ORNIS SVECICA 9:155–160, 1999

Nest-leaving in the Starling *Sturnus vulgaris*: an example of parent-offspring conflict?

ULF OTTOSSON

Abstract

It has been suggested that there will be a conflict not only between parent-offspring but also between siblings, about when to leave the nest. To investigate which part of the family initiates nest-leaving Starling nestboxes, with individually marked nestlings, were observed prior to, during and after nestlings had started to leave the nest. Parents may initiate nest-leaving by deacreasing the provisioning rate. It is suggested that the time of fledging is determined by sibling competion and the trade off between the possibility to be fed inside the nestbox or outside.

Ulf Ottosson, Department of Animal Ecology, Lund University, S-223 62 Lund, Sweden
Present address: 88, rue des Eglantiers, L-1457 Luxemburg
e-mail:ottosson@village.uunet.lu.se

Received 13 July 1999, Accepted 18 August 1999, Editor: S. Svensson

An early major decision for a juvenile bird to make is when to leave the nest. What makes them interested in leaving the comfort and security in a nest? Do nestlings initiate nest-leaving themselves or do parents try to force them out, e.g. by reducing feeding frequency (Trivers 1974, Davies 1976)? The timing of nest-leaving has been suggested to depend on the outcome of a conflict of interest between parents and their young about the time spent in the nest (Trivers 1985). But, since altricial bird nestlings will continue to be dependent on parental investment for at least another 10–12 days after they leave the nest, it may be logically wrong to suggest such a conflict. The time of nest-leaving may instead be a result of sibling competition over parental provisioning, which is an offspring-offspring conflict, that force nestlings to leave the nest to increase their possibility to be fed, despite a possibly higher risk of predation. Instead of waiting in the nest, a nestling can approach and follow the parents in an effort to increase its chances of monopolising delivered food. In this context the order of nest-leaving is of special interest, and this has been subject of discussion (Lemel 1989, Nilsson 1990, Nilsson & Svensson 1993). It has been argued that for birds breeding in nest-boxes it will be a subdominant nestling in less good condition that will leave first (Lemel 1989). In the nestbox the largest nestling will monopolise the feedings in the entrance hole and the only way for the other nestlings to be fed is to leave the nestbox. Several studies have actually shown that dominant nestlings have succeeded in monopolising feedings (e.g. Bengtsson & Rydén 1983, Gottlander 1987, Forbes & Ankney 1987, Kacelnik et al. 1995).

By observing Starling nests before and during nest leaving, I obtained information about the nest leaving process to elucidate the factors that determine this process.

Material and methods

This study was conducted in the Revinge area, 20 km east of Lund, southern Sweden. In this area some 500 nest-boxes are erected in tree rows in colonies of 15 or 40 nest-boxes. In this particular study individual nest-boxes from several of these colonies were included. Nest-boxes were chosen so that prior activities did not conflict with the aim of this study.

When nestlings were 14 days old they were ringed, weighed to nearest 0.5 gram with a Pesola spring balance and had their right tarsus measured with a calliper to nearest 0.05 mm. Further, each nestling was individually colour marked on its forehead with a small spot of non-poisonous acrylic-paint. Nest-

lings were size-ranked within broods both on tarsus and mass. To overcome the problem with different clutch sizes these ranks were transformed to fractional ranks by dividing the absolute ranks with clutch size+1, and the same was made for the nest-leaving order.

From two to four days before the expected fledging day (day 20), a total of 33 nests were observed, 9 in 1992 and 24 in 1993, during a total of 124 hours. The provisioning procedure was studied and registered either from a blind or with help of camcorders between one and three hours per day until fledging. In this late stage of the nestling period, one nestling is more or less constantly occupying the nest entrance and almost all feedings occur in the hole with the parent sitting on the outside of the nestbox. With the help of the individual colour marks on their forehead it was easy to determine which nestling occupied the entrance hole and who was fed. During an observation period we registered at what time a nestling started to occupy the entrance hole, when it disappeared from the hole and if fed, when and by which parent. We included only feeding frequencies obtained during observation periods longer than 15 minutes and feeding frequencies were corrected to that expected at 07 00 hours using linear regression, according to data from Sandell et al. (1996).

Nest-leaving order was also obtained by repeated visits to these and about 15 other nestboxes during the nest-leaving period. During these visits the number and identity of nestlings left were registered. When visiting nestboxes the observer did not touch the nestling to avoid disturbance that could cause premature fledging. Jump order was transformed to fractional jump rank in same way as the size ranks (see above).

Statistical analysis was made in SYSTAT (Wilkinson 1992). A p-value of less than 0.05 was considered significant.

