

Helping non-relatives: a role for deceit?

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Abstract. In birds and mammals with ‘helpers-at-the-nest’, some individuals not only feed unrelated offspring, but also compete to do so. Non-adaptive explanations for alloparental care do not predict competition for access to offspring that, in its most extreme form, can include kidnapping young from adjacent territories. A common adaptive explanation holds that allofeeding promotes a ‘social bond’, with non-relatives. This proximate hypothesis does not explain why the recipient later cooperates with or helps at the nest of its former benefactor. An extension of this hypothesis posits that, by helping to care for unrelated young, individuals may take advantage of a kin-recognition mechanism based on associations learned by nestlings while being fed. The deceived young later may offer assistance according to its perceived relatedness to the former helper. This mechanism, termed kinship deceit, may be a form of bet-hedging in cooperative breeding systems where mortality is high, where breeders can benefit from contributions by helpers, and where helpers normally assist relatives.

In avian and mammalian cooperative breeding systems, most alloparental helpers are close relatives of the young they rear (Emlen 1991). Nevertheless, unrelated helpers also occur; in birds these typically constitute less than 10%, but sometimes as many as 45%, of all helpers (e.g. papers in Stacey & Koenig 1990). Why unrelated individuals should help remains problematic. Here we note several allied phenomena that are difficult to explain under prevailing hypotheses, and draw attention to an alternative mechanism based on deception that could account for helping by non-relatives and associated behaviour such as kidnapping. We call this mechanism kinship deceit.

Helping (usually defined by provisioning behaviour) directed towards unrelated young can arise in several ways. Most commonly, adults may gain access to unrelated young when they disperse and join existing groups or if they reside in groups with multiple breeding units. Adult female Florida scrub jays, *Aphelocoma c. coerulescens*, often move between groups; most replace dead breeders, but some join as non-breeders and help provision their new group’s unrelated offspring (Woolfenden & Fitzpatrick 1984). In plural breeders (Brown 1987), groups may contain several breeding units, generating opportunities

for individuals to help at nests containing distantly related or unrelated young (e.g. Curry 1988).

Adoption, involving recruitment and care of dependent young from another group, is another source of unrelated helpers. Adoption can occur when juveniles immigrate into new groups or when a group expands its territory such that it subsumes areas inhabited by unrelated fledglings. Adoption has been seen in scrub jays (Woolfenden & Fitzpatrick 1984), Galapagos mockingbirds, *Nesomimus parvulus* (Curry 1988; unpublished observations) and Arabian babblers, *Turdoides squamiceps* (Zahavi 1990).

An extreme form of adoption, ‘kidnapping’, occurs when adults herd young from another territory into their own. Heinsohn (1991a) observed 14 instances (out of 87 group-years of study; Heinsohn 1991b) in white-winged choughs, *Corcorax melanorhamphos*, where kidnapping occurred during or following aggressive encounters between groups. Adult ‘kidnappers’ fed the fledglings they adopted; three young survived to become unrelated helpers in their new groups. Kidnapping differs from other forms of adoption in that kidnappers incur costs in recruiting unrelated offspring in addition to those associated with provisioning. Kidnapping may be

analogous to 'slave-making' in ants (Wilson 1971).

Helpers may also incur costs by competing for access to recipients. In green woodhoopoes, *Phoeniculus purpureus* (Ligon & Ligon 1978, 1983; Ligon 1983), Arabian babblers (Carlisle & Zahavi 1986; Zahavi 1990) and dwarf mongooses, *Helgale parvula* (Rasa 1977, 1986), helpers vie for chances to feed related and unrelated young. When woodhoopoe nestlings are small, for example, helpers deliver food via the parent female, but as the nestlings grow, helpers avoid the parent and feed the nestlings directly (Ligon & Ligon 1983). Woodhoopoe helpers also steal food items from each other and deliver them to young birds. The Lignons twice saw woodhoopoes enter neighbouring territories in a 'stealthy' fashion, and attempt to feed unrelated nestlings 'surreptitiously'; in one case the intruders succeeded and in the other they were chased off by the parents.

Why do helpers provision (and even kidnap) unrelated young, sometimes competing to do so? Several adaptive hypotheses for the expression of helping do not depend on helper-recipient kinship (Emlen 1991); most, however, cannot explain the observations described above because they fail to account for the unusual costs involved. One oft-cited alternative offers a partial explanation: by provisioning, helpers may foster the formation of 'social bonds' with recipient young, bonds that later benefit the helper either (1) by increasing the probability that the young will return the favour, or (2) by promoting development of coalitions beneficial in competing for breeding positions (Ligon 1983; Emlen 1991; Emlen et al. 1991). Heinsohn (1991a), for example, suggested that in white-winged choughs, which required helpers to reproduce successfully, selection may have favoured kidnapping because the resulting 'special bonds' cause kidnapped young to help their kidnappers.

