

Adoption as a gosling strategy to obtain better parental care? Experimental evidence for gosling choice and age-dependency of adoption in greylag geese

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Summary

Adoptions of unrelated young by successful breeders are a form of alloparental care which has been observed in many species of geese. Depending on costs and benefits to the parents, adoptions might represent an inter-generational conflict or a mutually beneficial strategy. Although most studies of wild populations suggest benefits of large brood sizes, incidental observations mostly report aggressive behaviour of parents towards lone goslings. No studies have investigated mechanisms and behaviour during adoptions in order to test whether adoptions are driven by parents or goslings. To test whether goslings might use adoption as a strategy to obtain better parental care, we carried out an experiment where lone greylag goose (*Anser anser*) goslings could choose between a dominant and a subordinate foster family. In a second experiment we also tested whether adoption was age-dependent. Except for one case, all lone goslings ($N = 16$) chose the dominant family. Parents showed very little aggression towards lone goslings at three days after hatch, but aggression increased until 9 days and remained high thereafter. At the same time as aggression increased, the chance of successful adoption decreased. In the first five weeks of life, goslings which had been adopted were no further away from parents than original goslings during grazing. These results show that goslings might choose foster families according to dominance. The fact that with increasing gosling age parents are less willing to adopt could be due to improved individual recognition and reflect decreasing benefits of gaining an additional family member. More detailed studies on state-dependent costs and benefits of adoptions are required to determine whether adoptions in geese represent conflict or mutualism, and why this changes with gosling age.

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Introduction

The provisioning of care to young by individuals other than the genetic parents is a behaviour that has been described in many animals and is broadly referred to as alloparental care (Riedman, 1982). Although at first sight investing resources into non-genetic offspring appears contradictory to the aim of maximising ones genetic contribution to future generations, particularly for cooperative systems it has been shown that alloparents can gain direct and indirect benefits (Clutton-Brock, 2002; Roulin, 2002; Koenig & Dickinson, 2004). Apart from cooperative breeding systems, alloparental care also occurs in other reproductive systems, including those with social monogamy and biparental care (Riedman, 1982). In birds various forms of brood mixing have been described, such as communal crèching, brood amalgamations and adoptions. The term adoption has been used in many different contexts. We define it as a form of alloparental care where one or several foreign young permanently join another brood, and the parents of the original brood exclusively provide all aspects of parental care to these young (Eadie et al., 1988). The fitness consequences and adaptiveness of this kind of alloparental care are little studied and understood (Emlen et al., 1991; Kalmbach, in press).

Geese are precocial birds with biparental care and are known to frequently adopt goslings that are not their own, with up to 50% of families containing adopted young (Zicus, 1981; Choudhury et al., 1993; Larsson et al., 1995). In wild populations, adopters appear to be almost exclusively successful breeders who have goslings of their own at the time of adoption (Zicus, 1981; Williams, 1994; Larsson et al., 1995). This observation has led to the traditional explanation of adoptions as 'reproductive error' due to imprecision of parent-offspring recognition at an early age (Jamieson, 1986; Emlen et al., 1991). Although adoptions are most common during the goslings' first week of life, they have also been observed throughout the whole brood rearing period of two to three months (Prevett & MacInnes, 1980; Choudhury et al., 1993; Williams, 1994). These observations suggest that adoptions can not only be explained by a recognition mistake between parents and goslings, as individual recognition is developed by the age of 10 to 15 days (Ramsay, 1951; Prevett & MacInnes, 1980). If adoptions are adaptive for the goslings

but gaining additional brood members is costly to parents, they would represent an intergenerational conflict (Pierotti, 1988). If, however, parents gain benefits from an increased family size, then adoptions might be mutually beneficial (Williams, 1994; Loonen et al., 1999).

