Behav Ecol Sociobiol (1997) 40: 253–260

José L. Tella · Manuela G. Forero · José A. Donázar
Juan J. Negro · Fernando Hiraldo

Non-adaptive adoptions of nestlings in the colonial lesser kestrel: proximate causes and fitness consequences

Received: 3 May 1996 / Accepted after revision: 19 January 1997

Abstract We examined the causes, costs and benefits of adoption in the altricial lesser kestrel *Falco naumanni*. Specifically, we tested the intergenerational conflict hypothesis, proposed to explain adoption in some birds. Adoptions involved 76% of the nests and 51% of the nestlings at a mean age of 25 days (12 days before fledging). Nest-switching nestlings were not in poorer body condition, more parasitized or younger than their siblings, and body condition and prey delivery rates of their parents did not differ from those of other parents. In the foster nest, adopted nestlings did not benefit from higher feeding rates or a prolongation of the nestling period. They did not have fewer nest-mates or achieve higher rank within the new brood. Thus, adopted nestlings did not improve their body condition and survival. Adult lesser kestrels seemed unable to finely discriminate beween their own and alien chicks. Foster parents bore the cost of an increase of prey delivery rates, although it did not affect their survival or subsequent reproductive performance. Therefore, our results do not support the intergenerational conflict hypothesis, and suggest that adoption in this species is non-adaptive. Traditionally, the lesser kestrel bred in cliffs where movement among nest-sites was restricted. Nowadays, about half of the colonies are in tiled roofs which facilitate nest-switching by nestlings. The high rate of adoptions may thus be explained as reproductive errors associated with the recent occupation of a new breeding habitat.

Key words Adoptions · Intergenerational conflict · *Falco naumanni* · Offspring recognition · Parental care

J.L. Tella (✉) · M.G. Forero · J.A. Donázar · J.J. Negro · F. Hiraldo
Estación Biológica de Doñana (CSIC),
Avda Mª Luisa s.n.,
E-41013 Sevilla, Spain
Fax: 34 95 4621125; e-mail: Tella@cica.es

Introduction

The care of young by conspecifics other than their biological parents (i.e. alloparental care) has been reported in a number of birds and mammals (Riedman 1982). In birds, some nestlings leave their nests apparently to seek adoption by foster parents. Adoption of nestlings is relatively common in semiprecocial species such as colonial sea-birds (Graves and Whiten 1980; Pierotti 1988; Morris et al. 1991; Saino et al. 1994; Jouventin et al. 1995), while brood amalgamation often takes place in precocial species such as waterfowl (Eadie et al. 1988; Williams 1994; Larsson et al. 1995). In these species adoption usually occurs early in the development of the nestlings and young can receive alloparental care over extended periods (Pierotti 1988). In contrast, altricial and semialtricial nestlings need certain flying capabilities to abandon their nest; adoptions usually take place close to fledging and the period of alloparental care is comparatively short (Bustamante and Hiraldo 1990; Kenward et al. 1993; Ferrer 1993; Redondo et al. 1995).

Proximal factors thought to be responsible for nest-switching are sub-standard parental care (Pierotti and Murphy 1987; Saino et al. 1994; Brown et al. 1995) or harassment by nest-mates (Pierotti and Murphy 1987; Redondo et al. 1995). In either case, nest-switching nestlings are assumed to be disadvantaged and to derive benefits if they get better care and/or reduced aggression in the foster nest. However, it is not clear why parents tolerate and often feed nestlings that are not their own (Redondo et al. 1995). This has been explained as the result of reproductive errors (Roberts and Hatch 1994) or non-recognition of visitors as strangers (Poole 1982; Holley 1984, 1988; Pierotti 1991; Kenward et al. 1993), sometimes due to unusually high densities (Patterson et al. 1982; Holley 1984; Bustamante and Hiraldo 1990; Donázar and Ceballos 1990; Ferrer 1993).

The cost of rearing unrelated young is highly dependent on the developmental strategy of the species. In precocial birds, the cost to a foster parent can be neg-

ligible (Patterson et al. 1982; Eadie et al. 1988; Larsson et al. 1995), and a strong selective pressure towards the avoidance of adoptions is not expected (Redondo 1993). In contrast, in semiprecocial and altricial birds, a foster parent may incur reproductive costs, including death of its offspring (Bustamante and Hiraldo 1990; Brown et al. 1995). In species incurring costs, adoption may still be adaptive due to (1) kin-selection (Waltz 1981), (2) reciprocal altruism (Pierotti 1980, 1982, 1988) or (3) dilution of predation risk on their own offspring (Eadie et al. 1988).

