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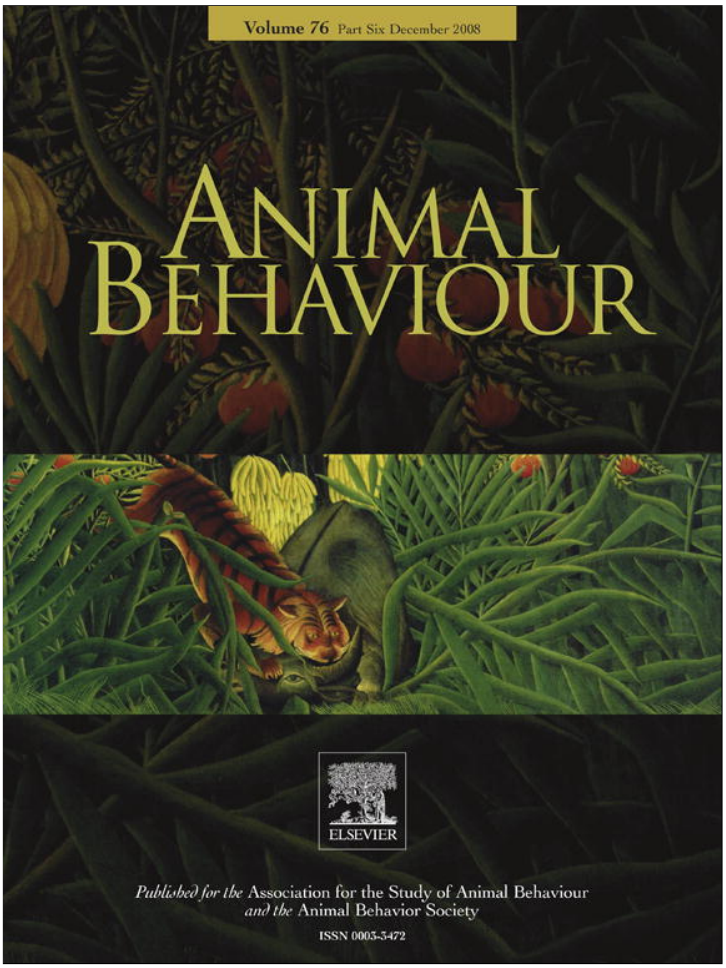

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Experimental evidence of vocal recognition in young and adult black-legged kittiwakes

HERVÉ MULARD*†, THIERRY AUBIN‡, JOËL F. WHITE*†, SCOTT A. HATCH§ & ÉTIENNE DANCHIN*

*Laboratoire d'Écologie, UMR 7625, Université Pierre et Marie Curie
†Konrad Lorenz Institute for Ethology, Austrian Academy of Science
‡Laboratoire Mécanismes de Communication, UMR 8620, Université Paris-Sud
§U.S. Geological Survey, Alaska Science Center, Anchorage

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Individual recognition is required in most social interactions, and its presence has been confirmed in many species. In birds, vocal cues appear to be a major component of recognition. Curiously, vocal recognition seems absent or limited in some highly social species such as the black-legged kittiwake, *Rissa tridactyla*. Using playback experiments, we found that kittiwake chicks recognized their parents vocally, this capacity being detectable as early as 20 days after hatching, the youngest age tested. Mates also recognized each other's long calls. Some birds reacted to their partner's voice when only a part of the long call was played back. Nevertheless, only about a third of the tested birds reacted to their mate's or parents' call and we were unable to detect recognition among neighbours. We discuss the low reactivity of kittiwakes in relation to their cliff-nesting habit and compare our results with evidence of vocal recognition in other larids.

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Keywords: black-legged kittiwake; long call; mate recognition; parent–offspring recognition; playback; *Rissa tridactyla*; vocal communication

Most mechanisms of social interactions (i.e. cooperation, mutualism or mating systems, see Hamilton & May 1977; Bateson 1978; Emlen 1994; Nowak & Sigmund 1998) assume the existence of individual recognition. For example, interactions between mates are important in species with biparental care, and in monogamous long-lived birds, mate recognition should promote parental coordination. In species forming long-lasting pair bonds, mate recognition is also likely to persist for years. In species with parental care, parents may need to recognize their young to avoid misdirecting parental care, and young may also need to recognize their parents to avoid infanticide, or simply to solicit parental care. Several hypotheses about the evolution of divorce also implicitly assume that recognition of mates and neighbours is prevalent (Cézilly et al. 2000). Finally, kin recognition may be involved in inbreeding avoidance.