Lazarus & Inglis (1986) have proposed that large broods are not costly to parents with respect to parental investment of which all offspring benefit simultaneously, such as vigilance or brooding behaviour ('unshared investment' *sensu* Lazarus & Inglis, 1986¹). As most of the post-hatch parental care in precocial species falls into the category of 'unshared investment', large broods should not be more costly than small broods for parents in such species. In fact, very few studies have actually tried to identify costs of raising large families in geese (Kalmbach, in press). Evidence from observational studies generally shows that larger families are more dominant, which leads to better access to high quality feeding areas, and that gosling growth and condition is enhanced, while no negative effects on adult survival or future reproduction are found (Seddon & Nudds, 1994; Williams et al., 1994; Lepage et al., 1998; Loonen et al., 1999). Although non-breeders have been found to have a higher return rate than breeders (Raveling, 1981; Petersen, 1992; Prop et al., 2004), amongst emperor goose *Chen canagicus* females those with larger families had higher survival than those with small families (Petersen, 1992). Of the three studies to date which have carried out brood size manipulations in geese, two have found strong evidence for a causal relationship between family size and social dominance, as well as gosling growth (Lepage et al., 1998; Loonen et al., 1999). Also, both parents and juveniles gain benefits from large families and long family association on the wintering grounds (Black & Owen, 1989a, b). It appears that on the whole large broods are more beneficial than costly to goose parents and their genetic offspring. Beside these indirect benefits of adoption via enlarged family size, it has been suggested that adoptions might provide direct benefits

¹ In the original paper by Lazarus & Inglis (1986) 'unshared investment' is defined as an act of parental care which is directed at the brood as a whole and of which therefore all offspring benefit equally (unshared = everyone gets all of the investment, not only a share). 'Shared investment' is defined as an act of parental care which benefits individual offspring to a different degree, up to the case of monopolization by one offspring, such as delivery of food items. Lazarus & Inglis (1986) argue that the costs of 'unshared investment' do not vary with brood size, while costs of 'shared investment' increase with increasing brood size.

of predation avoidance through predation dilution and the selfish herd effect (Hamilton, 1971; Eadie & Lumsden, 1985; Nastase & Sherry, 1997).

These results suggest indeed that adoption might be a beneficial strategy of parents to increase their family size, particularly when they can do so without incurring the costs of laying and incubating extra eggs. From the gosling's perspective, it has traditionally been assumed that adoption occurs as a salvage strategy after having lost its parents (Choudhury et al., 1993; Williams, 1994; Nastase & Sherry, 1997). However, from our own and other researchers' observations, it is often the case that original parents are still alive and present in the local feeding group, particularly in cases when adoptees are very young (K. Kotrschal, J. Prop, M.J.J.E. Loonen, pers. comm.). We suggest that adoption could also be an active strategy of goslings to obtain better parental care or higher social status (Pierotti, 1988).

In this study, we carried out behavioural experiments with a semi-captive greylag goose *Anser anser* population to test three hypotheses about the role of parents and goslings in adoptions. (1) If adoption is a strategy by goslings to obtain better parental care, goslings should be able to discriminate between parents of different quality, and, if given the choice, choose the higher quality family. (2) If an increase in family size entails mainly benefits and not costs, parents should be basically willing to adopt. (3) If adoption is a strategy by parents to decrease predation risk of their genetic offspring, we expect to see a difference in the distances between original and adopted goslings to the parents. Through aggressive or threatening behaviour goslings might be kept at the periphery of the group and predation risk could be skewed towards fostered young, thereby providing protection for original young (Öst & Bäck, 2003).

Methods

Study population and clutch manipulation

The study was carried out in the breeding seasons (March-August) of 2003 and 2004 with a captive population of greylag geese. The geese are kept on 0.5 ha area of grassland, bushes and water pools near the Biological Centre of the University of Groningen (The Netherlands). The population was started in 1992 with eggs that were collected from the wild. Wing feathers are clipped every year during moult to prevent geese from flying away. The

flock consisted of 76 (40 males, 36 females) and 63 (33 males, 30 females) adults and several juveniles in 2003 and 2004, respectively. All geese were individually marked with numbered aluminium leg rings and uniquely coded plastic neck rings, which are legible from a distance. From the start of the breeding season, the whole area was checked every day for new nests and eggs.