One explanation for adoption is based on the "arms race" concept. According to the intergenerational conflict hypothesis of Pierotti and Murphy (1987), nestlings would be selected to abandon their natal nests when they receive deficient parental care. This, in turn, generates a selective pressure for the adults to discriminate against visiting nestlings. Nestlings can be expected to win this "arms race" because benefits for them (i.e. survival) are higher than the costs for the foster parents (i.e. partial fitness reduction). Furthermore, selection will act more strongly on traits expressed early on life (e.g., the trait promoting nest-switching in the stressed nestlings) (Pierotti 1991; Redondo et al. 1995). Recent studies have found that this arms race explained the fostering behaviour of some semi-precocial species (Morris et al. 1991; Saino et al. 1994; Brown et al. 1995), but not in precocial ones (Williams 1994; Larsson et al. 1995). In altricial species this hypothesis has only been properly tested – and supported – in the white stork (*Ciconia ciconia*) (Redondo et al. 1995).

In this study we examined the patterns, costs and benefits of adoption in the altricial lesser kestrel (*Falco naumanni*). This is a colonial falcon in which adoptions have been previously reported (Donázar et al. 1991). We tested the following predictions derived from the intergenerational conflict hypothesis (Pierotti and Murphy 1987): (1) adopted nestlings receive sub-standard parental care prior to nest-switching, (2) nestlings acquire a higher rank in the foster brood or receive better parental care than in their natal nests, and (3) adoptions are costly to the foster parents, which should discriminate against foreing nestlings. In addition, we examined the effects of adoptions on fitness, in terms of post-breeding survival of both adults and fledglings, and the subsequent reproductive performance of adults.

Methods

The study was conducted in Los Monegros (north-east Spain), a pseudo-steppe area where lesser kestrels breed exclusively on tiled roofs of abandoned rural constructions (Tella et al. 1996a). Observations were conducted in 1993 in the three largest colonies (34, 34 and 17 pairs, respectively), and in one colony in 1994 (33 pairs). Adoptions were monitored in all pairs breeding in nest-boxes, which had been installed under the roof of the buildings in 1990. Nest boxes have an outside opening and a rear one-way mirror and trap-door to check the content of the nests from the inside of the building to minimize disturbance. Successive inspections of the nest-boxes never provoked abandonment by the parents, nor nest-switching of nestlings after handling.

Nest-boxes were installed in hollows under the tiles where lesser kestrels had nested in previous years. Nest-boxes had no effect on: (1) nest site availability, because they simply substituted former natural hollows, (2) inter-nest distance, (3) levels of parasite infestation, and (4) breeding success (J.L. Tella, unpublished work). These results suggest that the installation of nest-boxes did not bias our results.

We monitored 42 (45%) of the 93 nests containing nestlings in the four colonies under study. Focal nests were visited every 6 days from laying until the first adoption was detected. Those nests produced 133 nestlings (45% of the nestlings produced in the four colonies, $n = 295$). During the first visit after hatching nestlings were ranked according to their relative size among brood-mates and individually marked with numbered cloth bands. At age 2 weeks post-hatching, cloth bands were replaced with metal and PVC bands. Starting with the first detected adoption in a colony, visits to all focal nests were conducted every 4 days until 8 days after the last focal nestling fledged.

For analytical purposes, the date when nest-switching occurred was taken to be the mid-point between the visit when the foreign nestling was first noticed in a strange nest and the previous visit. A nestling was considered adopted only if it had been observed in a foster nest in at least two consecutive visits. The length of the eighth primary feather of the nestlings was used to estimate their hatching date and age (Donázar et al. 1991). Fledging date for each nestling was estimated by nest monitoring. Given that duration of parental care after fledging is short for lesser kestrels (5 days on average; Bustamante and Negro 1994), it was not considered in this study. During each nest inspection, all nestlings present were identified, and their body mass and length of the eighth primary feather were recorded. We also systematically counted the number of the two main ectoparasites of lesser kestrel nestlings (*Carnus hemapterus* and *Ornitophila gestroi*; Tella 1996). When we found banded non-focal nestlings in focal nests we also checked their nest of origin and took the same information as in the focal nests. At the focal colonies, 169 adult kestrels were trapped in their nests and banded with PVC bands. Body condition was calculated as the residuals from the regression of body mass on the cube of a measurement of body size (Potti 1993; Mateos and Carranza 1996; Blanco and Tella in press). We used wing length for adults, and the length of the eighth primary feather for nestlings, the best estimators of body size for the lesser kestrel according to Tella (1996). Due to seasonal and yearly changes in adult body mass, we obtained the residuals after controlling for capture date and year with two-way ANOVAs (Tella et al. 1997). Young were sexed according to plumage characteristics (Tella et al. 1996b).

Behavioural observations were conducted in all nests in the main colony using spotting scopes from a distance of 100 m, during 363 h/nest before the first adoption and during 555 thereafter until all nestlings fledged, over a total of 11 days in 1993 and 26 days in 1994. Surveys were done in two daily periods (0800–1200 hours and 1700–2100 hours), coinciding with the maximum activity of lesser kestrels. We observed about 15 nests simultaneously in each survey, and covered the whole colony every two consecutive surveys. We identified adult and nestlings by their band numbers, and recorded instances and the apparent causes of nest-switching of nestlings, as well as prey deliveries and aggression.

