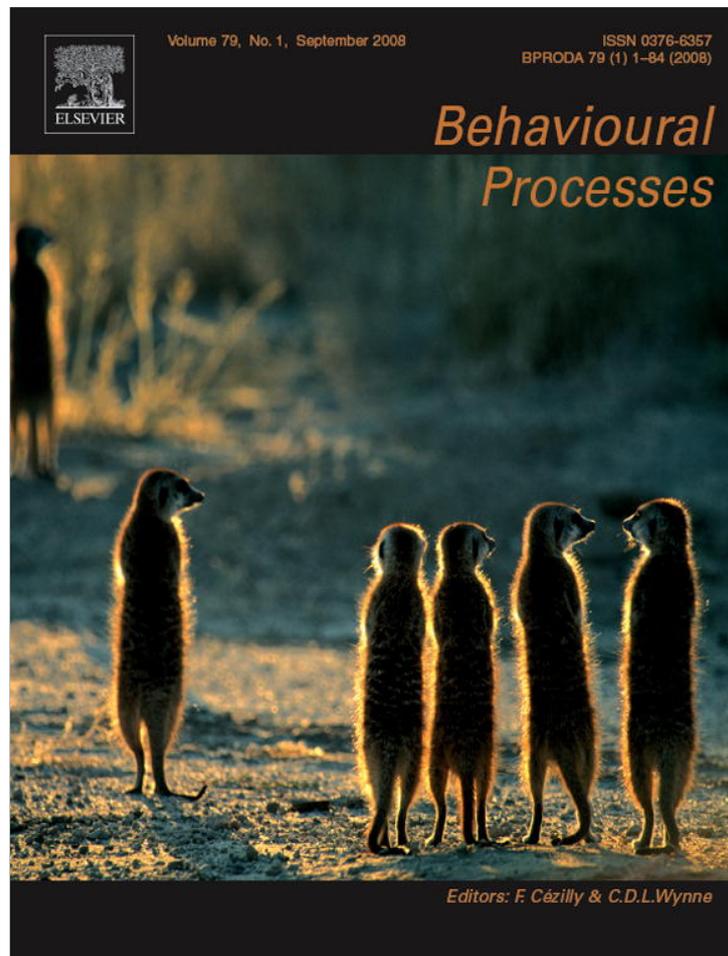


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The role of parent–offspring interactions during and after fledging in the Black-legged Kittiwake

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ABSTRACT

Most bird species endure a high mortality at fledging, and selection should favour parental behaviour diminishing these costs. Post-fledging parental care varies greatly among species and is often linked to parent–offspring recognition. In the Black-legged Kittiwake (*Rissa tridactyla*), fledglings need to return to the natal nest to be fed by their parents until independence. Rejections of fledglings by non-parent adults may be fairly violent, and parents are expected to recognize and help their chicks at the time of first return. However, previous cross-fostering experiments pointed out that parents are not able to recognize their chicks up to 15 days before fledging. In this paper, we study the behaviour of both parents and juveniles at fledging. We found that parents answered significantly more to their fledgling's calls than to those of others. Compared to silent juveniles, juveniles that called before landing were more likely to be accepted by their parents. No such pattern was observed with foreign juveniles, indicating that fledglings' voice may carry individual identity. Furthermore, fledglings found their way back to the natal nest faster when parents attended the natal nest and reacted to their offspring's calls than when they were absent or inactive. Such interactions may therefore diminish juvenile mortality at fledging.

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1. Introduction

In many birds species, the usually low estimates of juvenile survival rates suggest that fledging constitutes a difficult stage (Parker et al., 2003; Cam et al., 2003). For example, mortality at fledging reaches 68% in wood thrush fledglings *Hylocichla mustelina* (Anders et al., 1997) and 36% in brown thornbill fledglings *Acanthiza pusilla* (Green and Cockburn, 2001). Such high mortalities should favour parents expressing specific parental care at the time of fledging, a pattern that is observed in many bird species (e.g., Draganoiu et al., 2005; Middleton et al., 2007).