Although the social bond hypothesis has been invoked frequently, it offers no evolutionary explanation for why helper-recipient bonds should develop. More importantly, it fails to explain why such bonds should cause individuals to cooperate with, or act altruistically towards, unrelated helpers that had provisioned them. Our extension of the hypothesis addresses these issues: by feeding unrelated offspring, helpers may parasitize a kin-recognition mechanism based on

associative learning; the deceived offspring recognize those who care for them as kin and later help rear their provisioner's offspring (see Curry 1988). This hypothesis derives from the general concept that if kin-recognition mechanisms are imperfect, individuals may benefit by mimicking kinship cues, and thereby inveigle others into providing beneficence usually reserved for close relatives (e.g. Trivers 1971). Helping by unrelated individuals is of particular interest because the deceit is executed with altruism.

The kinship deceit hypothesis applies if most helpers assist relatives preferentially (e.g. Curry 1988; Emlen & Wrege 1988) because of some indirect fitness benefit. We expect to find kinship deceit in species where: (1) young animals recognize kin based on learned associations; (2) help increases the reproductive success of the breeder rather than the helper; and (3) close kin are not always available to provide help. Kinship deceit is not restricted to unrelated individuals because it is defined as deceit about the degree of relatedness.

If young animals preferentially help relatives and if they learn to recognize kin based on who feeds them as nestlings, then provisioning behaviour should predict recipients of subsequent help better than does kinship. Galapagos mockingbirds offer support for this prediction: facultative helping behaviour in this species is directed disproportionately to close relatives, but prior association better accounts for the observed pattern of helping than does relatedness (Curry 1988). The failure of breeders or helpers to alter provisioning when Curry switched nestlings in adjacent territories is consistent with assumption that individuals decide whom to help based on their presumed kinship with breeders, and not on their recognition of nestlings.

Below we evaluate the kinship deceit hypothesis by comparing it to other hypotheses that have been offered to explain why helpers might provision unrelated offspring.

The 'unselected' hypothesis championed by Jamieson & Craig (1987; Jamieson 1989, 1991) holds that provisioning by helpers is a non-adaptive by-product of selection for parental behaviour: the same stimulus-response mechanism that mediates parental feeding causes non-parents to exhibit alloparental care. According to this hypothesis, provisioning by helpers should be similar in form to parental feeding and should not

show evidence of adaptive modification (Jamieson 1991).

In their critique of Jamieson (1989), Emlen et al. (1991) reviewed several studies in which helpers discriminated between recipient young based on relatedness. Jamieson (1991) countered that such adaptive modification of helping had been demonstrated only in colonial and plural breeders and not in more prevalent singular breeders. We note, however, that Jamieson (1989, 1991) overlooked kidnapping and competition for opportunities to feed nestlings, and that singular-breeding woodhoopoes (Ligon & Ligon 1983) and scrub jays (Stallcup & Woolfenden 1978) exhibit related behavioural modifications that affect access to potential recipients.

Adaptive hypotheses are based on the premise that helping is favoured by selection because the helper accrues some return benefit that outweighs the cost of helping. Following Trivers (1985), we refer to cases in which individuals perform costly acts for others that induce subsequent benefits to the actor as 'return benefit altruism'. Four different models of return benefit altruism have been applied to provisioning of unrelated offspring; the kinship deceit hypothesis is a fifth. Below we evaluate the ability of these five models to explain 'special bonds' between non-relatives, competition to feed nestlings, and kidnapping.

Reciprocal Altruism

In reciprocal altruism (Trivers 1971) one individual (A) performs a costly act for another individual (B) and is later paid back by a costly act by B. Reciprocal altruism requires that individuals recognize each other, keep track of their interactions, monitor their partner for cheating, and cheat themselves if they can get away with it. Can reciprocal altruism explain the bonds between helpers and helped? The two-party Tit-for-Tat model of reciprocal altruism requires that there is some probability that two individuals will meet again; if there is only one or a known number of interactions the only evolutionary stable strategy is to defect (Axelrod & Hamilton 1981). In vertebrate cooperative breeding, there is typically only one 'turn' by each party: helper A feeds fledgling B, who later provisions A's young. Reciprocal altruism is therefore not a viable model for the bond between helpers and unrelated young they may provision (Koenig 1988).

Pseudo-reciprocity

In pseudo-reciprocity an individual (A) performs a costly act for another (B), but the return benefit to A is a by-product of self-serving behaviour by B rather than a costly act performed to benefit A (Connor 1986). Pseudo-reciprocity may apply where the return benefits helpers receive are experience or allies helpful in territory acquisition and defence, or in offspring care (Brown 1983; Connor 1986). However, pseudo-reciprocity does not predict competition to feed offspring or the formation of social bonds between helpers and those they help. In pseudo-reciprocity, individual A is selected to promote B's survival so that B can later perform selfish behaviour that incidentally benefits A; A's return benefit does not depend on a bond with B. Furthermore, A should prefer that other individuals pay the cost of ensuring B's survival and should not interfere with their attempts to care for B. It is also unlikely that helpers would try to prevent others from gaining experience.