To avoid any potential bias in our experiments due to genetic relatedness of goslings and parents, we prevented all eggs that were laid by the captive geese from developing through thorough shaking, and replaced them with eggs from a wild population. The wild eggs were collected by members of the Dutch Forestry Commission under a licensed control scheme for local goose populations, and obtained by us under licence from the Ministry for Agriculture, Environment and Fisheries (licence number FF/75A/2003/048). Wild eggs were initially kept in an incubator at 37.5°C and around 55% humidity and grouped by the stage of development, which was estimated by inspection with a lamp.

Shortly before hatching in 2003, groups of ten eggs were formed, of which three each were put into two nests, while the other four were hatched in the incubator. After hatching, the incubator goslings were kept with a pair of failed breeders in a smaller enclosure where a heating lamp was present as well as an outdoor part. The adults were kept with the goslings to avoid imprinting of goslings on humans. Although the female did not brood the goslings, the adults did not show aggression towards the goslings, and even defended the goslings against approaching humans. Through this procedure we obtained 'twinned' nests in the field, with broods of three goslings each hatched on the same day, while four more goslings of the same age were present in the foster-enclosure. In 2004, groups of 12 eggs were formed, of which three each were put into three nests in the field, and the remaining three hatched in the incubator and were kept with the foster parents. The fact that in 2004 groups of 3 twinned families existed is of no further importance to the experiments described in the present paper. Nests in the field were 'twinned' according to the original start of incubation, to avoid large differences in the time females had spent incubating within the sets of twin-families.

Gosling choice experiment

In 2003, we carried out a choice experiment where lone goslings were able to choose between two potential adoption families. For this, we built open cages

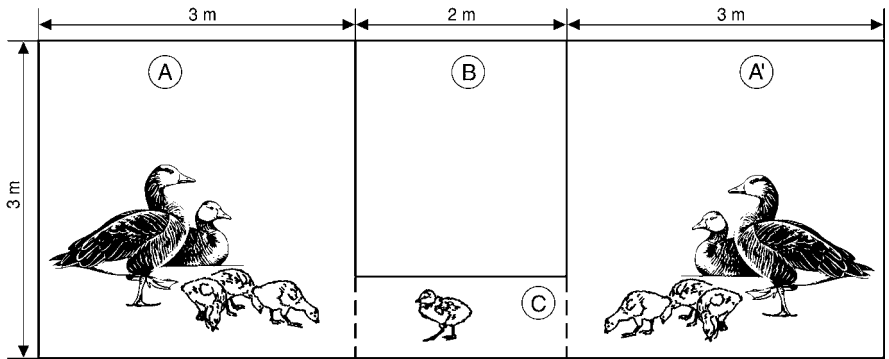


Figure 1. Schematic layout of the enclosure used for the gosling choice experiment with position of test gosling and families during testing phase. All separations were made with chicken wire. The separations between compartment C and A and A' contained doors where only goslings could pass through (indicated by the dashed line). Those doors were closed before the testing phase, i.e. during the interaction period of the experiment (see text).

in a separate part of the field, which contained four compartments (Figure 1). All separations between the compartments were made of chicken wire and it was possible for all geese to see through the fences. When goslings were two days old, the twinned families were placed in the compartments A and A' with some water, and left to get accustomed to the cages and surroundings for a minimum of one hour. Then both families were placed in compartment B, with water and food placed in the middle, while a lone gosling was placed in compartment C with food and water. The lone gosling came from the foster enclosure and was of the same age as the family goslings.

For a minimum of 30 minutes, the two families were left in part B, while the lone gosling was left in part C. All interactions between the two families were scored by two observers to determine which family was more dominant. As dominant was determined the family who had won more than 50% of the interactions. If this was not clear after 30 minutes, this period of the experiment was extended until dominance became clear, which lasted a maximum of 2 hours in one case. At the end of the interaction period, the families were again divided into parts A and A'. Immediately then the connections between part C towards A and A' were opened for goslings. The doors were too small for adults to pass through, therefore adults could not physically force the lone gosling into their family. The two meter distance between the doors to the two families also facilitated to clearly detect the choice of the gosling, as it was very unlikely that the gosling mistakenly went out the door of the non-

favoured family. It was noted which family the lone gosling joined, before it was removed and replaced in the foster enclosure. The whole experiment was carried out twice, once in the morning and once in the afternoon, with each set of twinned families, using two different goslings. After both runs of the experiment, the adults of the two families were weighed.