The quality of parental care, as well as the costs and benefits of adoptions were examined using the following variables: (1) feeding rates (prey deliveries/h) 2 days before and 2 days after adoptions took place, in both natal and foster nests of the adoptees; (2) body condition of parents and nestlings; (3) brood size and rank of the adopted nestling in both its natal and foster nests; (4) gender of nestlings; (5) prevalence – percentage of infected nestlings – and intensity – number of parasites by infected nestling – of ectoparasites; (6) survival of nestlings until fledging. Long-term fitness effects of adoptions for foster parents were examined through post-breeding survival and reproductive success the following year. Since lesser kestrels are highly philopatric, both adult and fledging survival were estimated by considering those birds not resighted in

subsequent years in the study area as dead (Tella et al. 1997). Accordingly, we searched banded birds in all 70 colonies in the population in 1994 and 1995, from February to August. Breeding success (clutch size and number of fledgings) of adults surviving until the next year was recorded in 1994 and 1995. For the analyses, we included focal birds as well as other adopted nestlings originated from non-focal nests. All variables were assessed for possible differences among years and colonies. Since no differences were found, we pooled data for further analyses.

Results

Frequency of adoptions

Of 133 focal nestlings 68 (51.35%) switched nests. Considering all nestlings in the study colonies, the proportion of male (24.45%, $n = 147$) and female (25.18%, $n = 139$) nestlings that switched nests did not differ significantly ($\chi^2 = 0.42$, $df = 1, P = 0.52$). Adoptions occurred when the nest-switching nestlings were 25 days old on average (SD = 4.48, range = 16–33 days, $n = 68$). The duration of foster care was about 12 days (i.e. about one-third of the nestling stage; Bustamante and Negro 1994).

Of the 68 nestlings that switched nests, 42 (62%) completed growth and fledged from their foster nest, 21 (31%) switched to a second foster nest from which they fledged, and 5 (7%) eventually returned to their natal nests. Adoptions affected 32 (76%) of the 42 focal nests. Ten pairs (23.8%) adopted nestlings, 5 (11.9%) had a nestling that moved to another nest, and 17 (40.5%) both produced nest-switching nestlings and adopted others. The number of nestlings adopted in each foster nest ranged from one to ten (Fig. 1). However, the mean number of adoptees simultaneously present in a given nest was low and similar in all of them (1.4 ± 0.7, $n = 27$ nests). The duration of the period of adoption was also comparable in most nests (10 ± 5.1 days, $n = 27$ nests).

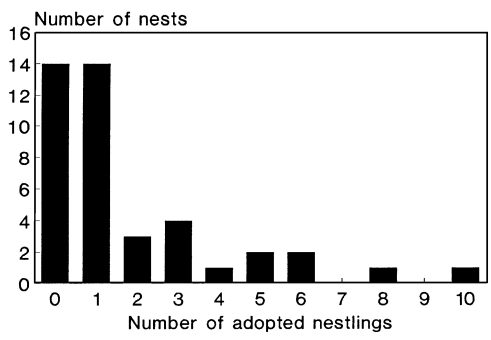

Fig. 1 Number of adopted nestlings in each lesser kestrel nest ($n = 42$ nests). All adopted nestlings were not always present at the same time

Proximal factors inducing nest-switching

On roofs, nestlings are able to leave the nest, walk over the roof and potentially switch nests. Actual nest-switching was observed for 21 nestlings; 20 were adopted and the remaining 1 returned to its natal nest. The main cause inducing adoptions was the nestlings following non-parent adults delivering prey. During the last 15 days of the nestling period, we recorded 917 feedings outside the nest boxes. On 160 (17.4%) of these occasions alien nestlings approached the adult delivering prey, 37 (4%) pirated food, 9 (0.9%) entered foster nests and were adopted, and only one was mobbed away by adults. Seven adoptions started when nestlings outside their natal nests were attacked by adults and rushed to shelter in other nests. Another nestling rushed in panic to a new nest when a peregrine falcon (*Falco peregrinus*) attacked a stock dove (*Columba oenas*) on the same roof. Three nestlings left their natal nests and inspected new ones, where they were adopted. No adults or predators were present in these three cases.

In 48 nests where the identity of both parents was known, there was no adult mortality before the nestling had abandoned the nest. Before nest-switching, the body condition of the parents of adoptees did not differ from that of parents whose nestlings did not move; feeding rates did not differ between nests abandoned by nestlings and others where all nestlings stayed (Table 1). In addition, nest-switching nestlings were not in poorer body condition than their siblings (Table 2); 15 (47%) of 32 nest-switching nestlings were in better condition than the mean of their siblings. There was no tendency for the smallest (i.e. lowest rank) nestling in a brood to leave the nest. On the contrary, in only 19 cases was it the youngest nestling that moved (27.9%), versus 49 occasions on which an older nestling moved.

We were unable to determine whether sibling aggression triggered nest-switching in the lesser kestrel. However, several factors make this unlikely. The occurrence of nest-switching is independent of both brood size in the natal nest, and rank of the switching nestling. Flying exercises are also unlikely causes of nest-switching since most nestlings were too young to perform exercises when they switched nests.

