saino et al. 1994; Brown et al. 1995). However, adoption may also be an obligatory strategy for the adopters, as in white-winged crows, *Corcorax melanorhamphos*, where individuals from one group actively kidnap youngsters from another group, these youngsters later becoming helpers in their adopters' group (Heinsohn et al. 1988; Heinsohn 1991).

In precocial birds there is no evidence that adoption reduces the fitness of adopters, and adopting may sometimes be beneficial to both adopters and adoptees. Adoption usually involves brood amalgamation by successful reproducers, as in ostriches, *Struthio camelus* (Bertram 1992) and many species of waterfowl (Anatidae) (Eadie et al. 1988). Adopters may benefit through preferentially reducing the chances of predation on their own young, through the selfish group effect, through enhanced growth rates of chicks in large families, through kin selection and reciprocal altruism, through better predator detection because of more numerous vigilant juveniles, and through increased dominance of larger families (Munro & Bédard 1977; Riedman 1982; Eadie et al. 1988; Choudhury et al. 1993).

Clearly there is no shortage of explanations for the adaptive advantage of maintaining adoption. However, one aspect of adoption that has not been discussed in the literature is the effect of the information obtained through social learning. We argue that when the set of behaviours associated with adoption is itself transmitted by social learning, 'adoptive' behaviour may spread even when selectively neutral or slightly deleterious for the adopters. We also suggest that information that is socially learnt in adoptive conditions may benefit both adopters and adoptees.

'ADOPTIVE' BEHAVIOUR PATTERNS

It is clear that adoption is a vehicle for the transfer of parental behaviour patterns across lineages

(Avital & Jablonka 1994). It is a vehicle for the 'phenotypic cloning' of some of the parents' behaviours that can involve the transfer of food preferences, foraging techniques, mate preferences, predator avoidance techniques, and niche preference. It is well established that parents can transmit such information to their young (see for example, Harris & Murie 1984; McFarland 1987, page 304; Cheney & Seyfarth 1990; Terkel 1996). Some phenotypic cloning is an inevitable effect rather than an evolved adaptive function of adoption. However, as an inevitable effect it may have important evolutionary consequences, even when the transmissible socially learnt information is not adaptive. These evolutionary consequences can be affected by genetic differences that influence social learning, but can also be independent of genetic differences between individuals. They may depend solely on socially transmitted information.

If adopters have, by chance, a distribution of socially transmissible traits that is different from that found in the general population, adoption may lead to the spread of these traits because of the inherently asymmetric transfer of information: adopters adopt the offspring of non-adopters as well as those of adopters, and transmit information to them, as well as to their own offspring. If adoptees later transmit their socially acquired behaviours through conventional parental care, and adoption does not lead to a reduction in fitness, a socially acquired behaviour that by chance was present only in the adopter fraction may increase in the population as a whole, even though it is selectively neutral (Avital & Jablonka 1996). As Cavalli-Sforza & Feldman (1981) emphasized, the spread of any cultural trait depends on its 'cultural fitness', that is, on the relative success of 'cultural parents' in transmitting a given 'cultural' behaviour pattern, and its effects on biological fitness (see also Boyd & Richerson 1985). The explanation of the distribution of behavioural phenotypes in a population with adopters and non-adopters must therefore take into account the dynamics of transfer of behavioural information by adoption, as well as the effects of the transmitted behaviours on fitness.

We believe that adoption itself can spread through social learning if it is correlated with a particular style of parental care (parenting-style). In feral cats, *Felis silvestris catus*, and domestic