Adoption willingness experiment

In 2003 and 2004, we carried out an experiment to test the willingness of parents to accept lone goslings into their family. When goslings were three days old, the twinned families were put into a fenced in area of 4×5 m each, which contained vegetation, a small ditch, and bowls with food and water. They were left to acclimatise for a period of at least one hour. In 2003, alternately the dominant or subordinate family of a twinned set received two lone goslings of the same age as the family goslings. These goslings were never those which had taken part in the choice experiment the previous day. The family which did not receive additional goslings was kept in the enclosure for the same length of time as the receiving family. In 2004, only one lone gosling was given to every family. Test-goslings were always of the same age as family goslings. All goslings were visually marked with colourful tape flags which were attached to the down. For 30 minutes, all aggressive interactions (biting, threatening, chasing) from the parents to the lone goslings were scored, as well as assessing whether adoption within the 30 minutes was successful. Successful adoption was determined by the continued absence of any aggression from parents towards goslings when they were close to the adults, and whether the gosling was being brooded by the female when brooding took place. Initially we carried out observations for 90 minutes, but found that the outcome of adoption did not change between the end of 30 minutes and 90 minutes. Goslings were either accepted within the first 10 to 15 minutes, or not at all. Those goslings which were accepted into families were allowed to remain with those families after the experiment.

In 2003, the experiment was repeated at ages 14 and 27 of the goslings, and in 2004 the experiment was repeated at ages 6, 9, and 14. For these repeated experiments we used goslings of another family as test-gosling, matching age as closely as possible (± 2 days) and not using the same gosling more than once per family. Goslings were then always returned to their original families after the 30 minutes. While at age 3 days all families had

three original chicks, family sizes at the later experiments varied, due to the experimental adoptions, naturally occurring adoptions, as well as gosling loss either to predation or to adoption.

Following distance

In 2003, all families which had adopted two chicks at age 3 days were observed in the field at gosling ages 4, 7, 10, 13, 16, 19, 28, and 34 days to determine distances between family members. For 30 minutes every 30 seconds the positions of all family members were noted on a grid, where the male was put as a reference into the centre of the grid. Distances were estimated in adult goose length. All observations were carried out by the same observer to avoid between-observer differences in estimating distances. Goslings were marked with colourful small tape flags attached to the down on the upper legs and the centre of the back.

For each observation day, all values were averaged to obtain one value for distance of original goslings and one value for adopted goslings with respect to the distance to the male and female parent. Goslings which had been adopted naturally in the field were included in the value for adopted goslings. As only the female parent broods the young, observations during brooding were not included in the analysis.

Data analysis

In the choice experiment we used every set of twinned families (= 'set of families') twice, each time with a new naïve gosling. To test whether the identity of the family set had an influence on the choice the goslings made, we used a GLM with binomial error, response variable 'choice', and predicting variable 'set of family'. There was no effect of the family set on gosling choice ($\chi^2 = 4.71$, $df = 7$, $p = 0.70$), and we therefore used an exact binomial test to check if the choice of the goslings for dominant and subordinate families differed from a 0.5 probability.