Consequently, individual recognition has been the focus of many studies in various taxa. In birds, most reported evidence involves vocal recognition. Among larids for example, chicks of laughing gulls, *Larus atricilla* (Beer 1969), black-headed gulls, *L. ridibundus* (Charrier et al. 2001) and black-billed gulls, *L. bulleri* (Evans 1970) recognize their parents vocally. Black-headed and slender-billed gulls, *L. genei*, also have individually distinct voices (Mathevon et al. 2003).

In the cliff-nesting black-legged kittiwake, *Rissa tridactyla*, as in many other bird species, the question of vocal recognition is unresolved. The black-legged kittiwake is a long-lived (Hatch et al. 1993; Cam et al. 2002), strictly monogamous seabird (Helfenstein et al. 2004) in which

Correspondence and present address: H. Mulard, Laboratoire Ecologie et Neurologie Sensorielles, Université Jean Monnet, 23 Rue Paul Michelon, 42023 Saint-Etienne Cedex 02, France (email: hmulard@snv.jussieu.fr). T. Aubin and J. F. White are at the Laboratoire Mécanismes de Communication, UMR 8620, Université Paris-Sud, Bâtiment 446, F – 91405 Orsay, France. S. A. Hatch is at the U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508-4626, Canada. E. Danchin is now at Evolution et Diversité biologique, Université de Toulouse, 118 Route de Narbonne, 31062 Toulouse Cedex 9, France.

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most successful pair members remain faithful across years (Coulson 1966; Naves et al. 2006). Such high mate fidelity has been shown experimentally to result from individual rather than nest site recognition (Fairweather & Coulson 1995). Despite equivocal evidence concerning the role of vocal recognition, we hypothesized that kittiwakes recognize and memorize the voice of their mate and neighbours over several years. Although Wooller (1978) found evidence for vocal recognition between mates, another study failed to detect any recognition during incubation (T. Aubin, N. Matevon, V. Staszewski & T. Boulinier, personal communication). The long call (the 'ki-tti-wake' call) contains an individual signature (Aubin et al. 2007), but it is unclear whether it is the whole call, or one of its components, that is the carrier. Recognition of chicks by parents is also controversial. Storey et al. (1992) showed that the calls of kittiwake chicks convey a much weaker individual signature than those of related species such as the herring gull, *L. argentatus*, supporting Cullen's (1956) suggestion that adult kittiwakes do not recognize their chicks until they are at least 25 days old. However, Roberts & Hatch (1994) reported that nonlocal chicks attempting to enter a neighbouring nest were more likely to be attacked and repelled by resident adults than locally born chicks. Parent recognition by chicks has not been studied in black-legged kittiwakes. In a previous study, we provided observational evidence that black-legged kittiwake chicks recognize their parents at the time of their first flight (Mulard & Danchin 2008). In this study, we used playback experiments to look at whether (1) offspring are able to recognize their parents, (2) mates are able to recognize each other and (3) they react differently towards their close neighbours versus more distant individuals. We also analysed which component of the long call is important for recognition, by broadcasting partial calls.

METHODS

Study Population

Middleton Island (north-central Gulf of Alaska, 58°25′N, 146°19′W) supports a large population of black-legged kittiwakes (25 000 birds in 1999, Gill & Hatch 2002). We studied kittiwakes nesting on an abandoned U.S. Air Force radar tower which enabled close observation and easy capture (Gill & Hatch 2002). The study plot was on vertical walls with uniform size and spacing of the wooden ledges that served as nest sites. Nest sites were observed from inside the building twice daily from early May to mid August 2006 to assess individual attendance and reproductive success. Chicks were marked on the head (1 cm wide mark that disappeared within 10 days) at hatching using nontoxic permanent colour pens (red or blue) and ringed at 25 days of age. Adults were captured with a small hook from inside the building during the preincubation period while they were on the nest. Both adults and chicks were ringed with U.S. metal and one to four Darvic colour rings (see Gill & Hatch 2002 and Gill et al. 2002 for more details). Similar methods have been used by all workers on kittiwakes since Coulson's pioneer study in the 1950s (Coulson & White 1956). Ringing was authorized by the U.S. Geological Survey. Precise laying and hatching dates were recorded (±0.5 days).