Post-fledging parental care varies greatly among bird species. In several species, juveniles become fully independent as soon as (or even before) they leave the nest. This is the case of Manx shearwaters (*Puffinus puffinus*), Gannets (*Sula bassana*) and most Procellariiforms. Their unique fledgling is usually overfed during the rearing stage, and outweighs its parents by up to 60% when the

latter leave the burrow, days before fledging (Ydenberg, 1989). The juvenile thus fledges by itself and starves for several days before it learns how to fish, continuing losing weight during that period. In the short-tailed albatross (*Phoebastria albatrus*), for instance, chicks fledge by themselves, soon after adults have deserted the colony (Hasegawa and DeGange, 1982). In other species however, there is a long post-fledging-dependent period, during which parents progressively stop caring for their young. In Passerines, for instance, the brood often fledges simultaneously and leaves the nest definitively (e.g., the house wren *Troglodytes aedon* (Johnson et al., 2004)), with parents still providing care for 10–14 days until independence. In several species, the brood is divided between parents, each of the parents taking care of specific fledglings (Draganoiu et al., 2005; Green and Cockburn, 2001; Leedman and Magrath, 2003; Lessells, 2002; Slagsvold, 1997). In blackbirds (*Turdus merula*) fledglings are fed at specific spots in the territory until full independence, but parents are apparently unable to recognize them and occasionally feed other juveniles (Edward, 1985). In razorbills (*Alca torda*), fathers have a better vocal recognition of offspring than mothers, and juveniles leave the male parent only after fledging (Insley et al., 2003).

In the Black-legged Kittiwake (*Rissa tridactyla*), fledglings have to return to the natal nest where parents feed them for about a fortnight (Cam et al., 2003; Danchin, 1988a,b), a period we call 'post-fledging dependence'. This long period of post-fledging parental care appears to be vital for juvenile survival

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because first year survival is positively related to the length of post-fledging dependence in that species (Cam et al., 2003). When attempting to return for the first time, fledglings land apparently randomly on many nests, often enduring attacks by resident adults. Risks of offspring mortality at that stage should have favoured parent–offspring recognition, as well as specific behaviours directed to the returning chicks.

However, cross-fostering experiments on young chicks (before 25 days) showed the absence of offspring recognition before that age (Cullen, 1956; Storey et al., 1992). The only evidence of individual recognition in this species concerns mates (Aubin et al., 2007; Wooller, 1978, 1979). However, chicks fledge at the age of 40 days on average (see Section 3) which leaves the possibility for parent–offspring recognition to develop before fledging. Although Kittiwake behaviour has been intensively studied for many years (Cam et al., 2003; Coulson, 1983; Cullen, 1956; Danchin, 1987, 1991; Danchin et al., 1998), fledging and post-fledging care have not been investigated. Here, we provide the first observational evidence for parent–offspring recognition at fledging in that species and propose a hypothesis about the function of such parent–offspring interactions.

We expected the existence of parent–offspring recognition at fledging. Parents are thus predicted to react more to their fledgling's calls than to any other fledgling's calls, and to accept their own fledglings while rejecting others. We also predicted that fledglings should come back to the natal nest faster when their parents are present and react to their calls than when parents are absent or non-reactive. Furthermore, parental attendance could be expected to increase at fledging, a pattern that would enhance parent offspring interactions. Finally, landing on narrow cliff edges is associated to specific behaviours such as pre-landing calls (Danchin, 1987, 1991). If these behaviours are acquired through learning during the fledging period, we might expect to see a change of fledglings' pre-landing call behaviour during the post-fledging period.

2. Methods

2.1. Studied population

The Black-legged Kittiwake (*R. tridactyla*) is one of the most common pelagic gulls in the northern portion of both the Atlantic and Pacific Oceans. It winters at sea, and breeds colonially on vertical cliffs from April to the end of August. There can be one to three chicks hatching in sequence usually within 2 days. Cliff-nesting physically constrains chicks to stay on the nest until fledging (Coulson, 1983; Cullen, 1956). A detailed description of the social displays of that species can be found in Danchin (1991).