Many of the breeding pairs in 2003 and 2004 remained the same. For the analysis of the aggression experiment, we therefore applied a mixed model with a nested random factor for family identity within years (Crawley, 2002; Venables & Ripley, 2002). The likelihood of successful adoption in our experiment was analyzed by using generalized estimating equations (GEE) to fit population average models to the data (Hosmer & Lemeshow, 2000). This

procedure is similar to generalized linear models, but particularly designed for binary longitudinal data, and it allows the inclusion of a random factor (family identity). Parameter estimates and significances are reported from the final model or, for non-significant variables, from the final model plus the respective variable. As response variable for the aggression test we used 'aggressive acts per minute' towards the gosling, combining aggression from the male and female of the family. To account for the fact that at age 3 in 2003 two goslings were added to the family, we used a per-gosling rate of aggression in the analysis. However, there was very little aggression shown by the parents at that age anyway. Because families were tested in the adoption willingness test at different gosling ages and on a varying number of occasions, we analyzed only the subset of 10 families which were all tested at the same gosling ages in 2004 for individual differences in adoption willingness. We employed a χ^2 test with counts of successful/unsuccessful adoptions per family to test for inter-family differences.

For the analysis of following distances we used $\log(\text{distance})$ in order to achieve normal distribution. We analysed the gosling-parent distances with mixed models with a grouped data structure to account for the fact that each family was sampled repeatedly over time (Crawley, 2002). The factor 'adopted' was coded so that the coefficient in the model represents the distances of adopted goslings to adults, while the coefficients of original goslings was set to zero. Data analyses were carried out using the open source software 'R' functions 'lme' and 'geese' for the mixed models and GEEs (Ihaka & Gentleman, 1996; Crawley, 2002; Venables & Ripley, 2002) and SPSS for Windows, version 11.0.

Results

In 2003, 17 paired females successfully completed incubation and hatched three chicks from wild eggs, leading to a sample size of 8 sets of twinned families. In 2004, 11 families with three goslings from wild eggs were obtained.

Gosling choice experiment

The choice experiment was carried out with 16 lone goslings. In all 16 cases, the goslings made an obvious choice when the doors between its compartment and the family compartments were opened. 15 chose the dominant

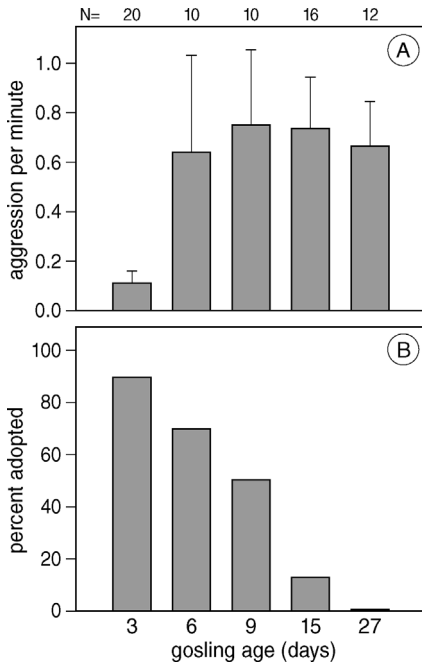


Figure 2. (a) Aggression from parents towards lone goslings and (b) rate of successful adoption during 30 minute experiments in relation to gosling age. Error bars represent ± 1 SE, and N denotes sample size.

family and 1 chose the subordinate family. This pattern was significantly different from a random choice (exact binomial test $p = 0.0005$). Adults from dominant pairs were not heavier than subordinates (males dominant: 3971 ± 107 g, subordinate: 4196 ± 150 g, $T_{14} = 1.22$, $p = 0.24$; females dominant: 3219 ± 164 g, subordinate: 3247 ± 192 g, $T_{14} = 0.11$, $p = 0.91$), and thus gosling choice was not related to adult weight (GLM with binomial error, dependent 'choice' predictor 'male weight': $\chi^2 = 1.39$, $df = 1$, $p = 0.24$).