Recording and Editing Playback Samples

Long calls (Tinbergen 1953, 1959; Cullen 1956; Wooller 1978, 1979; Danchin 1987) were recorded from individuals landing or resting at the nest site. An AKG D770 microphone (AKG Acoustics GMBH, Vienna, Austria), connected to a Marantz PMD670 recorder (D&M Holding Inc., Eindhoven, The Netherlands) was placed directly on the nest. Calls were thus recorded from less than 30 cm away. When necessary, calls were shortened (using CTWave32 software, Creative Technology Ltd, Dublin, Ireland) by silencing either the 'ki-tti' or the 'wake' part. Such a modification allowed us to preserve the rhythm of long-call series played back. Sound tracks were broadcast with a Marantz MA6100 and Audax AP080M4 loudspeakers (Applications Acoustiques de Composites, La Chartre sur le Loir, France). Every broadcast track contained 10 repetitions of the 'ki-tti-wake' call (see Fig. 1 and Aubin et al. 2007 for the detailed sonagram and nomenclature of the different parts of the call). All playbacks were made during the chick-rearing period (late July and early August), using recordings obtained during the 25 days preceding the experiment.

Test of Vocal Recognition Response in Chicks

We tested every chick for its ability to recognize its parents, by comparing its reaction to complete calls of (1) its parents, (2) unknown adults and (3) neighbouring breeders. We further tested whether the whole call was necessary to elicit a response by the chick, by comparing its response to playbacks containing only parts of its parents' long calls (i.e. the 'ki-tti' or the 'wake' part, see Fig. 1). Chicks were placed in the centre of a table (250 × 65 cm) in the tower with a loudspeaker at each end. Calls were broadcast from a randomly chosen end. To limit the impact of the manipulations on the chicks, we did all the tests in one experiment involving the successive playback of nine calls in random order: two complete parental calls (one for each parent), two incomplete parental calls containing only the 'ki-tti' part, two incomplete parental calls containing only the 'wake' part, two complete calls from distant, unknown adults, and one from a neighbouring breeder. Calls from unknown adults (recorded at least 10 nests away from that of the tested chick) were chosen randomly. Each tested call was separated from the next by at least 1 min, in which we placed the chick back in the middle of the table and let it settle. Calls were broadcast at an intensity level matching that of an adult (i.e. about 90 dB sound pressure level measured at 1 m from the source). We recorded whether the chick moved more than 40 cm towards the active loudspeaker, and whether it called back in response during the 25 s following the beginning of each playback. A chick displaying one of these responses was recorded as having reacted to the test call (see Table 1).

Chicks were tested at 20, 25 and 30 days of age. Older chicks were not tested because of risks of premature fledging. Overall, 35 chicks from 33 nests were tested for

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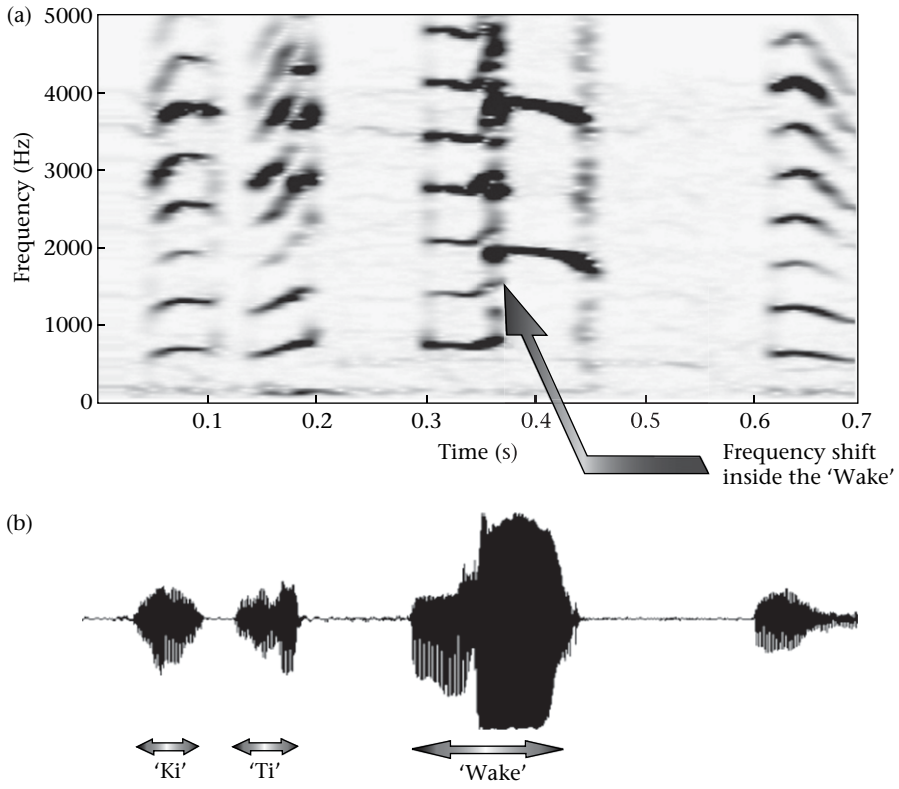

Figure 1. Long call of an adult kittiwake. (a) Frequency in relation to time. (b) Amplitude in relation to time. The nomenclature of the different parts of the call ('ki', '(t)ti', 'wake' and the frequency shift inside the 'wake') is given.

vocal recognition response. We tested 30 chicks more than once; two chicks died between 20 and 25 days old, three were tested only at 30 days, two were not tested at 25 days old and two others were not tested at 30 days old.