The study population was in Cap Sizun (Brittany, France) where a breeding population has been monitored since 1979 (Cadiou et al., 1994; Cam and Monnat, 2000; Cam et al., 2003; Danchin, 1987, 1988b; Danchin et al., 1998). From 1979 to 2002, a total of 949 adults and 12246 chicks were individually marked with a unique code of four or five colour rings. Every year, colonies were visited at least once a week from February to mid-June, and then daily until the end of August. This allowed us to determine egg laying date, hatching date, chick rank (i.e., the position of the chick in the hatching sequence of the brood) as well as the date of first flight and return. Every year, nests with chicks older than 30 days were visited twice a day to estimate the date of first flight, first return and last observation at the colony from mid-June to the end of August. Data for breeder attendance presented here were obtained in 1995 because we do not have appropriate data to study breeder attendance throughout the whole reproductive season in 1983–1985.

2.2. Observation of fledglings returns

Observations of first returns to the nest were performed by E.D. from 1983 to 1985, during specific observation bouts. Newly fledged juveniles were monitored daily during a total of 6400 nests*hours (57 fledglings from 46 nests in 1983, in 16 h of observations; 100 fledglings from 80 nests in 51 h of observations in 1984; 86 fledglings from 66 nests in 24 h of observations in 1985) to record details of the first return to the nest. Observations were made from a vantage point less than 10 m away from focal nests.

Observation focused on individually marked fledglings returning to their natal nest for the first time. Because the first absence usually lasts well above 24 h, our observation protocol (two visits per day) allowed us to ascertain that the chick was absent for the first time. We recorded (i) the sequence of visited sites on which the fledging was seen (sites might be nests or any other landing area); (ii) juvenile behaviour before (silent vs. calling) and after landing (aggression from or toward the fledgling, begging for food, calling); (iii) the reaction of the resident individual – adult or chick – (acceptance, rejection, feeding, leaving); (iv) the reaction of the parent at the focal-fledgling's natal nest (presence or absence of one or both parents, bow and moan, long-call, interest – head movements – towards the behaviour of the focal-fledgling, takeoffs and landings while calling; see Danchin (1991) for a description of these behaviours); (v) any other reaction of individuals on neighbouring sites (see Cullen (1956), Danchin (1987, 1988b), Tinbergen (1959), for description and significance of displays associated with landing).

Observation bouts were made during daylight (roughly randomly distributed between 8 a.m. and 9 p.m.) and lasted 116 min on average (max, 534 min; min, 15 min) and focused on nests where fledglings were missing. There was no correlation between date and observation bout length ($F < 1.65$, $p > 0.21$ for every year). If the fledgling returned to its nest during the observation bout, it was registered as a “short absence” and details of final landing were recorded. If the fledgling was still absent from its nest at the end of the observation bout, it was registered as a “long absence”. When a fledgling was still away from its nest on the second day it was then recorded as “first absence” in the first day, and as “subsequent absences” in the following days. Twenty-five years of detailed observations of fledging behaviour have shown that first absences shorter than 1 day are very rare. Thus, first absences observed during several consecutive days may still be first absences. However, we did not consider them as such because of the uncertainty due to the discontinuous nature of our observations. These obvious imperfections in our protocol, however, can only diminish our capacity to detect any pattern, making our analyses conservative.