Adoption willingness experiment

When goslings were 3 days old, there was very little aggression of prospective adoption parents directed towards the goslings (Figure 2a). As goslings grew older, aggression increased up to an age of 9 days, and then remained more or less at the same level (Figure 2a; age effect on aggression: coefficient 0.025 ± 0.01 , $p = 0.0135$). In agreement with the increasing ag-

gression, the rate of successful adoptions under our present conditions decreased from 90% at age 3 to 0% when goslings were 27 days old (Figure 2b; age effect on adoption: coefficient -0.345 ± 0.08 , $p < 0.0001$). Family size was not related to the level of aggression that was directed towards the lone goslings nor to the likelihood of a successful adoption during the duration of the experiment (family size effect on aggression: coefficient 0.082 ± 0.05 , $p = 0.11$; family size effect on adoption: coefficient 0.030 ± 0.14 , $p = 0.84$). Although gosling age appeared to be the most important factor which influenced adoption willingness, there also seemed to be differences in the individual propensity of parents to adopt (χ^2 -test of 10 families which were tested in 2004: $\chi^2 = 16.5$, $df = 9$, $p = 0.06$). However, the only family which had not accepted goslings at age 3 in 2003, accepted a gosling in 2004. Unfortunately, the only family which did not accept a gosling in 2004 at age 3 had not been tested at that age in 2003.

Following distance

Six of the eight families who had received two adoptees at age 3 could be followed for five weeks. The other two had lost their goslings during the first week. There was no difference in distances from adopted or original goslings to either of the parents (Figure 3; factor 'adopted' for distance to male: coefficient 0.06 ± 0.08 , $p = 0.48$; factor 'adopted' for distance to female: coefficient 0.06 ± 0.07 , $p = 0.38$). Although events of brooding were excluded from the analysis, goslings were on average closer to the female than to the male (distance to male: 2.0 ± 0.15 goose lengths; distance to female 1.2 ± 0.04 goose lengths; paired T -test: $T_{93} = 7.89$, $p < 0.0001$).

While older goslings were slightly further away from the female than younger ones (factor 'age' for distance to female: coefficient 0.007 ± 0.003 , $p = 0.0361$), the distance of goslings to the male did not change with age (factor 'age' for distance to male: coefficient -0.005 ± 0.004 , $p = 0.27$). Between families, there were significant differences in how far goslings were away from the father (ANOVA, effect of family identity on distance to male: $F_{5,82} = 7.07$, $p < 0.0001$), while distances to the mother varied much less (ANOVA, effect of family identity on distance to female: $F_{5,82} = 2.22$, $p = 0.0599$).

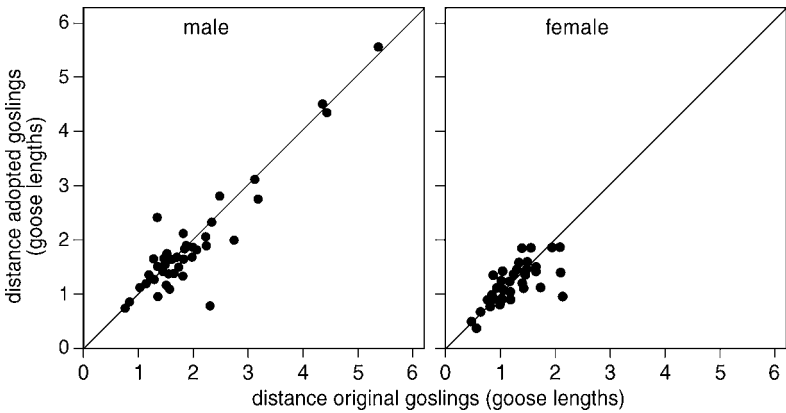


Figure 3. Average distances measured in goose lengths of adopted and original goslings to female and male parent during grazing. Incidences of brooding were not included, as these would bias distances towards the female parent. Adopted goslings were not further from the parents than original goslings, and all goslings were on average closer to the mother than to the father.

Discussion

Our results provide the first experimental evidence that lone goslings might choose foster families according to a characteristic which indicates quality. Goslings chose dominant families when given the choice between a dominant and a subordinate family. Being part of a dominant family could benefit a gosling through better access to resources as well as in the long-term through inheriting a higher social rank (Black & Owen, 1987; Mulder et al., 1995). If adoption would be a strategy of goslings to secure better parental care, the ability to discriminate between potential foster families before adoption on the basis of parental quality, would be hugely beneficial in order to avoid a lot of ‘trial and error’ by the gosling. Various authors have remarked that lone goslings usually have to endure attacks by families which they are trying to join, and that unsuccessful goslings disappear from the study area within a few days (Prevett & MacInnes, 1980; Choudhury et al., 1993; Larsson et al., 1995). However, these incidental records have to be interpreted with caution. In none of these studies goslings were marked individually and these observations were recorded as a side-effect of other observations. An unsuccessful adoption attempt, where aggression from the parents is involved, is much more likely to attract the attention of an observer than a successful adoption which happens without aggressive interactions.