Test of Vocal Recognition Response in Adults

As for chicks, we tested breeders for their ability to recognize their mate's long call, by comparing their responses to complete calls of their mates, of unknown adults and of neighbouring breeders. We also tested which part of the long call was involved in the recognition by comparing responses to the whole call and to playbacks containing only parts of its own or mate's long call. Calls were played back to chick-rearing individuals from an observation point 40 m from the base of the tower, with an amplitude (as heard from the tower nests) mimicking that of a bird calling from ca. 5 m. Thus the tested call was not louder than the general noise of the colony and the whole colony could hear the broadcast calls. We videotaped the behaviour of adults at only four to six neighbouring nests at a time; these sessions involved the playback of long calls coming from every breeder recorded in this subarea (three call types per adult: complete, and versions containing only the 'ki-tti' or the 'wake' components) and six complete calls of adults from other areas (i.e. non-neighbours). Each bird thus heard in random order the three types of its own and mate's call, six complete calls of non-neighbours, and the calls of all its recorded neighbours. This enabled us to check the response of the focal breeder to its mate's calls and that of its closest neighbours (less than 50 cm away) simultaneously. To analyse the response of neighbours, we kept only cases when neighbours reacted before the focal adult, to prevent situations where neighbours reacted to the calls of the focal individual. All calls were played back in random order every 20 s, with calls of the same individual at least 5 min apart. We analysed videotapes blindly as the observer did not know the identity of calling birds. Responses were recorded during the playback until 10 s after the end of the broadcast. Responding adults either suddenly moved the head towards the loudspeaker and/or called back in response.

Ethical Note

The study was approved by the French committee of animal ethics and carried out under Alaska State and U.S. Federal Fish and Wildlife permits. Chicks were measured and weighed every 5 days (see Gill et al. 2002 for more details). Playbacks were carried out at this time. Chicks were never kept away from their nests for more than 20 min. We observed the parents' behaviour for 10 min after putting the chick back on the nest. Most displayed normal behaviour shortly after the return of their chick, often feeding them. We followed 122 chicks from the age of 20 days (beginning of the experiment) to 35 days (youngest age of fledging). Eight chicks died during this time, four in our experimental sample (out of 35 chicks) and four in the other nests (out of 87). Chick mortality did

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Table 1. Chick maximal responses observed for each of the nine tested calls

Stimulus call		Number of chicks reacting by					
Origin	Type	Moving to loudspeaker	Calling back	Total	Number of chicks tested	McNemar's *S*	*P*
Unknown adult	Complete	4	1	4	2×34 (2 calls/chick)		
Neighbour	Complete	3	2	4	31	0	NS
Father	Complete	9	4	10	33	4.5	0.03
	'Ki-tti'	10	3	10	33	4.5	0.03
	'Wake'	4	2	6	33	0.67	NS
Mother	Complete	10	6	11	34	7	0.008
	'Ki-tti'	4	0	4	34	0	NS
	'Wake'	2	2	4	34	0	NS

McNemar's chi-square test associated with the paired comparison between total reactivity to unknown adult (used as reference) and the given tested call.

not differ between the manipulated and unmanipulated chicks ($\chi^2_1 = 1.9$, $P = 0.17$), suggesting that the experiment did not increase mortality significantly. Furthermore, external reasons were involved in the deaths of three of our manipulated chicks: one lost its father before 20 days and probably died as a consequence, and two chicks born on exposed nests disappeared simultaneously during a storm. There is thus no tangible evidence that our manipulations increased chick mortality.

Statistical Analysis

For statistical analysis we used the SAS package (SAS Institute Inc., Cary, NC, U.S.A.). Hereafter, the term 'maximal response' depicts focal birds' responses as the maximal level on a 4-point scale: 0 for no response; 1 for movement towards the loudspeaker (for chicks) or head movements (for adults); 2 for call(s) in reply; 3 for movements and call(s) in reply. The variable 'reactivity' depicts focal birds' responses as a binary effect: 0 for no response detected and 1 if the focal bird reacted (maximal response $\geq$1) to the broadcast call. Using these variables makes analyses conservative because chicks are unlikely to react more than once to unknown adults, whereas they usually do so for parents (see Results). The analysis using the maximal response over different tests thus maximizes the reaction to unknown adults. Since the same individual was tested for response to different types of call, we used paired chi-square tests (McNemar's test, McNemar 1947; *S* is the value of the test) to investigate whether chicks/adults moved and/or called differently to the different tested calls. This test allows paired comparison between binary coded variables.