Pay-to-stay

Gaston (1978) suggested that individuals might enter a territory and feed unrelated offspring as payment to the breeder for the helper's access to local resources. Pay-to-stay may be a form of reciprocity but it has not been explicitly modelled as such. Because the breeder is never in the position of owing the helper, there is no alternation of costly acts as in reciprocal altruism.

The deceit hypothesis may be considered an alternative to pay-to-stay: immigrants may feed unrelated young not as payment, but because they benefit by deceiving the breeder's offspring. The breeder may tolerate the immigrant if the benefit of additional feeding is greater than the cost of having its offspring deceived. Pied kingfishers, *Ceryle rudis*, may provide an example: most auxiliaries ('primary' helpers) are sons of the breeding pair, but breeders accept additional unrelated immigrants in harsh environments (Reyer 1984, 1986); these 'secondary' helpers may feed unrelated nestlings primarily to improve their chances of succeeding the breeding male, but those that become breeders occasionally also receive help from the nestlings they provisioned (Reyer 1986). Pay-to-stay, like pseudo-reciprocity, does not predict continuation of helper-fledgling social bonds beyond fledgling independence.

Dominance Interactions

Arabian babblers feed unrelated adults and young, and dominant birds actively interfere with the attempts of subordinates to feed nestlings. Carlisle & Zahavi (1986) call such behaviour 'status' exhibition and Zahavi (1990, page 125) extends the status explanation to all forms of helping: 'no model of group selection, kin selection, or reciprocity can explain why babblers do not exploit the tendency of others in the groups to help, and certainly does not explain the reason for investing in hindering other babblers from acting as altruists'.

Kinship deceit cannot explain the feeding of unrelated adults. However, if babbler nestlings learn to recognize those who feed them as kin, then such behaviour may be explained as competition for kinship bonds. Helpers of equal relatedness to nestlings may compete for a limited number of 'kinship bonds', which would not be deceit as defined here. In complex groups of babblers, however, relatedness varies and opportunities may arise for helpers to deceive nestlings about their degree of kinship. Babbler group members occasionally adopt 'alien' fledglings but this may reflect deception by the fledgling rather than the helper (Beecher 1988).

Kinship Deceit

Kinship deceit can explain social bonds, kidnapping, and competition for opportunities to feed unrelated nestlings. We suggest that competing to provision represents competition for kinship bonds, and that when distantly related or unrelated helpers are involved (e.g. Ligon & Ligon 1978) then kinship deceit may occur. Offspring will form 'kinship' bonds, through associative learning, with the helpers that fed them, and the deceiving birds should continue the sham as long as they can benefit from it.

The kinship deceit hypothesis would benefit from a formal model to investigate how patterns of relatedness, mortality, and parental and nestling counterstrategies would affect the evolutionary stability of deceit. We do not attempt such a model here, but point out some general issues that would need to be addressed. First, kinship deceit should be more common in unpredictable environments with high mortality. Helpers should prefer to recruit young relatives as allies

because kinship deceivers will suffer the cost of having their offspring deceived in return. However, if mortality is high, helpers should hedge their bets against the loss of related young and attempt to deceive unrelated young. Second, breeders without related helpers may also tolerate kinship deceivers because the cost of having one's offspring deceived may often be small compared with the benefits of having helpers. Third, if kinship deceit spreads in a population, the necessary correlation between kinship and helping will decrease. This in turn may favour modification of kin-recognition rules. For example, a rule might shift from recognizing anyone who feeds you as kin to only those who feed you the most (which might select for more competition to feed nestlings). However, failing a shift to self-referent phenotype matching or the appearance of 'recognition alleles' (Sherman & Holmes 1985), any change in the kin-recognition mechanism will still allow occasional kinship deceit. The frequency of kinship deceit may remain low in a population because of efforts of true kin to thwart it. Selection may favour increased vigilance for deceivers by parents and other kin which may, in turn, favour new deceiving strategies.

The kinship deceit hypothesis predicts that deceived helpers should perceive non-kin as kin. This perception should manifest itself in non-helping contexts, providing a possible test. For example, observations that individuals avoid breeding with unrelated adults that fed them as nestlings would support the kinship deceit hypothesis. Zahavi (1990) offered the tantalizing observation that 'babblers that attend to a fledgling that is not related to them avoid breeding with it'. Zahavi did not state how he was able to attribute responsibility to the helper; the kinship deceit hypothesis predicts that the fledgling would be responsible for preventing the mating.

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