Result

Time in the nest

In most nests nestlings started to fledge 21 days from hatching of the first egg (range 18 to 23; Figure 1) and the nest-leaving generally spanned over two days (Ottosson in prep.). The time in the nest was related to the tarsus length of the largest nestling in a nest, on the day of ringing (P=0.029, r= 0.24, n=84) but not to mass (P=0.612, r=0.06, n=84). Average tarsus length or average mass of the clutch showed no relation to the time in the nest, nor did brood size.

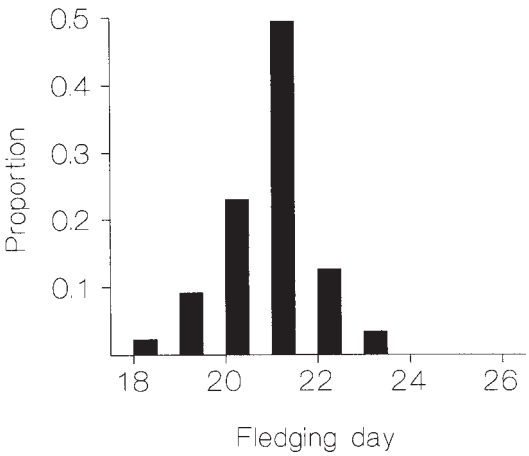

Figure 1. Time of nest-leaving: the number of days between the day the first nestling hatched and the day the first nestling left the nest-box. The bars show the proportion of recorded nests.
Tid för utflygningen: antal dagar i holken mellan den dag då den första ungen kläcktes och den dag den första ungen lämnade holken. Staplarna visar proportion av registrerade bon.

Feeding

During the first part of the nestling period parental feedings were delivered inside the nestbox. Later parents fed nestlings from the entrance hole but the nestlings were still sitting inside. When the nestlings reached 17–18 days of age they started to occupy the entrance hole, where they also were being fed. The average proportion of time when the entrance hole was occupied by a nestling increased as the fledging date was approached, from a very low proportion to about 70% of the time on the day before fledging (Figure 2). The size rank, both tarsus and mass rank, did not influence the proportion of time that the nestlings occupied the entrance hole.

Starling parents decreased their provisioning rate before the fledging of the first young (Figure 3a). The difference in provisioning rate between two days before fledging and on the day of fledging, before any young had fledged, was significant (Figure 3a; t-test t_{23}=2.62, P=0.015). When nestlings had started to leave the nest, those behind seemed to get the same amount of food as before any had left (Figure 3b). Nestling size, here tarsus rank and mass rank, did not influence the number of feedings a nestling received. In the three nests that we observed after more than two nestlings had left, only one of the parents continued to feed the remaining nestling(s).

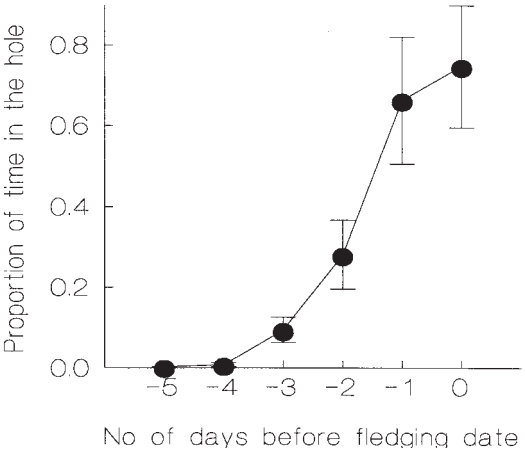

Figure 2. The average summed proportion, per nest, of observed time that nestlings spent in the hole versus the number of days before the day of fledging of the first nestling in a nest. *Den totala tid som ungarna i en holk vistades i holköppningen redovisad som proportion av observationstiden i relation till antal dagar till dess att den första ungen lämnade boet.*

Nest-leaving

During our observations we saw when 15 nestlings actually left the nest, eight (53%) of them left the nest directly after they had been fed. Further, 13 of the 15 nestlings (86.7%) had been fed at least once (average 1.4 feeds) during the last 15 minutes. Of the same 15 nestlings, five were the first to leave their respective nest, four of these five nestlings left in conjunction with a feeding, and all had been fed at least once the last 15 minutes.

Jump order

The order in which the nestlings left the nest was not correlated to their size, here fractional tarsus rank at ringing on day 14 (P=0.14, r=0.19, n=59) or with fractional mass rank (P=0.88, r=0.02, n=59). However, there was a tendency towards a correlation between a nestlings condition, here the residual of the regression of mass versus tarsus length and the fractional nest-leaving order (P=0.088, r=0.23, n=56; Figure 4). This tendency disappears, however, if the few nestlings in poorest condition are removed. Nestlings in better than average condition did not tend to leave earlier. Hence, there was no correlation over the whole range of residual conditions.

