The presence of kleptoparasitic fledglings is associated with a reduced breeding success in the host family in the barn owl

Motti Charter[1], Ido Izhaki[2], Alexandre Roulin[3]

[1]Shamir Research Institute, University of Haifa, Katzrin, Israel

[2]Department of Evolutionary and Environmental Biology, University of Haifa, Haifa 31905, Israel

[3]Department of Ecology and Evolution, Biophore, University of Lausanne, 1015 Lausanne, Switzerland

Corresponding author: Motti Charter, Shamir Research Institute, University of Haifa, Katzrin, Israel. E-mail: chartermotti@gmail.com

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Abstract

Fledgling birds sometimes abandon their own nest and move to neighboring nests where they are fed by host parents. This behaviour, referred to as "nest-switching", is well known in precocial birds that are mobile soon after hatching and can easily reach foster nests. In contrast, due to the difficulty of observing nest-switching in territorial altricial birds, the causes and consequences of moving to others' nests are poorly known in this group of birds. Nest-switchers can be adopted by the foster parents or they can steal food from the host parents meant for their offspring, a form of kleptoparasitism, which may result in reduced breeding success of the host nest. In Israel, 12 barn owl fledglings left their natal nests and were found in 9 host nests out of 111 monitored nests (8.1%). Nest-switchers that fledged earlier in the breeding season flew shorter distances to reach host nests probably because the density of nests with younger nestlings is higher early in the season. The number of host nestlings fledged and the percentage of nestlings fledged was lower in host nests than in nest without switchers. The occasional nest-switchers were always older than host nestlings (respectively 80 and 50 days of age, on average) and host parents fledged fewer young when nest-switchers occupied host nests with younger nestlings. This suggests that nest-switchers are kleptoparasites because the presence of the older alien fledglings is associated with a lower breeding success of the host parents.

Keywords: nest-switching, parasitism, host nests, barn owls, kleptoparasite

Introduction

Nest-switching describes the situation where nestlings abandon their natal nest and move to the nest of a host family (Riedman 1982). This behavior is relatively frequent in precocial animals because soon after hatching the young have the ability to move between nests by walking or swimming (Roldán and Soler 2011). The frequency of nest-switching should be higher in colonial than territorial species because the distance between nests can be very short in the former. From the point of view of the host parents, the presence of nest-switchers in a host brood is often described either as a form of adoption (Riedman 1982) or of misdirected parental care where the nest-switchers parasitizes the host family by stealing resources intended to the host young (Roldán and Soler 2011). Kleptoparasitic fledglings should cause a reduction in the fitness of host nests, whereas in the case of adoption, the presence of nest-switchers can provide fitness benefits to the host family if, for example, it reduces the likelihood that the host offspring are depredated (Eadie et al. 1988, Williams 1994, Lengyel 2002, Kraaijeveld 2005).

The causes and consequences of nest-switching have been the focus of intense research in precocial species, whereas information about nest-switching in altricial species is fragmentary. In comparison to colonial altricial species in which nestlings can walk, such as in Lesser Kestrels (*Falco naumanni*) and Alpine swift (*Apus melba*) (Tella et al. 1997, Bize et al. 2003) to reach a host nest, in territorial species nest-switching occurs only after fledging because moving to another family requires the ability to fly. For this reason, the frequency of nest-switching is low in territorial altricial birds because of the difficulty of detecting a nest-switcher without intensive fieldwork and/or tracking devices and because in territorial species the distance between nests may reduce the chances of a nest-switcher from reaching certain nests. Nest-switching may therefore be more prevalent in areas with higher breeding density, which increases the probability that fledglings locate other nests (Bustamante and Hiraldo 1990, Kenward et al. 1993, Donazar and Ceballos 2008, Frumkin 2008).