2.3 Statistics

Statistical analyses were made using the SAS® package (SAS Institute, 1999). In order to correct for pseudo-replication, we used generalized mixed models for some analyses and report the Z statistics. All tests were two-tailed. We mainly used three-dependent variables: the proportion of short versus long absences (Fig. 2), the number of nests visited per absence (Fig. 3) and the proportion of noisy versus silent landings (Fig. 4). The first two variables quantify a fledgling's difficulty in finding its way back to its nest. The proportion of noisy versus silent landings is linked to the importance of acoustic displays in recognition and to the learning of certain social behaviours linked to the landing on narrow cliff edges. *p*-Values below 5% were interpreted as significant. The following analyses rely on data gathered during 1983–1985. The proportion of short versus long absences did not vary significantly across years (taking all absences: $F_{2,181} = 0.2$, $p = 0.8$, $n = 182$; taking only

first absences $F_{2,64} = 2, p = 0.15, n = 65$). For each absence date, the number of visited nests did not vary significantly across years (for example for absences on day 0: $F_{2,64} = 1.21, p = 0.3, n = 65$; absences on day 1: $F_{2,21} = 0.98, p = 0.39, n = 22$; etc.). Similarly, the proportion of silent landings did not vary between 1984 and 1985 (taking all absences: $F_{1,178} = 0.57, p = 0.45, n = 179$; taking only first absences: $F_{1,83} = 3.4, p = 0.07, n = 84$; sample size regarding this aspect of chicks behaviour was very low in 1983 and not sufficient to allow comparisons with other years). Thus, data from 1983 to 1985 were pooled in all further analyses.

3. Results

3.1. Parental attendance at fledging

In 1995, 197 nests were monitored from nest building to the end of the breeding season. Fledgling's first absences (i.e., fledging) occurred approximately 40 days after hatching (mean \pm 95% confidence interval = 39.7 ± 1.7 days, $n = 197$ in 1995; Fig. 1). After their first return, they were fed regularly on the nest during approximately 11 days (10.7 ± 0.6 in 1995, $n = 197$). In almost 30 years of studies, we never saw fledglings being fed by their parents outside the natal nest. The only exception was that of a relatively old banded chick that fell out from its isolated nest to a ledge 1.5 m below and that was fed until fledging by its marked parents. Thus returning to the nest appeared to be important for post-fledging survival.

Parental attendance (at least one parent) was close to 100% until chicks were about 15 days old (Fig. 1). It then declined progressively until fledging. First absences occurred when parental attendance was of about 65% on average. However, parental attendance increased significantly for 2 days immediately after the first absence of the first chick (attendance in day -1 and 0 differed, $t_{134} = 3.45, p = 0.0007$; attendance in days 0 and 1 did not differ, $t_{120} = 1.81, p = 0.07$; but attendance between days 0 and 2 differed, $t_{114} = 3.8, p = 0.0002$, parental attendance being higher on days 0 and 1 than before or after; see Fig. 1). After 2 days, parental attendance came back to values similar to before fledging and remained at about 60% for 15 days after fledging (Fig. 1).

Second chicks usually fledged 2.4 ± 0.6 days after the first chick. Parental attendance was thus significantly higher during the first return of the first chick than that of the second or third ones ($p = 0.0002$ between days 0 and 2).

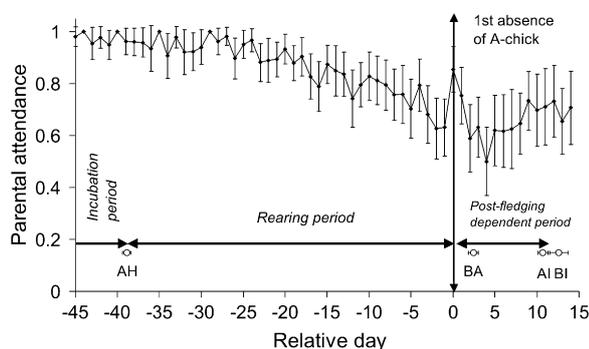


Fig. 1. Parental attendance from 45 days before to 13 after the fledging of the first chick. Data from 1995 (197 chicks coming from 8 different adjacent cliffs). Relative day means the observation Julian day minus the Julian day of the first flight of the first chick. Parental attendance is the proportion of nests occupied by at least one breeder. Data (parental attendance, hatching, first flight of the chicks, last observation of the first and the second chick) are given as mean \pm the confidence interval for $\alpha = 0.05$. Main life-history events are abbreviated as AH = "A-chick hatches"; BA = "first absence of B-chick (if existing)"; AI = "independence of A-chick"; BI = "independence of B-chick".