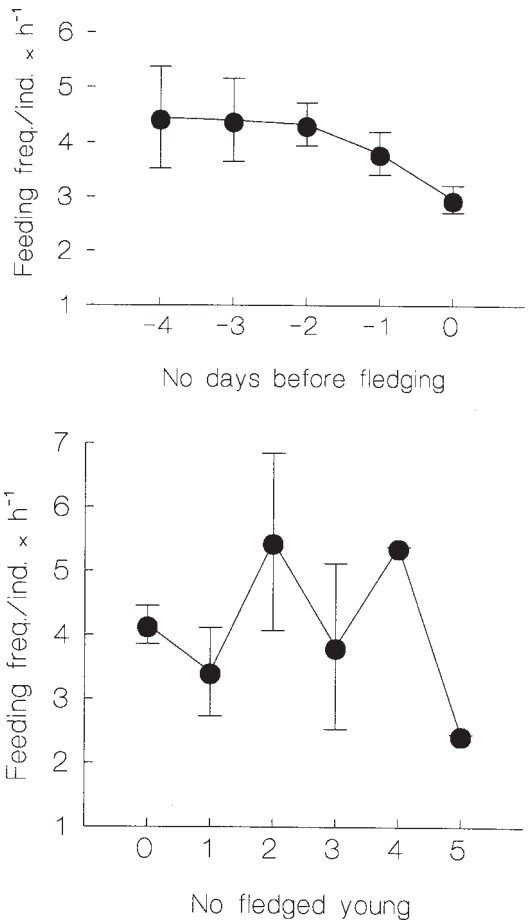

Figure 3. The average number of feedings per individual and hour versus (upper) the number of days before the day of fledging of the first nestling in a nest and (lower) the number of fledged nestlings, horisontal bars show standard error. *Det genomsnittliga antalet matningar per individ och timme i relation till (övre) antal dagar till dess att den första ungen lämnade boet och (undre) antal ungar som flugit ut.*

Discussion

The nest-leaving process in the Starling generally spans over more than one day (Ottosson, unpupl. data). This is what one would expect since the asynchronous start of incubation in the Starling produces a size hierarchy with one nestling almost one day younger than its nest-mates. This size hierarchy last at least until the nestlings are 14 days old (Ottosson 1997).

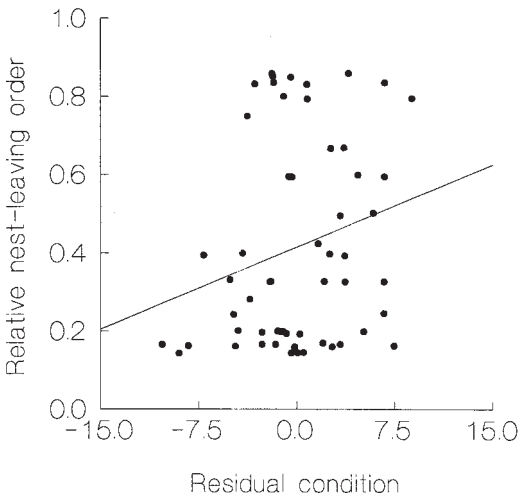

Figure 4. Individual nestlings' order of nest-leaving plotted against condition, here the residual for the regression between mass and tarsus length.
Individuella ungars relativa holklämningsordning i relation till kondition, här mätt som residualen för regressionen vikt mot tarslängd.

The parents seemed to initiate nest-leaving by decreasing the provisioning rate towards the end of the nestling period (Figure 3a). To reduce the amount of food brought to the nest is also the most obvious way in which parents could manipulate their young to leave (c.f. Davies 1976, 1978). The benefit for parents to have the nestlings outside the nest-box can be shorter foraging trips and a decreased risk of loss of the hole brood.

Alternatively, the decrease in provisioning rate may be an effect of a decrease in nestling demand after they have left the most intense period of growth (c.f. Ottosson & Smith, in prep.). This is supported both by the result that the provisioning rate per nestling was constant after nestlings had started to leave the nest (Figure 3b), and by the result that nestlings that actually were observed leaving the nest left shortly after a feeding. So it is not necessarily so that Starling parents decrease the provisioning rate in order to force the nestling out of the nest as have been shown in other studies (Lemel 1990, Nilsson & Svensson 1993).

One does observe parents flying around in front of the nestbox calling and with food in their beaks in a way that one, at least as a human, interprets as a way of enticing the nestlings to leave. Unfortunately, it is hard to evaluate the importance of this behaviour, but it remains as an anecdotal fact.