Even though nest-switchers have often been considered as being adopted by host parents (Riedman 1982), few researchers could examine whether the presence of a nest-switcher is associated with a fitness reduction at the host nest. Even though in some colonial species parents can identify their biological young from nest-switchers (cliff swallow *Hirundo pyrrhonota*; Stoddard and Beecher 1983), act aggressively to the nest-switchers (white stork *Ciconia ciconia*; Redondo et al. 1995) and repel the alien young that try to invade their nest (Adélie penguins *Pygoscelis adeliae*; Beaulieu et al. 2009), in a number of territorial species parents are apparently not able to discriminate between their biological offspring and nest-switchers, as found in the barn owl (*Tyto alba*) and sparrowhawks (*Accipiter nisus*) (Roulin et al. 1999, Frumkin 2008). The question therefore remains open about whether in territorial birds, nest-switchers are adopted or should be considered as parasites.

In colonial species, the presences of nest-switchers has been found to cause a reduction in adult fitness (Common Tern *Sterna hirundo*; Saino et al. 1994), breeding success (Western and ring-billed gulls *Larus occidentalis* and *L. delawarensis*; Carter and Spear 1986; Brown 1998) and lower weights in host nestlings (white stork; Redondo et al. 1995), whereas no negative effects were reported in lesser kestrels (Tella et al. 1997). Even though nest-switchers have been found in a number of territorial species of Strigiformes and Falconiformes (barn owl, eagle owl *Bubo bubo*, Tengmalm's owl *Aegolius funereus*, **goshawk** *Accipiter gentilis*, ospreys *Pandion haliaetus*, sparrowhawk, Egyptian vulture *Neophron percnopterus*; Kenward et al. 1993, Roulin 1999, Gilson and Marzluff 2000, Penteriani and Del Mar Delgado 2008, Frumkin 2008, Donazar and Ceballos 2008, Kouba et al. 2017), none of these studies have reported an association between the presence of nest-switchers and reduction of breeding success at the host nest. Nest-switchers could cause a decline in reproductive success because in territorial species nest-switching can occur only after fledging implying that the nest-switchers may often be older, and hence potentially larger, stronger than the young in the host nest. As a consequence, nest-switchers may be competitively superior to their host nest mates and outcompete them in the acquisition of parental food resources. Even though older nest-switchers may have a similar weight as younger host nestlings [from the age of 40 days to fledging time, nestlings naturally lose body mass (Almasi and Roulin 2015)], nest-switchers are still developmentally more advanced and hence more competitive.

To the best of our knowledge, reduced breeding success as a result of nest-switchers has not yet been reported in any territorial bird species. During the 2011 breeding season, one of the authors found two barn owl nests with a nest-switcher and dead host nestlings (Charter unpubl. data). This convinced us to perform an observational study the following year to determine whether nest-switchers frequently visit other nest boxes and whether their presence is associated with a reduction of breeding success at the host nest. Barn owls have the potential to be host parents because barn owls do not discriminate against nest-switchers (Roulin 1999) or foster nestlings in cross-fostering experiments (Charter unpubl. data), pairs breed asynchronously (Charter et al. 2015) and the breeding density in Israel is one of the highest in the world (Meyrom et al. 2009, Charter et al. 2010). In Israel, barn owls typically have one brood per year and have relatively large brood sizes compared to other populations (Charter et al. 2015). The presence of a nest-switcher may reduce the quantity of food available to each host nestling because barn owl parents do not increase prey deliveries in nests where nestlings were experimentally added (Roulin et al. 1999). The presence of nest-switchers may reduce breeding success of the host family in cases when they are older than the host nestlings. Indeed, if a nest-switcher invades a host family containing younger nestlings, it may have a competitive advantage to obtain food from foster parents. However, in some cases the host nestlings can be older than the invading individual (Roulin 1999) because, in contrast to most other bird species, barn owl fledglings return to the nest after having taken their first flight for approximately one month (Simmons and Cramp 1983).