Table 1 Body condition of the parents and feeding rates (number of feedings/h) before adoptions in **A** nests with nest-switching nestlings, **B** nests without nest-switching nestlings. Values are mean ± SD

	A	B	Test
Body cond. of males	1.13 ± 5.07 ($n = 18$)	0.14 ± 4.22 ($n = 15$)	ANOVA $F = 0.56$, $P = 0.47$
Body cond. of females	-1.02 ± 3.55 ($n = 16$)	0.36 ± 2.08 ($n = 19$)	ANOVA $F = 0.18$, $P = 0.68$
Feeding rates	2.79 ± 1.38 ($n = 21$)	2.49 ± 1.17 ($n = 12$)	*U*-test $Z = -0.56$, $P = 0.57$

Table 2 Body condition and parasite load in nest-switching nestlings (**A**) and their siblings (**B**) 2 days before departure. Prevalence refers to the percentage of infected nestlings, and intensity to the number of ectoparasites by infected nestling. Values are mean ± SD or percentage

	A	B	Test
Body Cond.	1.01 ± 15.70 ($n = 32$)	-1.35 ± 15.39 ($n = 32$)	Wilcoxon test $Z = -0.23$, $P = 0.81$
Prevalence *C. hemapterus*	8.06% ($n = 62$)	12.29% ($n = 122$)	$\chi^2 = 0.76$, $P = 0.38$
Intensity *C. hemapterus*	4.40 ± 3.49 ($n = 5$)	2.20 ± 1.33 ($n = 15$)	*U*-test $Z = -1.30$, $P = 0.19$
Prevalence *O. gestroi*	12.90% ($n = 62$)	15.57% ($n = 122$)	$\chi^2 = 0.23$, $P = 0.63$
Intensity *O. gestroi*	1.12 ± 0.33 ($n = 8$)	1.26 ± 0.44 ($n = 19$)	*U*-test $Z = 0.74$, $P = 0.46$

Another reason to move might be that nest-switching nestlings were suffering from higher ectoparasitic infestations than their siblings. However, the prevalence and intensity of the two main haematophagous ectoparasites were low and no differences were found between nestlings that moved and those that did not (Table 2).

Benefits for a moving nestling in the foster nest

The adopted nestling may benefit by improved food provisioning in at least three ways: (1) obtaining a higher feeding rate; (2) prolonging its nestling stage by joining a less-developed brood; (3) obtaining a higher rank in the foster brood. In all cases, an improvement in body condition and survival is expected.

The duration of the nestling stage in nests with adoptees (35.4 ± 4.7 days, range 23–43, $n = 27$) did not differ from that in nests with no adopted nestlings (34.7 ± 6.1 days, range 26–44, $n = 9$) ($U = -0.40$, $P = 0.68$). Moreover, 20 nestlings moved to nests where their nestling period was actually shorter than that of their siblings in the natal nest, 14 had a nestling period of a similar length, and only 10 had a longer nestling period (Sign test, $Z = 1.20$, $P = 0.23$, $n = 43$).

Only 24 (44.4%) nest-switching nestlings moved to foster nests which, two days before the adoption occurred, showed higher feeding rates than their natal nests; in 19 (35.2%) nests, feedings were lower and in 11 (20.4%) nests were equal. (Sign test, $Z = 0.91$, $P = 0.36$, $n = 54$). After adoptions took place, provisioning rates in foster nests (3.89 ± 3.93 prey/h, $n = 39$) were not significantly higher than in the natal nests of the adoptees (3.57 ± 3.02 prey/h, $n = 39$) (Sign test $Z = 0$, $P = 1$, $n = 39$). Regarding the new rank of the adoptee in the foster brood, only 12 (22%) nestlings were adopted in nests with fewer nest-mates, 32 (58%) gained more nest mates and 11 (20%) were adopted in brood of the same size. Additionally, 18 (28%) out of 64 lowered their previous rank in the foster brood, 18 (28%) kept the same rank, and 28 (43%) achieved a higher rank (Sign test, $Z = 0.44$, $P = 0.66$, $n = 63$).

On average, adopted nestlings did not improve their body condition in their foster nests. On the contrary, two days after the adoption started, 19 (70%) adopted nestlings were in poorer condition and only 8 (30%) were in better condition than their siblings remaining in their natal nests (Wilcoxon test, $Z = 2.56$, $P = 0.01$). Nonetheless, nestling survival did not differ between adopted and non-adopted nestlings ($\chi^2 = 0$, $df = 1$, $P = 1$, $n = 184$), nor their survival until the next breeding season ($\chi^2 = 0.81$, $df = 1$, $P = 0.37$, $n = 166$) (Fig. 2).

Immediate costs of nest-switching for the moving nestling

Adult lesser kestrels may steal nestlings and practise cannibalism (Negro et al. 1993); and thus they can potentially inflict serious injuries on intruder nestlings. Of 917 observed visits of adults to their nests while foreign nestlings were nearby, the adults attacked foreign nestlings 94 (10.2%) times. However, no injuries were detected.