There was no significant correlation between size rank, here both tarsus rank and mass rank, and the nest-leaving order. Further, the proportion of individuals which were known to have left first was more or less equal between tarsus rank categories one to four. This can be explained by a relatively low variation in size between the synchronous nestlings in the clutch (Ottosson 1997). However, there was a tendency for the condition of the nestlings on the day of ringing to correlate with the nest-leaving order.

Starling nestlings leave the nest in the later part, not at the end, of the period of parental investment (Trivers 1972) and the time of nest-leaving will not, therefore, be subject to the traditional parent-offspring conflict as proposed by Trivers (1985). However, one part of the parent-offspring conflict (Trivers 1974), the intra-generational conflict, includes sibling conflict/competition over current parental investment. Towards the end of the nestling period the proportion of time that the nestlings spend in the entrance hole increases and so does probably also the competition for this favoured position. It seems, however, that no single individual tried or were able to monopolise parental investment by occupying the entrance hole permanently. But as the competition in the nest increases an individual nestling has to trade the possibility of being fed inside against outside the nest-box, and this may be the factor that triggers the nestling to leave.

Acknowledgement

I thank Johan Bäckman, Måns Bruun, Mariano Cuadrado, Daniel Dzierzanowski, Thomas Ohlsson, Maria Sandell, Liv Wennerberg and Karl Wettermark for valuable help with the fieldwork. I also thank Henrik G. Smith, and Mikael Svensson for discussion and constructive criticism on the manuscript. The project was financed by a grant from the Swedish Natural Sciences Research Council to Henrik G. Smith.

References

Bengtsson, H. & Rydén O. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit (*Parus major*). *Behav. Ecol. Sociobiol.* 12: 243–251.

Davies, N. B. 1976. Parental care and the transition to independent feeding in the young spotted flycatcher *(Muscicapa striata). Behaviour.* 59: 280–295.

Davies, N. B. 1978. Parental meanness and offspring indepen-

dence: an experiment with hand-reared great tits *(Parus major). Ibis.* 120: 509–514.
Forbes, M. R. L. & Ankney, C. D. Hatching asynchrony and food allocation within broods of Pied-billed Grebes *Podilymbus podiceps. Can. J. Zool.* 65: 2872–2877.
Gottlander, K. 1987. Parental feeding behaviour and sibling competition in the pied flycatcher *(Ficedula hypoleuca). Ornis Scand.* 18: 269–276.
Kacelnik, A., Cotton, P. A., Stirling L. & Wright J. 1995. Food allocation among Starlings: sibling competition and the scope of parental choice. *Proc. R. Soc. Lond. B.* 259: 259–263.
Lemel, J. 1989. Body-mass dependent fledging order in the great tit. *Auk.* 106: 490–492.
Nilsson, J. & Svensson, M. 1993. Fledging in altricial birds: parental manipulation or sibling competition? *Anim. Behav.* 46: 379–386.
Ottosson, U. 1997. *Parent-offspring Relations in Birds: Conflicts & Trade-offs.* Ph.D. Thesis, Dept of Ecology, Animal Ecology, Lund University, Sweden.
Trivers, R. L. 1974. Parent-offspring conflict. *Am. Zool.* 14: 249–264.
Trivers, R. L. 1985. *Social Evolution.* Menlo Park. Bejamin/Cummings
Wilkinson, L. 1992. *SYSTAT for Windows, Version 5,* Evanston, IL. SYSTAT.

Sammanfattning

Utflygningen hos stare Sturnus vulgaris*: exempel på en konflikt mellan föräldrar och ungar?*

Ett av de första viktiga beslut en fågelunge skall ta, är när den skall lämna holken. Vad är det som får dem att lämna bekvämligheten och säkerheten i boet? Bestämmer ungarna själva när de skall lämna boet eller är det föräldrarna som på något sätt tvingar ut dem (Trivers 1974, Davies 1976)? Det har föreslagits att tiden i boet bestäms av en avvägning, där konkurrens om mat som får dem att lämna boet för att öka sina chanser att bli matade ställs mot en högre predationsrisk (Lemel 1989, Nilsson 1990, Nilsson & Svensson 1993). Det har då också antagits att det, bland framförallt hålhäckande fåglar, är en subdominant individ som ”sticker först” då det kan tänkas att en dominant individ monopoliserar föräldrarnas matningar (Lemel 1989). Genom att studera starholkar på Revingefältet, utanför Lund, före och under bolämnandet försökte jag få informatiom om hur holklämningsprocessen styrs.