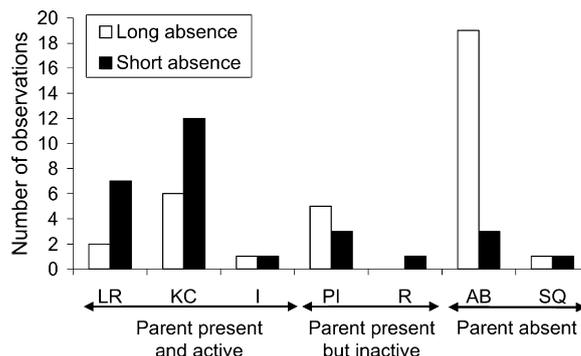


Fig. 2. Distribution of long (white bars) and short (black bars) first absences according to parental behaviour. Long first absences are those in which the first return of the newly fledged juvenile occurred after the first observation bout following the departure of the juvenile. Short ones are those for which the first return occurred during the first observation bout after the first absence of the juvenile. Parental activity. LR, parent(s) took off and landed on the nest while uttering the long-call; KC, parent(s) kittiwaked and/or chocked spontaneously on the nest; I, parent(s) reacted to the behaviour of its young without calling; PI, parent(s) present but did not react in any way; R, parent(s) present but rejected it when it landed on the nest; AB, parent absent; SQ, parent absent and the nest occupied by a squatter.

3.2. Absence duration and parental activity

Short first absences (see Section 2 for definition) were more frequent when at least one parent was on the nest (Fig. 2, cases "active" plus "inactive") than when both parents were absent (cases "absent" plus "squatters"; Fig. 2, $\chi^2_1 = 4.9, p = 0.027, n = 62$). Short first absences were more common in the presence of active (parents reacting to the chick, even calling back, $n = 29$) than inactive (parents oblivious to the chick, $n = 9$) parents (Fig. 2, $\chi^2_1 = 12.5, p = 0.0004, n = 62$).

Short absences were less frequent in first than subsequent returns (45% and 82%, respectively, $t_{180} = 5.4, p < 0.0001$). Absence duration in subsequent returns still depended on parental attendance ($F_{1,37} = 4.9, p = 0.033, n = 120$; Generalized mixed model including fledgling identity as a random factor: $Z = 1.5, p = 0.062$) but no longer on parental activity. Furthermore, parents tended to react more to their young's call during first than subsequent return ($F_{1,72} = 2.2, p = 0.15, n = 114$; Generalized mixed model with fledgling identity as a random factor: $Z = 1.9, p = 0.031$). Thus, in subsequent returns juveniles did not seem to have any difficulty in finding their way back, and experienced fledglings typically waited for their parents' return to come back directly to their nest to beg for food immediately.

3.3. Parent-offspring recognition during post-fledging dependence

We gathered 129 observations (involving 50 chicks) when the focal fledgling called (either from another nest or while flying) with at least one parent attending the natal nest. Parents reacted in 86 cases (67%), and called significantly more often in reply than did other adults (40% vs. 5%, respectively, $t_{256} = 7.4, p < 0.0001$). Focal fledglings did not always reply to their parents' calls, but in six cases, parental calls were directly followed by the first return of the focal fledgling that obviously changed its trajectory after its parent(s) called.