Materials and Methods

We monitored 253 barn owl nest boxes in the Beit Shean Valley, Israel (32º30´N, 35º30´E) and nest boxes occupied by a breeding pair were visited 4 to 5 times from 15 April to 15 July 2012 when the oldest nestlings were 30 to 60 days old (Charter et al. 2010, 2012). Data was collected on laying date (determined by back-calculation, using nestling wing length as a proxy of age and considering an incubation period of 32 days, Roulin 2004), brood size at hatching (number of nestlings that hatched) and number of fledglings (the number of nestlings when the oldest individual was 53 days old). Fledging success was calculated as the number of fledglings divided by the brood size at hatching. All nestlings were ringed before fledging and we therefore could identify an individual as a nest-switcher when it was found in another active nest than the one where it had been ringed. A "natal nest" was defined as the biological nest where nest-switchers hatched and later fledged from and a "host nest" was defined as a nest in which we found a fledgling born in another nest. Nests were visited at fledging time for other purposes than recording nest-switching events. For this reason, our study is descriptive and we discuss several alternative hypotheses to explain the cause and consequences of nest-switching. **We used non-parametric analyses because the sample size is small**. Mann-Whitney U tests were used to compare breeding parameters between nests with and without nest-switchers and breeding success between host nests with one or two nest-switchers. Spearman's correlation was used to examine whether breeding parameters at the nests where a nest-switcher was born and where it was later found were correlated (note that in two natal nests, we did not know the brood size at hatching explaining variation in sample size). Since barn owl breeding success is related to laying date(Charter et al. 2015), breeding parameters at the host nests (n = 9, laying date range = March 11- May 10) were compared only to breeding parameters observed in nests without any nest-switcher (n = 59, range = March 11- May 12) with similar laying dates. Wilcoxon signed-ranks tests were used to compare breeding parameters at the natal and host nests that the nest-switchers visited and also to compare the mean rank of the within-brood age hierarchy of nest-switchers in their natal nest and of their siblings that did not switch nest. Statistical analyses were performed using the software SPSS for Windows version 23. All statistical tests are two-tailed and P-values smaller or equal as 0.05 considered significant.

Results

During the 2012 breeding season, 111 out of 253 nest boxes (43.9%) were occupied by barn owl pairs with median laying date being March 20 (range = Jan 1-May 12), of which 9 nest boxes (8.1%, laying date: median = March 28, range = March 11-May 10) were host nests for 12 nest-switchers. Eggs were laid earlier in the breeding season in the natal nests of the nest-switchers (median = March 4, range = Feb 2-April 9) compared to the host nests that they visited (median = March 28, range = March 3- May 10; Wilcoxon signed-rank test: Z = -

2.673, n = 9, p = 0.008) (Fig. 1). In contrast, we detected no difference in brood size at hatching between the natal (median = 6 hatchlings, range = 5-10) and host nests (median = 6 hatchlings, range = 5-8; Wilcoxon signed-rank test: Z = -1.13, n = 7, p = 0.26). The median distance between the natal and host nests (815 m, n = 9, range = 112-4315 m) was positively related to the date when the first egg was laid at the natal nest of nest-switchers ($r_s = 0.67$, n = 9, p = 0.05) but not at their host nest ($r_s = 0.41$, n = 9, p = 0.28). The laying dates at the natal and host nests were positively related ($r_s = 0.76$, n = 9, p = 0.02) indicating that nest-switchers select active nests non-randomly but those with host nestlings of a similar age. The 12 nest-switchers originated from 9 different families and in three host nests 2 nest-switchers were siblings born in the same nest box and were found on the same day in the host nest at a distance of 112, 215 and 291 m from the natal nest. The rank in the within-brood age hierarchy of the nest-switchers in the natal nest was the 1st born in five cases, the 3rd born in 2 cases, the 4th born in 1 case, the 5th born in 3 cases, and the 6th born in 1 case. The mean rank in the within-brood age hierarchy did not differ between nest-switchers (median = 3, n = 9, range = 1-6) and the siblings from their natal nests that did not switch nests (median = 4, n = 9, range = 3-5) (Wilcoxon signed-rank test: Z = -0.84, n = 9, p = 0.40). The nest-switchers were older (median = 81 days, n = 9, range = 69-97) than the host nestlings (median = 51 days, n = 9, range = 43-59) in all 9 host nests (Wilcoxon signed-rank test: Z = -2.67, n = 9, p = 0.008).