Nest-switching nestlings are also exposed to predators when they walk over the roofs. Although we have not recorded predation attempts during our observations in focal colonies, up to 17 avian species prey upon nestling and fledgling lesser kestrels in this population (Tella et al. 1996a; Blanco and Tella, in press).

Offspring recognition

We observed 16 male and 15 female parents of nest-switching nestlings feeding their offspring in their new

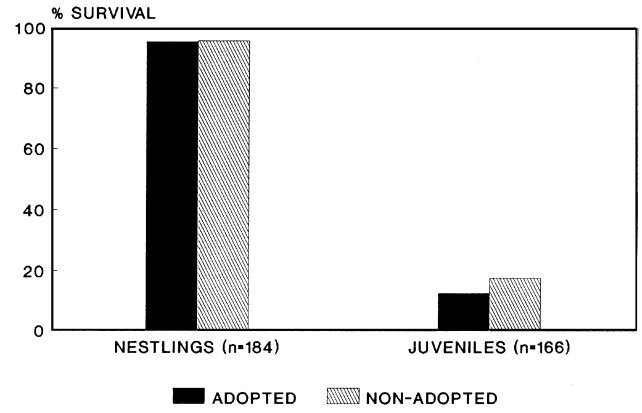

Fig. 2 Survival of adopted and non-adopted nestlings until fledging, as well as that of the survivors (juveniles) until the subsequent breeding season

adoptive nests. Two males and two females were observed feeding their nestlings when they fell from the roof to the ground and stayed there for some days. These qualitative observations suggest some degree of individual nestling recognition independent of circumstantial cues such as nest-hole recognition. However, at least 11 males and 13 females also fed alien nestlings when they apparently tried to feed their own nestlings in foster nests (61.6% of 171 feedings), and attacked their own offspring 30 times (17.6% of feedings, $n = 171$). Similarly, the parents occasionally attacked their own offspring (10.8% of 485 feedings) when they were outside the nest. On the other hand, when alien nestlings were inside their foster nests during feedings ($n = 82$ feedings by 13 males and 10 females) they were never attacked by foster parents.

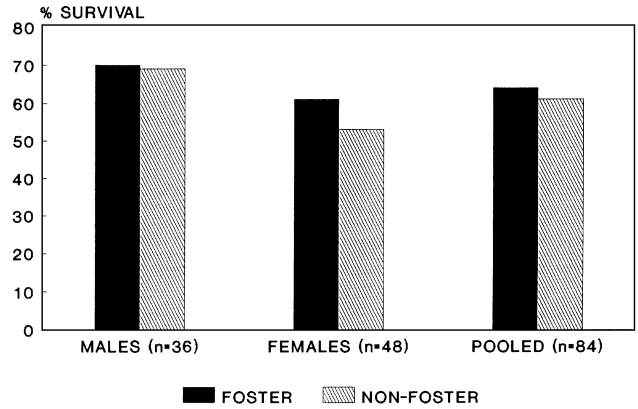

Fig. 3 Post-breeding survival of foster and non-foster parents until the subsequent breeding season

Costs for the foster parents

The brood size of abandoned nests before adoptions, (3.31 ± 1.27 nestlings, $n = 55$) was similar to that of nests with adopted nestlings (3.32 ± 1.86, $n = 66$) ($U = 0.05$, $P = 0.96$). Although some nests both lost and received nestlings (see above), this interchange resulted in fewer nestlings in natal nests (2.24 ± 2.26, $n = 45$) than in the receiving ones (4.45 ± 2.40, $n = 69$) ($U = 4.89$, $P = < 0.0001$). As a consequence, feeding rates generally increased in a higher proportion when an adoption took place ($+1.49 \pm 3.82$ feedings/h, $n = 24$) compared to nests where the number of nestlings remained constant ($+0.45 \pm 1.67$ feedings/h, $n = 27$), while feedings diminished after a nestling left (-0.90 ± 2.45 feedings/h, $n = 31$) (Kruskal-Wallis test, $Z = 10.85$, $P = 0.004$). These relative changes of feeding rates were closely related to the changes in brood size ($r_s = 0.40$, $P = 0.0003$, $n = 83$) as a result of nest-switching of nestlings.

The increased parental effort did not seem to affect the post-breeding survival of parents, which was the same for both foster and non-foster parents (males: $\chi^2 = 0.01$, $df = 1$, $P = 0.93$, $n = 36$ females; $\chi^2 = 0.31$, $df = 1$, $P = 0.57$, $n = 48$; pooled: $\chi^2 = 0.14$, $df = 1$, $P = 0.79$, $n = 84$) (Fig. 3). Furthermore, the breeding success of surviving foster adults the following year did not differ from that of surviving non-foster adults (Table 3).

Discussion

A nestling is expected to leave its natal nest and stay in a foster nest only if the obtained benefits exceed the costs. In the lesser kestrel, the potential costs involved in nest-switching were an increased risk of predation during moving and initial mild aggression by the foster parents. The potential benefits were not apparent; nestlings did not move to nests with lower brood size, not did they obtain a higher rank, extended parental care or higher survival in the new nest.