Age-dependency of adoptions

From the parents' standpoint, we found that aggression towards lone goslings increased with gosling age, which went hand in hand with a decreased willingness to adopt. This supports the hypothesis that the main mechanism for adoptions is error in recognition from the parents point of view, and that with increasing precision of individual recognition and decreasing risk of rejecting one's own gosling, adoptions become less frequent (Eadie et al., 1988). However, the experimental results have to be treated with caution with respect to the potential success of adoptions in the wild. Although we found that aggression towards lone goslings increased with increasing gosling age, we cannot rule out that over time spans longer than 30 minutes, adoptions might still have occurred. Also, in our setup test goslings were taken from intact families, and this might have influenced their behaviour in seeking adoption. Although the captive geese are used to the presence of humans and were given time to adjust to the cages (which they also voluntarily visit during non-experimental times), the captive situation might have increased aggressive behaviour. Field observations from other studies support the decreasing occurrence of adoptions as goslings grow older (Prevett & MacInnes, 1980; Choudhury et al., 1993; Nastase & Sherry, 1997), although some authors have reported adoptions up until families left the brood rearing areas (Zicus, 1981; Williams, 1994). In our study we found no evidence that adoptions in greylag geese occurred at ages older than two weeks, neither during our experiments nor naturally on the field (pers. obs.).

While increased precision of individual recognition is a likely mechanism to explain the covariation of gosling age and decreased frequencies of adoptions (but see Williams, 1994), it remains difficult to explain the functional aspect of this pattern. If increasing brood size was costly to parents, one would expect that recognition mechanisms had developed which also allow accurate discrimination of own and foreign goslings at very young ages, particularly in colonial precocial species (Keller, 1997; Komdeur & Hatchwell, 1999). The age-dependent pattern might indicate that costs and benefits of increasing family size change in relation to gosling age. For example if goslings are most vulnerable to predation during the first week after hatching, both parents and adoptees might gain the largest benefits of predation dilution at young gosling ages. Predation dilution has been shown to be an important factor explaining crèche formations in ducks (Munro &

Bedard, 1977), although these crèches usually involve much larger numbers of offspring than adoptions in geese (e.g., Choudhury et al., 1993; Larsson et al., 1995). Also, the risk of rejecting your own gosling is likely to decrease with age, which might affect the benefit of adoption. On the other hand, empirical studies have shown that benefits of large families in geese act throughout brood rearing and in the wintering areas (reviewed in Kalmbach, in press). It remains puzzling that an increase of family size at a later age is so avidly rejected (this study; Prevett & MacInnes, 1980; Choudhury et al., 1993; Kalmbach, in press). An alternative explanation could be that in order to gain the (later) benefits of large broods, families have to work as a well co-ordinated unit. This might be much easier achieved if family members join at a young age, as the early phase is likely to be important for imprinting, social learning, establishing group coherence and group coordination (e.g., Black & Owen, 1987; CoussiKorbel & Fragaszy, 1995; Avital et al., 1998; Fritz et al., 2000). Because gosling age and individual recognition will always be confounded, it is difficult to separate the influences of these two factors on adoptions. In our analysis of spacing behaviour we could not detect any difference between original goslings and those adopted at 3 days old. An important question is whether complete integration is also achieved in later adoptions.

Are adoptions driven by the gosling?