mice, *Mus domesticus*, solitary and communal caring styles have been observed (Feldman 1993; König 1994). Gubernick & Klopfer (1981) have suggested that the communal style in cats improves the chances of the litter's survival by providing them with potential adopters if the mother is injured, killed or neglectful. Young learn the parenting-style and other behaviour patterns from the parent, and this increases the chance that they themselves employ a similar style as parents (Berman 1990; Fairbanks 1996). A potential candidate for a parenting-style that may be correlated with adoptive behaviour in colonial species, where adoption is initiated by straying young, is relatively high tolerance towards foreign young. Animals vary in their degree of tolerance or aggression towards both their own young and other individuals (Southwick 1968). The tolerant behaviour or aggressive behaviour may be copied by the offspring including the adoptee, and lead to a higher frequency of adoption by adopters' offspring when adults. Aspects of a maternal style of caring affect aggressive behaviour in mice (Benus & Röndigs 1996), and the level of aggressiveness may be related to the style of caring, leading to the perpetuation of maternally induced behaviour patterns. When adoption is initiated by the adopters rather than adoptees as in brood amalgamation or in the active kidnapping by adult white-winged coughts, adopters actively recruit young, and this behaviour is observed and may be learnt by the young. Hence we do not consider the adopting behaviour as a distinct 'meme' (Dawkins 1976), but rather as an effect of a general style of parenting. We expect this style of parenting to be modulated by the ecological, energetic and social circumstances of the parents. The tendency to adopt can be expressed and socially transmitted when the conditions are compatible with the adopting behaviour, as, for example, in favourable conditions where parents may show more tolerance towards their own and foreign young. However, in similar ecological, energetic and social conditions, we expect young reared by adopting parents to have a higher tendency to adopt than young reared by non-adopting parents.

Although we believe that general parenting-style rather than specific 'adopting behaviour' is transmitted, it is possible that when parents adopt more than one young during a breeding season,

the parental style of older adoptees who observe the adopting behaviour of their adoptive parents may be further reinforced. In group-living species, the spatial structure of the colony and the relative position of adopting families may also influence the tendency of adoptees to adopt in the future. If adoption is common in a particular region of the colony, young within this region, including adoptees, may learn by observation, and the tendency to adopt may diffuse from this locality. The more adoption instances observed, the greater the efficiency of learning, so that in such cases adoption is positively frequency dependent. Inter-generational breeding-site tenacity may increase the spread of adoption even further in such cases. However, 'seeding' new areas in the colony with the adoptive phenotype can also lead to the spread of the adoptive behaviour in the population.

MODELS FOR THE SPREAD OF ADOPTION

In the following section we present two simple models exploring the effects of transmission of behaviour patterns from caring adults to young that need not be their genetic offspring. We ignore additional reinforcement and group-effects on the transmission dynamics. We assume that the tendency to adopt is a part of the parenting-style such as tolerance towards straying young, or a tendency to gather young together. Such styles of parental care are socially learnt by adoptees as well as by biological offspring. This social learning of the style of parenting results in a tendency for both biological offspring and adoptees to adopt. We further assume that adoption is selectively neutral. This assumption is based on data showing that in some cases of adoption there is no obvious fitness cost to the parents. For example, in the common eider, *Somateria mollissima*, adoption is of no apparent advantage or disadvantage for the adopting parent (Bustnes & Erikstad 1991). Neutral effects of adoption on adopters' fitness were also found in the white-winged scoter, *Melanitta fusca deglandi* (Kehoe 1989), barnacle goose, *Branta leucopsis* (Larsson et al. 1995) and Hawaiian monk seals, *Monachus schauinslandi* (Boness 1990), among other species. However, even if the assumption of neutrality is relaxed, and adoption somewhat decreases the fitness of

adopters, the models indicate that it can still spread.

Model I: Adoption by Reproducers

In this model all individuals in the population are reproducers and all have the same average number of biological offspring. There are two types of reproducer: adopters (frequency u) and non-adopters (frequency $1 - u$). The probability of transmitting the adopting behaviour by an adopter is p . Q is the probability that an adopter will take an adoptee when it encounters one. In the adopter subpopulation the number of young reared by the parents equals the number of genetic offspring that remain with their parents (did not become adoptees) plus the number of adoptees each pair of parents has adopted. Adoptees may come from adopter and from non-adopter parents with equal probability. The proportion of adoptees lost by adopters and acquired by other adopters does not alter the average number of the adopters' young. However, adopters can also adopt young that originate from non-adopter parents. We assume that adoption incurs no fitness cost.