Laying date and brood size were similar at the nests that hosted a nest-switcher and at the nests without nest-switchers (Table 1), whereas brood size at fledging (without counting nest-switchers) and fledging success (i.e. the percentage of young that successfully fledged) was significantly lower in host nests with a nest-switcher than in the nests without switchers

(Table 1). There was no difference in the number of fledglings between nests that had one (n = 6, median = 1.5) or two nest-switchers (n = 3, median = 1) (Mann-Whitney U = 8.0, p = 0.79). Brood size at fledging was lower if a nest-switcher invaded a host nest containing young rather than old nestlings (Spearman's correlation between brood size at fledging in the host nest and age of the host nestlings when nest-switchers visited their nest: $r_s = 0.85$, n = 9, p = 0.004; Fig. 2). In contrast, the number of host nestlings was not related to the age of the nest-switchers ($r_s = -0.27$, n = 9, p = 0.49), distance between the host and natal nest boxes ($r_s = -0.017$, n = 9, p = 0.97) and the host laying date ($r_s = -0.56$, n = 9, p = 0.12). In five of the 9 host nest boxes we found either 1 (n = 2) or 2 (n = 2) dead natal nestlings inside the nest boxes; they were very thin and looked like they died from starvation and in one nest box there was only one natal nestling that was still alive, very thin and was also injured with puncture wounds to the chest cavity. The proportion of nests with nestlings older than 30 days of age where we found at least one dead host nestling was significantly higher in the host nests (55.6%, 5 out of 9 nests) than in nests without nest-switchers (5.9%, 6 out 102 nests) (Fisher Exact Test p < 0.001).

Discussion

At least 8.1% of the barn owl pairs hosted nest-switchers, and these nests fledged fewer young than nests without nest-switchers. Interestingly, the percentage of nest boxes occupied in this study (43.9%) was an average year for the study site (for the period 2002 - 2016 the mean percentage of nest boxes occupied is 46.1%, range 25.7 - 65.9%, Charter unpubl. data). The extent of the reduction in breeding success was more pronounced when nest-switchers invaded nests with young than old host nestlings. Early in the season nest-switchers invaded host nests that were located closer to their natal nests than later in the season. Even though nest-switchers were always older than their host nest mates, there was a positive correlation between the laying dates of the natal and host nests indicating that nest-switchers select host nests with nestlings that were globally of a similar age. Nest-switchers appear to select nests where host nestlings are younger probably because this gives them a competitive advantage (Roulin et al. 2012) to monopolize food items that the parents hunt for the biological offspring. There is a possibility that the reduced breeding success was not caused by nest-switchers but rather the nest-switchers selected nests not only with younger nestlings but also with fewer host nestlings in order to reduce competition. We do not think this was the case because we found fresh dead host nestlings in 4 out of 9 host nests and in one case a very thin nestling was injured as if it had been attacked. Although possible, it is doubtful that the low reproductive success in host nests was due to host nestlings contracting diseases from nest-switchers. In a nest in 2015 where we installed a video-camera, we observed a nest-switcher attacking host nestlings and stealing food (Charter 2015). Furthermore, if the host nestling died from a lack of prey before the nest-switchers arrived, then we would expect that the nest-switchers select nests where the parents bring more food because they too would suffer from a lack of food.

Since nest-switchers were always older than their new host nest-mates, young fledged from earlier laying pairs may have more opportunities to find a potential host nests to invade compared to young fledged later in the season. Individuals that switched nests were not older or younger than their siblings not found in a host nest. This means that regardless of the hatching rank in the natal nest, nest-switchers in our study area seek host nests with younger nestlings. As also found by **Kouba et al. (2017**), the absence of hatching rank effect on the probability to switch nest also suggests that nest-switching is not necessarily performed by the individuals that are in poorest condition (later born nestlings are usually in poorer condition, Roulin 2002). Thus, nest-switching may not be a strategy to improve body condition but an opportunistic behaviour to parasitize other families. Similarly to this study, both sparrowhawk (Frumkin 2008) and goshawk (Kenward et al. 1993) nest-switchers were also older than host nestlings. Interestingly, in the osprey and eagle owls nest-switchers were younger than their new host nest-mates (Gilson and Marzluff 2000, Penteriani and Del Mar Delgado 2008) perhaps because parents feed preferentially the younger offspring of the brood. Further studies are required to examine how nest-switchers are able to obtain food from foster parents and how they can outcompete host nestlings.