In our study goslings chose dominant pairs as preferred foster families. Whether the actual dominance or number of won interactions were the trigger for the goslings' choice is not certain, however. Apart from dominance, we only measured body mass of adults as additional characteristic, which was not related to dominance and therefore not to the goslings' choice. Other characteristics which reflect parental status or quality and that are potentially related to dominance might have been used as a signal by the gosling, such as carotenoid based coloration of legs and bill or plumage characteristics and health etc. (Hill & Montgomerie, 1994; Petrie, 1994; Horak et al., 2001). It cannot be excluded that goslings might react to more subtle cues, such as differences in behaviour of goslings from dominant and subordinate pairs. In most natural goose populations which have been studied, dominance is correlated to brood size (Prevett & MacInnes, 1980; Zicus, 1981; Black & Owen, 1989a; Lepage et al., 1998; Loonen et al., 1999). In our experiment,

goslings were not able to choose between differently sized families, as all parents had three original goslings. However, since in natural populations family size is usually correlated with dominance status, brood size might be an easy way for a gosling to estimate dominance.

For altricial and semi-precocial bird species, it has been proposed that adoptions are driven by offspring which receive inadequate parental care from their own parents, and therefore seek adoption into another brood (Pierotti & Murphy, 1987; Redondo et al., 1995; Brown, 1998). Although we have shown that precocial goslings chose foster families according to a characteristic of family quality, in order to determine whether adoption represents an active strategy by goslings it will be crucial to determine the potential benefits of adoption to the gosling. Studies of the functional reasons, rather than the mechanisms of adoption, would be most meaningful with wild populations. The captive situation might influence social patterns, competition for food, and potentially also predation pressure (e.g., Lamprecht, 1986). As in other species, benefits are likely to vary with the state of the gosling prior to adoption, such as its condition, age, family size and dominance of the original family (Morris et al., 1991; Brown et al., 1995; Jouventin et al., 1995; Bize et al., 2003). This excludes goslings which have inadvertently lost their family, as adoption is the only (and adaptive) choice for them (Choudhury et al., 1993; Williams, 1994; Larsson et al., 1995). Our choice experiment mimicks that situation, as the goslings were 'orphaned' at the time of the experiment and did not have to make the decision to leave their own family. It still remains to be shown whether goslings actively leave their family to seek adoption in the wild.

Adoption as inter-generational conflict or mutualism?

In species where parents actively feed offspring, the adoption and subsequent feeding of extra offspring often results in increased costs and decreased reproductive output of the foster parents (Pierotti & Murphy, 1987; Morris et al., 1991; Brown et al., 1995; Redondo et al., 1995). Under such circumstances, adoption represents an intergenerational conflict, where young are trying to obtain foster care which adults should be selected to avoid giving (Pierotti, 1988; Brown, 1998). In geese and other precocial species however, where parental investment usually benefits all brood members simultaneously (unshared investment *sensu* Lazarus & Inglis, 1986), costs of caring for additional offspring are likely to be much lower. Most studies of

brood size in geese suggest neutrality or benefits of large broods to parents and goslings (Lessels, 1986; Black & Owen, 1989b; Gregoire & Ankney, 1990; Petersen, 1992; Seddon & Nudds, 1994; Lepage et al., 1998; Loonen et al., 1999). Rather than representing an inter-generational conflict, adoption in geese might be a mutually beneficial strategy (Williams, 1994), or by-product mutualism (Connor, 1995; Clutton-Brock, 2002), which is driven by the gosling but, at least at young ages, also beneficial to the parents. As for goslings, benefits for parents would be expected to vary with the initial state of the parents, such as dominance, family size or condition. Although our data suggests inter-family differences in the propensity to adopt, they were not explained by family size.

In this study we show that within a few days of hatching goslings possess the ability to choose adoption families in a way that could maximise benefits of adoption for the gosling, and that parents did not discriminate against adopted goslings. While recognition failure is the most likely mechanism to explain the strongly age-dependent parental willingness to adopt, it remains difficult to explain this pattern functionally, particularly given the empirical evidence for benefits of large broods. Clearly more studies, particularly experimental ones, are needed to understand the state-dependent costs and benefits of adoptions to goslings as well as parents.

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