Foreign fledglings were rejected by the nest occupant in 87% of the cases (75 of 86 cases, in 56 cases by an adult, in 19 cases by a chick, Table 1), and accepted by an adult in 5 cases. In the last six cases, the nest occupant left the nest immediately after the landing of the juvenile. Such occupants were probably squatters (Cadiou et al., 1994; Danchin, 1988a; Monnat et al., 1990). We

Table 1
Reaction of adults attending a nest when a chick landed on their nest according to the chick's landing behaviour

Chicks landed on	Another nest			Natal nest					
	An adult or another chick			At least one parents			A squatter		
	Chick did not call before	Chicks called before	Total	Chick did not call before	Chicks called before	Total	Chick did not call before	Chicks called before	Total
Adult does not react	0	0	0	2	31	33	0	2	2
Adult reacts by									
Accepting the chick	4	1	5	6	46	52	0	1	1
Rejecting the chick	61	14	75	3	2	5	4	14	18
Leaving the nest	3	3	6	1	4	5	0	2	2
Total of reactions	68	18	86	10	52	62	4	17	21
Total	68	18	86	12	83	95	4	19	23

also recorded 23 returns (Table 1) to natal nests that were occupied by known squatters. 18 (78%) of these juveniles were rejected, two provoked the departure of the squatter, two did not provoke any reaction from the resident adult, and the remaining one managed to stay after having been hit violently. Finally, among 95 cases of landings on the natal nest in the presence of at least one parent, 62 triggered parental reaction (Table 1). In 52 cases parents performed a full greeting display (Kittiwake and downward and upward chocking), or fed the returning juvenile. In five cases they rejected their juvenile (the parent eventually accepted the juvenile in three instances), and in the five last cases the parent left the nest. Adults thus recognized their fledglings in 91% of the cases (52 out of 57 without including cases when adults left the nest). Thus, fledglings are significantly less rejected by their parents than by other adults ($\chi^2_1 = 133.3, p < 0.0001$).

When landing at natal nests, fledglings that called were significantly more likely to be accepted by adults than silent ones ($\chi^2_1 = 8.1, p = 0.0045$) on the natal nest. This pattern was not found on foreign nests ($\chi^2_1 = 0.023, p = 0.88$), suggesting that foreign adults rejection was independent of juvenile landing behaviour. This suggests that juvenile calls carry an individual signature.

3.4. Fledgling behaviour: number of sites visited and occurrence of pre-landing calls

The mean number of sites visited was significantly greater during first returns than subsequent ones (Fig. 3, $t_{124} = 7.6, p < 0.0001$). The number of nest visited by juveniles that successfully returned to their nest on the first day varied greatly (on average 7.7 ± 6.1 , ranging from 1 to 23, $n = 31$). The percentage of silent landings was affected by the status of the return (first vs. subsequent, $F_{1,417} = 38.6, p < 0.0001$), the status of the nest (natal vs. foreign, $F_{1,417} = 19.0, p < 0.0001$) and the interaction between both param-

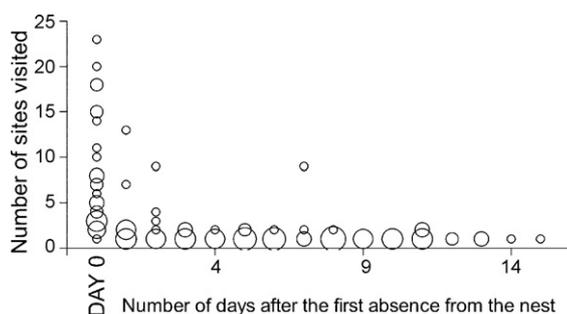


Fig. 3. Number of sites visited during the first and subsequent returns to the natal nest. Only successful attempts ($n = 126$) are shown here. Day 0 is the day of the first absence, and the size of the circles is proportional to the number of observations.