If adoptees did not receive improved parental care, why did they move? Adopted nestlings seemed to reach their foster nests in a fortuitous way. Nestling lesser kestrels usually rush to the opening of their nests when the parents deliver prey. Most observed adoptions started during feedings, when neighbouring nestlings attempted to steal prey. Rushing at the adults is a common behaviour in fledgling falconiforms (Poole 1982; Kenward et al. 1993; Donázar and Ceballos 1990). Other nestlings moved to foster nests as a result of attacks from adult kestrels or predators. The adopted nestlings may not have returned to their natal nests because they did not know the way back or because it would mean re-exposure to attacks and predation. In fact, the five nestlings that did return to their natal nests were in foster nests that were closer to their original nests (52 ± 33.3 cm, $n = 5$) than nestlings who did not return (109.8 ± 66.6 cm, $n = 32$) ($U = -2.17$, $P = 0.029$).

Even though adopted nestlings did not derive obvious benefits from adoption, an increase in their inclusive fitness could still be possible. The abandonment of their natal nests, with the subsequent brood reduction, would permit an improvement in the condition and survival of their parents and siblings (Dijkstra et al. 1990). However, the survival of the adults in nests where adopted nestlings originated did not differ significantly from that of adults in nests that had no brood reduction, and was no higher than that of foster adults with increased

Table 3 Breeding performance of fostering and non-fostering adults in the subsequent breeding season

	Fostering adults	Non-fostering adults	*U*-test
Clutch size	4.33 ± 0.97 ($n = 15$)	4.37 ± 1.30 ($n = 8$)	$Z = 0.00$ $P = 1.0$
Fledglings	2.28 ± 0.93 ($n = 25$)	2.25 ± 0.96 ($n = 12$)	$Z = 0.15$ $P = 0.88$

broods ($\chi^2 = 0.15$, $df = 2$, $P = 0.93$). Mortality of nestlings until fledging was negligible (< 5%) for both adopted and non-adopted nestlings. In sum, indirect kin-selected benefits were not a likely ultimate cause for the adoptions we observed.

The question that remains is why foster adults tolerated alien young. Adults that fostered alien nestlings had to provision an enlarged brood during a relatively long period, potentially affecting the survival of foster parents (Dijkstra et al. 1990; but see Korpimäki and Rita, in press). Nonetheless, the increase in feeding rates may be partially due to the true parents of the adopted nestlings feeding them along with the foster parents. Other unmeasured negative fitness effects might occur for the foster parents, such as immune system depression and a rise in parasite loads (Sheldon and Verhulst 1996). However, if they do occur, these effects must be subtle because the survival of foster parents was not reduced in the following year compared to other adults. A reduction of future reproductive output (Dijkstra et al. 1990) is not expected, since the breeding success of foster parents in the year following that of adoption was the same as that of other parents.

The high rate of nestling adoptions found in the lesser kestrel can hardly be explained in terms of the intergenerational conflict hypothesis (Pierotti and Murphy 1987). Even though there were no apparent long-term costs for the foster parents, there were no obvious benefits for the moving nestling. The situation that we observed in the lesser kestrel may be explained by one of the following hypotheses:

1. Adoptions occur because foster parents would obtain benefits in terms of dilution of predation risk on their own offspring (Eadie et al. 1988). However, this hypothesis is unlikely because predation occurs mainly in early breeding stages, affecting complete broods (authors, unpublished work).

2. Adoptions might have developed in a context of high inbreeding. Adults would derive indirect benefits from adopting related nestlings (i.e. through kin selection). Lesser kestrels are extremely philopatric and the population in Monegros is relatively isolated (authors, unpublished work). In addition, if kestrels engaged in extra-pair copulations or if nest parasitism through egg dumping occurred, foster parents could enhance direct fitness by adopting their own offspring (Saino et al. 1994). However, a concurrent study using DNA fingerprinting revealed a low incidence of extra-pair fertilizations (3.4%) and brood parasitism (7.4%) in the same colonies (Negro et al. 1996). The probability of adopting a closely related nestling were thus very low. In addition, the same study showed large inter-individual genetic differences. Thus, high inbreeding is unlikely (Kuhnlein et al. 1990).

In any case, it is not clear why an adult should incur any costs in helping any young that does not appear to need that help. The same reasoning may be used to discount the occurrence of reciprocal altruism. Although mutual exchange of nestlings was observed (10.5%), and even if this occurs in different breeding seasons, the absence of clear benefits for the moving nestlings makes the existence of this mechanism unlikely.

3. Adoptions are successful because lesser kestrels have not developed a fine-tuned kin-recognition mechanism. In species where the risk of alloparental care is high, mechanisms to discriminate and expel intruders are usually well developed (Redondo 1993). Species phylogenetically related to the lesser kestrel are solitary and only use circumstantial cues (through the presence of offspring inside the nest hole) to recognize their kin (Dijkstra et al. 1990; Wiebe and Bortolotti 1994; Korpimäki and Rita in press). This also seems to occur in some colonial species where the risk of adoption is low due to the relative isolation of nests, such as the cliff-nesting kittiwake (*Rissa trydactila*) (Roberts and Hatch 1994). In this context, a negative response by the adults would be maladaptive due to the potentially high cost (Beecher et al. 1991; Redondo 1993). After all, even a very discriminting adult still risks mistakenly expelling or injuring one of their own nestlings (Knudsen and Evans 1986; Hébert 1988).