After adoption, the frequency of adopters in the next generation (u') is:

$$u' = up + upQ(1 - u)$$

$$u'/u = p + pQ(1 - u)$$

The frequency of adopters will grow when $u'/u > 1$, that is,

$$p + pQ(1 - u) > 1$$

$$1 + 1/Q - 1/pQ > u$$

When u is close to 0 (adopters are rare), u will increase when:

$$p + pQ > 1$$

$$p(1 + Q) > 1$$

$$p > 1/(1 + Q)$$

Hence adoption will spread when rare if transmissibility (p) is greater than 0.5. When $p < 0.5$, the adoptive behaviour will gradually fade away. A

steady state will be reached when $u'/u = 1$, that is, when:

$$p + pQ(1 - u) = 1$$

$$1 + 1/Q - 1/pQ = u$$

These results show that when there is no fitness cost associated with adoption, the asymmetrical pattern of transmission from adults to non-offspring young can increase and maintain adoption, when both its transmissibility and the probability of acquiring an adoptee are sufficiently high. The effect of the social learning of adoption is likely to be seen most often in species showing brood amalgamation, where Q is large. Any pattern of behaviour that can be transmitted by both conventional parental care and by adoption may increase in the population when neutral, and even when deleterious as long as the bias formed by the asymmetrical transmission through adoption is large relative to the selective disadvantage.

Model II: Adoption by Non-reproducers

In this model the population has both reproducing and non-reproducing individuals that can be either adopters or non-adopters. Individuals can have either of two styles of parenting, 'adoptive' (i.e. behaviour likely to lead to adoption) or 'non-adoptive' (i.e. behaviour that does not lead to adoption), but the 'adoptive' style leads to actual adoption only in non-reproducers. Instances in which non-reproducers adopt are seen in emperor penguins, *Aptenodytes forsteri*. In these birds only adult non-breeders adopt young, sometimes even by forcefully kidnapping them from their biological parents. Adoption seems to benefit the young, but its advantages to the adoptive parents seem to be non-existent if not negative (Jouventin et al. 1995).

As in the previous model we assume that the system of transmission is purely cultural. We do not propose that adoption as such is socially learnt, but rather that a parenting-style that leads to adoption is learnt from the parents by both genetic and adopted 'offspring'. As above, we assume that there are u adopters and $1 - u$ non-adopters in the population. If the individual parenting the young has the 'adoptive' parenting-style, the 'student' acquires the 'adopting'

behaviour with probability p . There is always a fraction (a) of the population that reproduces and a fraction $(1 - a)$ that does not reproduce, or fails to rear offspring. The probability of a non-reproducer-adopter taking an adoptee is Q . Only non-reproducing individuals with the 'adoptive' parenting-style actually adopt. Reproducers do not adopt, but those with the 'adoptive' parenting-style transmit it to their offspring with probability p . The different proportions of each type of individual are therefore: reproducers-adopters, au ; reproducers-non-adopters, $a(1-u)$; non-reproducers-adopters, $u(1-a)$; non-reproducers-non-adopters, $(1-u)(1-a)$.

The fraction of offspring adopted by non-reproducers is equal to the encounters between adopter-non-reproducers and reproducer-non-adopters multiplied by the chance of taking an adoptee: $u(1-a)a(1-u)Q$. The offspring of reproducer-adopters do not change cultural parents (their carers are always adopters, whether or not they are genetic or adopting parents). The frequency of individuals with the 'adoptive' parenting-style in the next generation is therefore:

$$u' = \{p[au + u(1-a)a(1-u)Q]\} / a$$

(we divide the right hand term by a to keep the population size constant, since each reproducer produces $1/a$ of the offspring that make up the next generation):

$$u' = up + u(1-a)(1-u)pQ$$

$$u'/u = p + (1-a)(1-u)pQ$$

u will spread as long as $u'/u > 1$

$$u < 1 - 1/[pQ(1-a)] + 1/[Q(1-a)]$$

at equilibrium $u'/u = 1$, so:

$$u = 1 - 1/[pQ(1-a)] + 1/[Q(1-a)]$$

When u is very rare (close to 0) u will spread when:

$$p + (1-a)pQ > 1$$

$$p[1 + (1-a)Q] > 1$$

$$p > 1/[1 + (1-a)Q]$$

Thus, when adoption is neutral and rare, the fraction of adopters will grow providing a sufficiently large fraction of the population consists of non-reproducers, and there are enough potential adoptees. The higher the p , the more chance a rare adopter phenotype will spread. It is clear that if an adopter who is a somewhat poor reproducer but a much better adopter than the norm arrives in the population, its 'adoptive' parenting-style will increase. Any culturally transmissible trait associated with an adopter will also increase (unless it is very deleterious). The maintenance of adoption is somewhat less likely under the assumptions of model II than under those of model I.