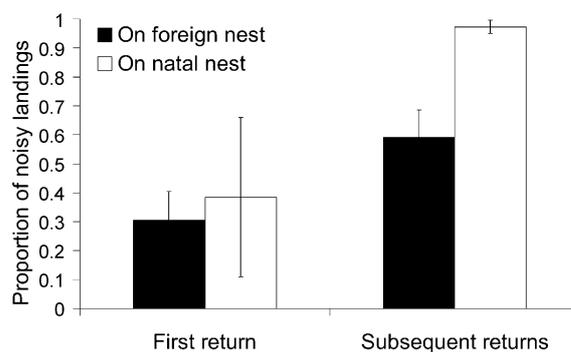


Fig. 4. Mean proportion of noisy landings according to return (first vs. subsequent) and nest (natal vs. foreign) status. The status of the return ($F_{1,417} = 38.6, p < 0.0001$), the status of the nest ($F_{1,417} = 19.1, p < 0.0001$) and the interaction between the two ($F_{2,417} = 5.6, p = 0.0187$) were significant ($n = 652$ landings displayed by 228 different fledglings; SAS Mixed Procedure with fledgling identity as random parameter: $p < 0.0001$).

eters ($F_{2,417} = 5.6, p = 0.019$, 652 landings displayed by 228 different fledglings; mixed model with fledgling identity as random factor: $Z = 4.68, p < 0.0001$, Fig. 4).

4. Discussion

4.1. Parent-offspring recognition in Kittiwakes

The existence of the post-fledging dependence period suggests the existence of some parent-offspring recognition avoiding mis-directed parental care. All the previous studies failed to show such recognition in Kittiwakes before the age of 25 days (Cullen, 1956; Storey et al., 1992). Our study thus provides the first evidence for parent-offspring vocal recognition in that species at the time of fledging when chicks are on average 40 days old. Parents reacted more than foreign adults to their juvenile's calls. In several observations, reacting parents were unable to see their fledgling, suggesting that vocal recognition is involved in kin recognition. This is supported by our observation that (i) fledglings were rejected more often by their own parents after silent than noisy landings and (ii) the fact that this pattern was not observed when landing near foreign adults. Whatever the mechanisms involved, our result suggests that recognition is not perfect because erroneous rejection or acceptance were observed.

Adoption is frequent in many bird species (Carter and Spear, 1986; Holley, 2000; Morris et al., 1991; Plissner and Gowaty, 1988). It also occurs at a detectable rate in Kittiwakes (Helfenstein et al., 2004; Roberts and Hatch, 1994) in spite of its cliff-nesting habit. In that species, most adoptions occur during the first 10 days after hatching, adoption of fledglings remaining exceptional

(Danchin, pers. obs.). Thus the trade-off between costs of efficient parent–offspring recognition and benefits of adoption also exists in that species. If the costs of taking care of a foreign juvenile are lower than those of rejecting its own ones, then adults are expected to show intermediate level of recognition as we observed (Avital et al., 1998; Riedman, 1982).

Our results suggest that parent–offspring recognition exists in Kittiwakes but develops late. Such delayed development may result from the strong constraints on chick movements imposed by cliff-nesting. Recognition only develops just before fledging, which may have a strong effect on fitness. Parents have the opportunity to learn their offspring's voice when chicks flap wings on the nest while uttering their characteristic harsh long-call during the 10 days before fledging.

Our results further suggest that parent–offspring vocal recognition helps fledglings to find their way back to their natal nest, a stage that may affect fitness. Recognition of parents by chicks has already been demonstrated in Larids (Beer, 1969, 1970a,b, 1979; Charrier et al., 2001; Evans, 1970). However, evidence that chicks are recognized by parents (Buckley and Buckley, 1972; Miller and Emlen, 1975) is rarer and is thought to be limited to periods of parental investment on mobile offspring (e.g. in razorbills *Alca torda* (Ingold, 1973)). Our study fits this view, since parents sometimes adopt young chicks, but appear to recognize their offspring and reject foreigners after fledging. Play-back experiments would be necessary to demonstrate that vocalizations are the basis of parent–offspring recognition at the time of fledging in Kittiwakes (e.g. Lengagne et al., 2001).