Before the existence of towns and villages, lesser kestrels may have nested in cliffs. However, at present only 4% of the Spanish colonies are in cliffs. The remaining colonies are found in human constructions, 50% in wall holes and 44.8% on roofs (González and Merino 1990). Building walls are similar to cliffs in the sense that nests are not usually in contact (Negro and Hiraldo 1993). In these colonies nest-switching is mainly limited to the fledging period and adoptions are not frequent (Donázar et al. 1991; authors, unpublished work). However, in colonies located on tiled roofs the young can easily walk between nests and engage in adoptions at an early age. It is not known for how long the lesser kestrel has been breeding on tiled roofs, but in the evolutionary history of this species, nesting in human dwellings is certainly a recent event.

To conclude, we believe that the high rate of non-adaptive adoptions of lesser kestrels resulted from reproductive errors related to the evolutionarily recent occupation of a new substratum for breeding. In this context, proximal factors causing nest-switching arise from the tendency of any young raptor to solicit food from adults passing close to their nests, as well as a tendency to run to any available hole to avoid conspecific attacks or predation. It would be difficult for adults to evolve response to adoption, because of the costs of misidentification of kin. As a balance between the risk of adoption and of rejection of kin, selection should favour acceptance by lesser kestrels of all nestlings that are in the nest due to the low cost of rearing alien nestlings.

Unless new selective pressures appear non-adaptive adoptions will persist. However, if the species suffered chronic food stress, costs for foster parents would increase and they would be expected to develop finer offspring recognition systems. On the other hand, there would be selection for chicks to seek better parental care. In this hypothetical scenario an arms race may

develop fitting the intergenerational conflict hypothesis. The fact that this conflict occurs in some species but not others could be related to the particular stage of their evolutionary histories at the time they were studied. It is possible that the current adoptive behaviour of some species is ultimately derived from changes in food or breeding substratum availability promoting nest-site clumping.

Acknowledgements We thank R. López, M. Villarroel, I. Sánchez, I. Bisson, Y. Menor, A. Riba, O. Ceballos, G. Blanco and M. Pomarol for their help with the field work. T. Redondo and R. Simmons made many helpful comments, and I. Bustamante helped with the English translation. K.M. Brown critically reviewed the manuscript and improved it substantially. This study was financed by the CICYT PB 90–1021 project. Logistic support was also provided by the D.G.A.; we thank M. Cabrera for her help. J.L.T. was in receipt of an FPI predoctoral grant from the M.E.C.

References

Beecher MD, Beecher IM, Lumpkin S (1981) Parent-offspring recognition in bank swallows (*Riparia riparia*). I. Natural history. Anim Behav 29:86–94

Blanco G, Tella JL (in press) Protective association and breeding advantages of choughs nesting in lesser kestrel colonies. Anim Behav

Brown KM, Woulfe M, Morris RD (1995) Patterns of adoption in ring-billed gulls: who is really winning the inter-generational conflict? Anim Behav 49:321–331

Bustamante J, Hiraldo F (1990) Adoptions of fledglings by black and red kites. Anim Behav 39:804–806

Bustamante J, Negro JJ (1994) The post-fledging dependence period of the lesser kestrel (*Falco naumanni*) in southwestern Spain. J Raptor Res 28:158–163

Dijkstra C, Bult A, Bijlsma S, Daan S, Meijer T, Zijlstra M (1990) Brood size manipulations in the kestrel (*Falco tinnunculus*). J Anim Ecol 59:269–285

Donázar JA, Ceballos O (1990) Acquisition of food by fledgling Egyptian vultures *Neophron percnopterus* by nest-switching and acceptance by foster parents. Ibis 132:603–607

Donázar JA, Negro JJ, Hiraldo F (1991) A note on the adoption of alien young by lesser kestrels *Falco naumanni*. Ardea 79:443–444

Eadie J McA, Kehoe FP, Nudds TD (1988) Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. Can J Zool 66:1709–1721

Ferrer M (1993) Natural adoption of fledglings by Spanish imperial eagles *Aquila adalberti*. J Ornithol 134:335–337

González JL, Merino M (1990) El cernícalo primilla (*Falco naumanni*) en la Península Ibérica. Serie Técnica, ICONA, Madrid

Graves JA, Whiten A (1980) Adoption of strange nestlings by herring gulls, *Larus argentatus* L. Z Tierpsychol 54:267–278

Hébert PN (1988) Adoption behaviour in gulls: a new hypothesis. Ibis 130:216–220

Holley AJF (1984) Adoption, parent – nestling recognition and maladaptation in the herring gull *Larus argentatus*. Z Tierpsychol 64:9–14

Holley AJF (1988) Intergenerational conflict in gulls. Anim Behav 36:619–620

Jouventin P, Barbraud C, Rubin M (1995) Adoption in the emperor penguin, *Aptenodytes forsteri*. Anim Behav 50:1023–1229