Similar results to those of this model are obtained from modelling socially transmitted helping behaviour performed by non-reproducers (results not shown).

In the two models we have assumed that the adoption behaviour patterns were neutral and that the number of biological offspring is unaffected by the behaviour. The possibility of oblique transmission enabled this selectively neutral trait to increase in frequency when rare. The transmissibility of the trait and the mode of transmission determine the increase in the trait's frequency up to the equilibrium point.

MATCH-MAKING

As the models in the previous section have shown, adoption can spread and be maintained in a population even if it does not have any adaptive advantage. However, it is possible that adoption has advantages that result from the information obtained under the adoptive conditions. We consider the possibility that in some species adoptive behaviour may lead to an 'arranged marriage' between the adopter's genetic offspring and the fostered offspring, and enhance the fitness of the adopter's genetic young when compatibility between mates is important.

A certain degree of similarity in habits and experience seems to be important in species where both parents contribute to parental care and the pair bond is stable and long term. Compatibility seems to be an important criterion of mate selection in geese and jays (Black 1996). In the barnacle goose, the preferred mate is one born in the same year, with whom the individual has associated in early life, and who comes from the same

natal area (Choudhury & Black 1994). The choice of familiar, same-age partners seems to improve bonding between mates, decrease the duration of courtship, lead to earlier mating, and make more efficient use of resources (McFarland 1987; Black & Owen 1995; Black et al. 1996). In geese, adoption of foreign young by successful reproducers may increase the chances that genetic offspring will mate with the foster siblings, and thus ensure similarity in habits among mates without paying the price of inbreeding. From the point of view of the adopting parents, such an 'arranged marriage' enhances their offspring's fitness by providing them with adequate future mates. Hence this form of 'match-making' should be more common in species in which both parents care for the young, where they pair for life, or where a high level of compatibility between mates is required. We expect this type of informational benefit through sexual imprinting to be particularly significant when adoption involves brood amalgamation, especially when the broods are large and amalgamation occurs after the development of kin recognition, decreasing the chances of inbreeding. We thus add one more function to the many functions suggested to explain brood amalgamation, such as diluting predation risk to one's own offspring, kin selection, reciprocal altruism, predator detection (Eadie et al. 1988) and accidental brood mixing following territorial aggressiveness (Savard 1987). Eadie et al. (1988) found that in North American anatid species with long-term pair bonding and biparental care, brood amalgamation is common. Brood amalgamation leads to familiarity and similarity in habits between unrelated young. If the match-making hypothesis we suggested is correct, preferential mating between non-siblings belonging to amalgamated broods in some of these anatid species should be found under some conditions. To the best of our knowledge, such data have not yet been published. Match-making may also play a role, albeit indirect, in adoption by replacement (foster) males. By sexually imprinting the adopted female offspring on characters that are unique to them, the fostering males may contribute towards the reproductive success of their own sons or male siblings, since they are likely to be preferred by the imprinted adopted daughters when they choose their mate. In fact, this effect of sexual imprinting leading to future preference for the male kin of the father as mates, may be applicable not only to adopter fathers but

also to genetic fathers. The significance of this effect will be determined by the patterns of dispersal of juvenile male and female offspring, and the likelihood of encounters between imprinted daughters and the father's male kin.

When match-making is an important function of adoption, the timing of sexual imprinting and the pattern of dispersal are expected to determine the age at which young are adopted, and possibly also the preferred sex of the adoptee. We expect that (1) the timing of sexual imprinting should coincide with or follow adoption, and (2) adoptees will mate more often than random with their foster siblings. Preferential mating will occur most commonly in colonially breeding species, when both male and female siblings tend to breed on the same territory and there are advantages in finding compatible mates.

DISCUSSION

Evolutionary biologists study adopting behaviour by examining the effects of this pattern of behaviour on the genotypic fitness of adopters and adoptees. We have taken up a different perspective, which is based on parenting as a channel of socially transmitted information, and which looks at 'cultural fitness'. In a population containing both adopters and non-adopters, the transmission of behaviour patterns is inherently asymmetrical because adopters transfer information to both their own young and to the young of non-adopters, whereas non-adopters cannot transfer information to the young of adopters. Adoption can lead to the spread of adopters' behaviour patterns when the average number of 'cultural offspring' of an adopter is larger than that of a non-adopter, even if most of these 'cultural offspring' are not genetic offspring and the genotypic fitness of the adopter is lower than that of a non-adopter. Since even non-reproducer adopters can transfer patterns of behaviour, their influence on the frequency of phenotypes in the population may not be zero. If adopters transmit other patterns of behaviour (e.g. a food preference, or a sexual preference) these preferences can subsequently be transmitted by the 'students' to the next generation by normal parental care (Avital & Jablonka 1996). The frequency of the pattern of behaviour will grow as a function of its efficiency of transmission by adopters in the population.