När starungarna var 14 dagar gamla ringmärktes de och biometriska data togs. Dessutom märktes de individuellt, inom holken, genom att pannorna färgades med olika färger. För att komma runt problemet med olika stora kullar används vid storleksjämförelser och uthoppsordning, relativa ranker d.v.s. en unges individuella rank divideras med kullstorlek+1. Totalt observerades 33 bon under 124 timmar från 2–4 dagar före förväntad uthoppsdag, dag 20, tills alla ungar hoppat ut. Under observationerna, som gjordes från gömsle eller med videokamera, registrerades vilka ungar som uppehöll sig i holköppningen och vilka som blev matade. Uthoppsordningen registrerades genom upprepade besök till dessa holkar och till ytterligare 15.

Botid

I de flesta holkar började ungarna hoppa ut när de var 21 dagar gamla och i allmänhet hoppade den sista ungen ur boet dagen efter den dag först ungen hade hoppat ut.

Matning

Under de första 16–17 dagarna efter kläckningen matar starföräldrarna ungarna inne i holken, men därefter börjar ungarna att tigga från holköppningen, i vilken matningen också sker. Att den tid som holköppningen är ockuperad av en unge ökar mot slutet av botiden illustreras i figur 2. Starföräldrarna minskade matningsfrekvensen mot slutet av botiden och skillnaden mellan matningsfrekvensen två dagar före uthoppsdagen och uthoppsdagen var signifikant (Figur 3a, *t*-test t_{23}=2.62, P=0.015). Ungarnas storlek, här tarslängd, påverkade inte antalet matningar som en unge fick och i de tre bon som vi observerade efter det att mer än två ungar hoppat ut matade bara ena föräldern.

Uthopp

Vi observerade direkt när 15 ungar lämnade boet, och 8 av dessa lämnade direkt efter det att de blivit matade och 13 hade blivit matade åtminstone en gång de senaste 15 minuterna.

Uthoppsordning

Ungarnas uthoppsordning var inte korrelerad till storlek, tarslängd, eller vikt vid ringmärkningstillfället, dag 14. Men det fanns en tendens till att en unges kondition, här residualen av regressionen vikt mot tarslängd, var relaterad till ungarnas relativa hoppordning. Då en unge med residualen noll ligger på regressionslinjen, här vikt mot tarslängd, innebär detta att ungar med förhållandevis låg vikt i förhållande till sin storlek, allmänt ansedda vara i sämre kondition, tenderar att lämna boet tidigare än ungar i bättre kondition.

Det verkar som om föräldrarna initierar uthoppsprocessen genom att sänka matningsfrekvensen mot slutet av boperioden (Figur 3a). Att dra ner på

matningen är ju också det mest naturliga sättet för föräldrarna att locka ut ungarna. Fördelen för föräldrarna att få ut ungarna ur holken kan antas vara de kan få kortare väg till födosökplatserna och att risken för att förlora hela kullen genom predation minskar.

Alternativt är det så att matningsfrekvensen minskar därför att ungarnas efterfrågan på mat minskar när de passerat de mest intensiva tillväxtfasen. Detta bekräftas delvis av att matningfrekvensen per unge var mer eller mindre konstant även efter det att ungar börjat lämna boet. Det är alltså inte säkert att det är för att tvinga ungarna ut ur holken som starföräldrarna sänker matningsfrekvensen. Starföräldrar observerades också flyga framför holken med mat i näbben på ett sätt som åtminstone en mänsklig betraktare tolkar som om de försöker locka ungarna ut ur boet. Tyvärr är det svårt att utvärdera betydelsen av detta beteende men det är åtminstone ett anekdotiskt faktum.

Det fanns ingen relation mellan storlek eller vikt och uthoppsordning, vilket eventuellt kan förklaras av en relativt liten variation inom kullarna. Däremot fanns det en tendens till att fåglar med sämre kondition hoppade ut före de i något bättre kondition.

Starungar lämnar boet under den senare delen, inte vid slutet, av den tid som föräldrarna investerar i dem och uthoppstiden är därför inte ett resultat av en föräldrar-unge konflikt *sensu* Trivers (1985). Men i slutet av botiden ökade starungarnas tid i holköppningen och då troligen också konkurrensen inom kullen om denna position. Det verkar dock inte som om någon unge ville eller kunde monopolisera föräldrarnas matningar genom att ockupera holköppningen. Men då konkurrensen mellan syskonen ökar måste den enskilda ungen göra en avvägning mellan möjligheterna att få mat i holken mot möjligheten att bli matad utanför och det är ju inte osannolikt att detta beslut påverkas av ungens kondition.