Kenward RE, Marcström V, Karlbom M (1993) Post-nestling behaviour in goshawks, *Accipiter gentilis*: Sex differences in sociality and nest-switching. Anim Behav 46:371–378

Knudsen B, Evans RM (1986) Parent-young recognition in herring gulls (*Larus argentatus*). Anim Behav 34:77–80

Korpimäki E, Rita H (in press) Effects of brood size manipulations on offspring and parental survival in the European kestrel under fluctuating food conditions. Ecoscience

Kuhnlein U, Zadworny D, Dawe Y, Fairfull RW, Gavora, JS (1990) Assessment of inbreeding by DNA fingerprinting: development of a calibration curve using defined strains of nestlingens. Genetics 125:161–165

Larsson K, Tegelström H, Forslund P (1995) Intraspecific nest parasitism and adoption in the barnacle goose: effects on survival and reproductive performance. Anim Behav 50:1349–1360

Mateos C, Carranza J (1996) On the intersexual selection for spurs in the ring-necked pheasant. Behav Ecol 7:362–369

Morris RD, Woulfe M, Wichert GD (1991) Hatching asynchrony, nestling care, and adoption in the common tern: can disadvantaged nestlings win?. Can J Zool 69:661–668

Negro JJ, Hiraldo F (1993) Nest-site selection and breeding success in the lesser kestrel *Falco naumanni*. Bird Study 40:115–119

Negro JJ, Donázar JA, Hiraldo F (1993) Kleptoparasitism and cannibalism in a colony of lesser kestrels (*Falco naumanni*). J Raptor Res 26:225–228

Negro JJ, Villarroel M, Tella JL, Kuhnlein U, Hiraldo F, Donázar JA, Bird DM (1996) DNA fingerprinting reveals a low incidence of extra-pair fertilizations in the lesser kestrel. Anim Behav 51:935–943

Patterson IJ, Gilboa A, Tozer DJ (1982) Rearing other peoples' young: brood mixing in the shelduck *Tadorna tadorna*. Anim Behav 30:199–202

Pierotti R (1980) Spite and altruism in gulls. Am Nat 115:290–300

Pierotti R (1982) Spite, altruism, and semantics: a reply to Waltz. Am Nat 119:116–120

Pierotti R (1988) Intergenerational conflicts in species of birds with precocial offspring. Proc Int Ornithol Congr 19:1265–1274

Pierotti R (1991) Infanticide versus adoption: an intergenerational conflict. Am Nat 138:1140–1158

Pierotti R, Murphy EC (1987) Intergenerational conflicts in gulls. Anim Behav 35:435–444

Poole A (1982) Breeding ospreys feed fledglings that are not their own. Auk 99:781–784

Potti J (1993) Environmental, ontogenic, and genetic variation in egg size of pied flycatchers. Can J Zool 71:1534–1542

Redondo T (1993) Exploitation of host mechanisms for parental care by avian brood parasites. Etología 3:235–297

Redondo T, Tortosa FS, Arias de Reyna L (1995) Nest-switching and alloparental care in colonial white storks. Anim Behav 49:1097–1110

Riedman ML (1982) The evolution of alloparental care and adoption in mammals and birds. Q Rev Biol 57:405–435

Roberts BD, Hatch SA (1994) Nestling movements and adoption in a colony of black-legged kittiwakes. Wilson Bull 106:289–298

Saino N, Fasola M, Crocicchia E (1994) Adoption in Little and Common Terns (Aves; Sternidae): Nestling benefits and parent's fitness costs. Ethology 97:294–309

Sheldon BC, Verhulst S (1996) Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. Trends Ecol Evol 11:317–321

Tella JL (1996) Condicionantes ecológicos, costes y beneficios asociados a la colonialidad en el cernícalo primilla. PhD thesis, University of Barcelona, Spain

Tella JL, Negro JJ, Donázar JA, Hiraldo F (1996a) Costs and benefits of urban nesting in the Lesser Kestrel (*Falco naumanni*). In: Bird DM, Varland DE, Negro JJ (eds) Raptors in human landscapes. Academic Press, London, pp 53–60

Tella JL, Donázar JA, Negro JJ, Hiraldo F (1996b) Seasonal and interannual variations in the sex-ratio of lesser kestrel *Falco naumanni* broods. Ibis 138:342–345

Tella JL, Forero MG, Donázar JA, Hiraldo F (1997) Is the expression of male traits in female lesser kestrels related to sexual selection? Ethology 103:72–81

Waltz EC (1981) Reciprocal altruism and spite in gulls: a comment. Am Nat 118:588–592

Wiebe KL, Bortolotti GR (1994) Energetic efficiency of reproduction: the benefits of asynchronous hatching for American kestrels. J Anim Ecol 63:551–560

Williams TD (1994) Adoption in a precocial species, the lesser snow goose: intergenerational conflict, altruism or a mutually beneficial strategy? Anim Behav 47:101–107

Communicated by M.A. Elgar