Adoption can also lead to its own transmission when it is linked to a socially transmissible style of parental care.

In colonial species the transmissible style of parental care that is likely to be associated with a tendency to adopt is tolerance to one's own as well as towards others' straying young; in other cases, adoption may be a socially learnt abducting or amalgamating behaviour. As the models presented above have illustrated, when rare, socially learnt 'adoptive' behaviour will spread in the population even if it does not have any adaptive advantage.

Adoption can have benefits for the adopting parents that are the consequence of sharing or exploiting useful, socially learnt information. Match-making through parentally guided sexual imprinting on foster siblings may be an important advantage of adoptive behaviour, mainly in some species with precocial young. When there are clear adaptive advantages to adoption, the rate at which the socially transmissible adopting behaviour spreads will rapidly increase, since the number of 'cultural offspring' (which includes both biological offspring and adoptees) of an adopter will be much higher than that of non-adopters (who have only genetic offspring).

There is another way to look at the complex of behaviours and circumstances leading to adoption. Instead of looking at the benefits and costs of adoption for the adopter and adoptee separately, we may look at the benefits and costs to an individual of the total set of behaviour patterns leading to socially learnt adoptive behaviour, a set that includes the fact of having been an adoptee. From this perspective we arrive at the conclusion that adoption is adaptive for the adoptee when the chances of needing non-parental care when young are high. Most available data indicate that the benefit to the adoptee is much greater than the damage to the adopter (if any); if the chances of becoming an adoptee are significant, and if individuals who are adoptees early in life and benefit greatly must 'pay the price' by becoming adopters in later life, adoption will spread. Of course, if the correlation between becoming an adoptee and being an adopter is weak, a selfish type of adoptee who does not adopt will invade the population. However, we suggest that social learning to become an adopter may provide a strong functional correlation between the two roles: the young adoptee cannot help but acquire

the parental style associated with the 'adoptive' behaviour, along with other behaviours transmitted by the adoptive parent. Hence, if the unit of analysis is not 'adoptive' behaviour, but rather the more inclusive 'adopter-adoptee behavioural set', adoption will be adaptive if the chances of being deserted when young are high enough and the cost of being deserted is large. In addition, as [Pierotti \(1991\)](#) has suggested, the asymmetry between benefits and costs in adopters and adoptees will result in more intense selection on the adoptee to manipulate the adopter, than on the adopter to avoid adopting, leading to the adoptee having a selective edge over the adopter, and (usually) 'winning' the inter-generational conflict.

In this paper we have concentrated on the effects of social learning, and have not considered the interaction between the cultural and genetic inheritance systems. However, such interactions will have important and interesting evolutionary effects. Any adaptive, learnt behaviour may be genetically assimilated if the adaptive advantage persists for a sufficiently long time, and if the efficiency of learning enhanced by genetic assimilation increases fitness ([Haldane 1959](#)). Thus, if socially learnt 'adoptive' behaviour is adaptive in the long term, selection for its partial genetic assimilation may occur. Complete genetic assimilation of 'adoptive' behaviour is unlikely as long as adoption is dependent to some extent on environmental conditions. [Laland \(1994a, b\)](#) has considered another important aspect of the interaction between the cultural and genetic inheritance systems. He has shown that sexual imprinting, which is a socially learnt mate preference, may sometimes lead to the spread of a genetically determined inferior preferred trait, such as a certain plumage colour. When the adoptive behaviour is itself the sexually imprinted trait, it may spread through sexual selection, for example when males exhibit their parental aptitude and style of care during courtship feeding. However, the interactions between sexual imprinting and the 'adoptive' parenting-style have yet to be explored by modelling.

ACKNOWLEDGMENTS

We are very grateful to Marion Lamb for her detailed and constructive criticism of drafts of this paper, and to the referees for their helpful and valuable comments.

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