Post-fledging parental care may also influence fitness either immediately or on the long-term. Previous studies have documented the importance of the post-fledging period of dependence for juvenile survival rates in Kittiwakes (Cam et al., 2003). Juveniles with longer-dependent periods show higher local survival rates during the first winter, and higher reproductive success as adults (Cam et al., 2003). Here we show that the duration of the first absence may also be influenced by parental attendance and activity, suggesting that parents actively help their offspring to return to the nest. Juveniles taking a long time to return may be attacked by other adults and more exposed to predation. Post-fledging parental care owing to parent–offspring recognition may therefore diminish the energetic costs of the first return, and affect post-fledging survival and thus fitness.

We are aware that our methods and conventions are not perfect. In particular our definition of short and long absences is very crude. However, these imperfections are unlikely to be responsible for the detected patterns. In fact, they mainly diminished our power to detect patterns, and our analyses are thus conservative (see Section 2). This implies that reported patterns are biologically sound and probably even stronger than estimated here. Our methods could have been improved either by increasing the length of observation bouts, or by using transponders recording the exact time and duration of first absence and possibly the number of landing attempts. Other parameters could also affect the intensity of parent–offspring interactions, like mean colony breeding success and density, fledgling quality, predation risks, luminosity or weather. For example, one may expect adults to react more to healthy than unhealthy fledglings, because of the higher benefits they may expect from high quality offspring. Vocal interactions are also likely to be used more often in foggy weather, and therefore parents may be more prone to react to their offspring in such conditions. Furthermore, since we pooled data from several years and pairs, it is unlikely that the other unaccounted variables can have affected our results significantly, but they may explain a part of the recorded individual differences (revealed by the significant Individual effect obtained in every generalized mixed model).

4.2. Change in parent–offspring interactions after the first return

Behaviour of newly fledged juveniles changed from first to subsequent returns to the nest. During their first flight, juveniles visited numerous nests randomly, demonstrating their capability to land on any kind of nest. Their difficulty was thus mainly in locating their natal nest, which they have never seen from outside before. Newly fledged juveniles are often silent, while during subsequent flights, juveniles usually fly directly to their nest and call before landing as adults do (Danchin, 1987, 1988a). The reason why newly fledged juveniles remain silent during their first return attempt is unclear because selection should favour juveniles capable of calling at that time. In fact, adult Kittiwakes show the same pattern: individuals landing on an unknown site are much more often silent than those landing on their own nest, the latter usually uttering a pre-landing call (Danchin, 1987, 1988a). This suggests that pre-landing calls are typical of confident individuals (Danchin, 1987, 1988a).

In parallel, parental behaviour changes in two ways around fledging. They first react to the absence of their chick by staying on the nest thus increasing their attendance. They also become more reactive to the voice of their offspring. These two components however disappear in only 3 days, implying that parents are much less likely to be present at the time of the return of their second offspring. This reduced post-fledging parental care to second fledglings, combined with sibling aggression and reduced food availability throughout development (Roberts and Hatch, 1994), may explain the long-term fitness consequences of hatching rank in that species (Cam et al., 2003). Post-fledging parental care may therefore play a crucial role in individual fitness and population demography.

Most species experience high mortality rate before recruitment, but few studies have focused on the early stages after fledging in order to understand what selective pressures may constrain fledgling survival. This study suggests that parent–offspring interactions may influence fledging success and, in turn, affect offspring survival. In Kittiwakes the nest seems to be the “meeting point” for parents and offspring, a function that is mediated by parent–offspring vocal interactions at the time of the first return. Parent–offspring recognition is common in Larids (Beer, 1970a; Charrier et al., 2001; Storey et al., 1992; Tinbergen, 1959), which suggests that it is an ancestral feature in this taxon. Cliff-nesting in Kittiwakes seems to have delayed the development of parent–offspring recognition (Cullen, 1956; Storey et al., 1992) to the time of fledging, a moment when it may impact fitness significantly. This led to the evolution of an unusual pattern of nest use where the nest is still used for a fortnight after fledging, while in most bird species the nest is deserted definitively by both breeders and juveniles immediately after fledging.

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