In our study area, the population of barn owls is very dense due to the provision of many nest boxes (Meyrom et al. 2009, Charter et al. 2012) and man-made structures (Meyrom et al. 2008). This system has probably generated an unnatural system where nestlings are able to reach other nests very easily. A similar situation prevails in Switzerland where seven foreign barn owl fledglings were observed (1.4 nest-switcher found per year) during a 5 years study of 257 barn owl nests. Whereas in Israel the median distance between the natal and host nest was only 815 m (max 4315 m), the mean distance in Switzerland was five times longer (on average 5.4 km). Thus, in Switzerland nest-switching may be less frequent implying that the fitness consequence of this behaviour for the host nest may be negligible (Roulin 1999) in contrast to Israel where this behaviour may be much more frequent. Another difference between the studies was that in Israel all the host nestlings were young and before fledging age (could not fly), whereas, in Switzerland 6 out of 7 of the host nests had already fledglings. In Switzerland, the nest-switchers may therefore reach the host nest later in the breading season due to the greater distances between the natal and host nests. Thus, nest-switching may be a form of parasitism (Roldán and Soler 2011) at least in Israel and we propose that a nest-switcher is a kleptoparasite because the presence of nest-switchers was associated with reduced breeding success in the host nest.

Nest-switching **in barn owls** has also been anecdotally recorded in the Netherlands (de Bruijn 1994), Germany (Schmidt 1993) and the USA (Looman et al. 1996). Thus, our observations are probably not exceptional resulting from specific environmental conditions that prevailed during the study period. **Our study presents the first hint about the possibility that nest-switchers are parasites. We believe that despite the low sample size, we should nevertheless publish such results because of the huge difficulty to document such data in wild animals. This study should therefore be considered as a stimulation for further studies and** more data are required to assess the frequency of nest-switching, for instance by using GPS devices to track the movements of barn owl fledglings. This would also help determine the amount of time nest-switchers spend in host nests to test whether only longer stay reduces reproductive success. We also need specific studies using cameras to examine whether nest-switchers attack or kill host nestlings and how the nest-switchers find or select the host nests.

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Figure Legends

Figure 1. Comparison between the percentage of distribution of laying dates of parasites nestlings (white, n = 12), nests that were not host nests (black, n = 93) and host nests (grey, n = 9).

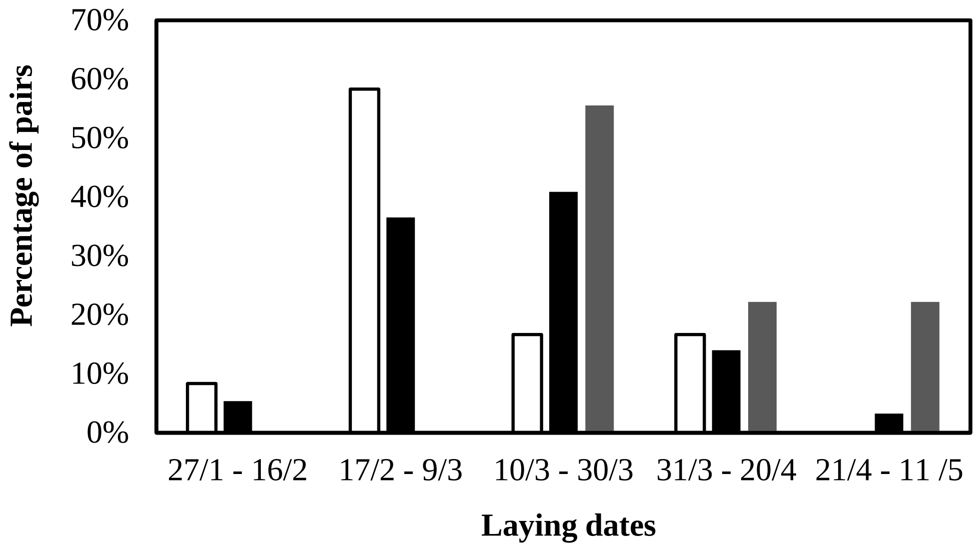

Figure 2. Relationship between the number of host nestlings per nest that fledged and the age (in days) of the host nestlings when the nest-switchers were found. **Circle= nests that had one nest-switcher and squares= nests that had two nest-switchers.**

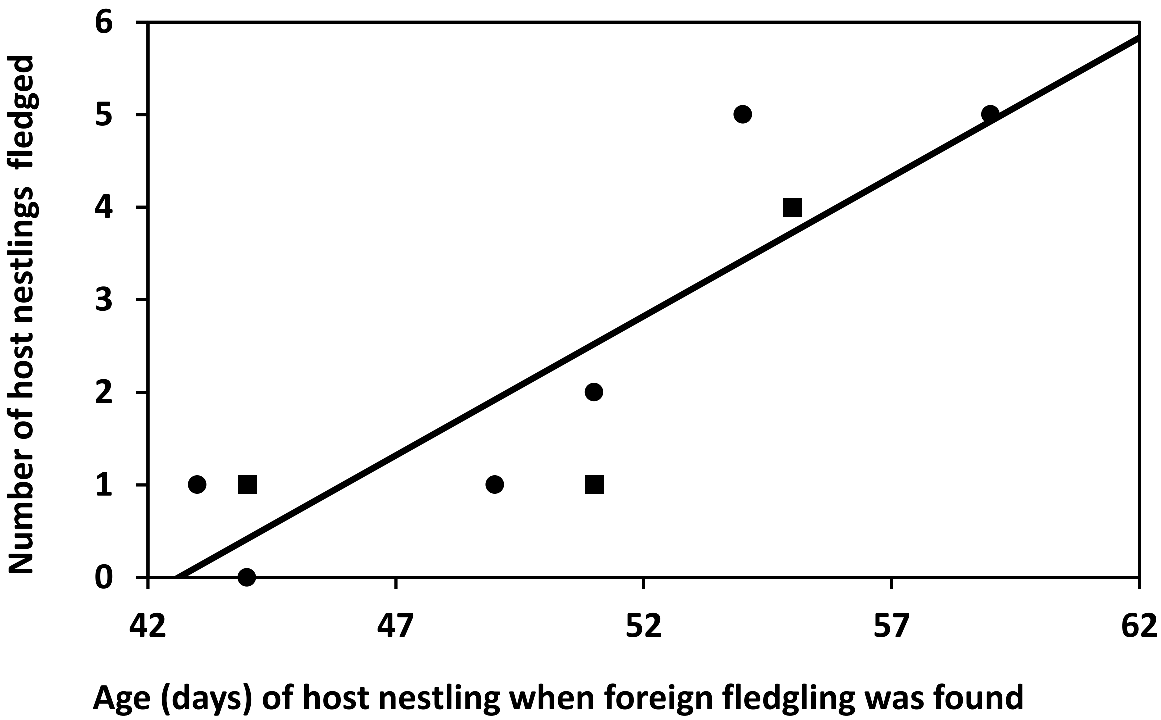

Table Legend

Table 1: Comparison between the breeding parameters of host nests with foreign fledglings to nests without a nest-switcher during March 11 to May 12 2012.

Breeding parameter	Host nests (n = 9) Median (range)	Nest without nest-switcher (n = 59) Median (range)	Statistics
Laying date	March 28 (March 11-May 10)	March 25 (March 11-May 12)	U = 245.0, p = 0.71
Brood size at hatching	6 nestlings (5-8)	7 nestlings (1-10)	U = 176.5, p = 0.10
Number of fledglings	1 fledgling (0-5)	5 fledglings (0-9)	U = 126.5, p = 0.011
Percentage of young fledged	20% (0-100%)	80% (0-100%)	U = 148.5, p = 0.032