To test the repeatability of chick reactivity, we used the kappa coefficient (κ, Cohen 1960) of the McNemar's test, which estimates the strength of the agreement between classes (when the observed agreement exceeds chance agreement, κ is positive with its magnitude reflecting the strength of agreement). When paired comparisons were not possible (i.e. typically when individuals did not react at all to a certain category of calls), we did simple chi-square tests. To test for repeatability of chick reactivity across ages, we also built a logistic regression model of chick reactivity as a function of age as a fixed dependent variable (with a logit link and a binomial distribution of errors). Similar models were also used to test for an influence of the order of calls in the playback on chick reactivity, and to detect differences in reactivity between types of incomplete calls (as specified in the Results). Post hoc McNemar's chi-square tests were then used to identify which kind of calls were the source of the observed differences.

RESULTS

Vocal Recognition of Parents by Chicks

Complete calls

We first analysed the change in reactivity with chick age. A chick reacting to any of the nine broadcast calls was recorded as 'reactive'. Of 30 chicks tested at least twice, 14 (47%) never reacted, and 33% reacted at two or three different ages. We found no difference in overall chick reactivity according to age (McNemar's chi-square test between 20 and 25 days: $S_1 = 2.7$, $\kappa = 0.58$, $N = 30$, $P = 0.1$; between 25 and 30 days: $S_1 = 0$, $\kappa = 0.55$, $N = 28$, $P = 1$). For a given type of call, chick reactivity also did not differ across ages (binomial logistic regression of reactivity to each type of call as a function of chick age: $P > 0.14$). The order of the calls in the playback did not influence chick reactivity (binomial logistic regression of reactivity as a function of the order of diffusion in the playback session: $F_{1,953} = 0.02$, $P = 0.64$). We thus pooled the observations across ages, and kept only the maximal response to each class of calls for every chick.

We then compared this maximal response towards the father's call to the one observed towards any of the two unknown adult calls. Chicks reacted more to their father than to unknown adults (Table 1). They tended to call more ($S_1 = 3$, $N = 33$, $P = 0.08$) and to move more towards the active loudspeaker ($S_1 = 2.8$, $P = 0.09$) when hearing their father's than unknown adults' voices. Chicks reacted also significantly more to their father than to neighbouring breeders ($S_1 = 7$, $N = 30$, $P = 0.008$). Since chicks heard twice as many complete calls from unknown adults than from their father (and thus had twice as many opportunities

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to react to unknown adults than to their father), this analysis is conservative.

Chicks also reacted more to their mother's calls than to those of unknown individuals (Table 1), calling ($S_1 = 5$, $N = 34$, $P = 0.03$) and moving towards the loudspeaker ($S_1 = 6$, $N = 34$, $P = 0.01$) more often when hearing their mother's voice than that of an unknown adult. Chicks also reacted significantly more to their mother than to neighbouring breeders ($S_1 = 7$, $N = 31$, $P = 0.008$). As for fathers, this analysis is conservative.

At the age of 20 days, seven chicks reacted more to at least one of their parents (out of 33 chicks, 21%) than to unknown adults: four chicks (out of 30, 13%) to their father and six chicks (out of 25, 24%) to their mother, while none of them reacted to unknown individuals. Thus, we found a significant difference in reactivity towards parents versus unknown adults (number of chicks reacting to their father versus unknown adult: simple chi-square test: $\chi^2_1 = 4.26$, $P = 0.04$; mother: $\chi^2_1 = 6.8$, $P = 0.009$; paired chi-square tests were not possible since 20-day-old chicks never reacted to unknown individuals).

Chicks did not show differences in response towards neighbours and unknown adults. Within the chicks tested, only two called back to a neighbour's call. One of them, having lost its father a few days before the 20-day test, was subsequently alone on the nest most of the time, and may have learnt the voice of the tested adult which was its closest neighbour, and was repeatedly seen on the tested chick's nest.

Incomplete calls

We built a general mixed model with reactivity depending on the type of call (without taking into account reaction to parents' complete calls) and chick identity as a random factor to test whether chicks reacted more to playbacks containing only parts of the long call. We found a significant effect of the type of call ($F_{1,130} = 2.72$, $N = 168$, $P = 0.004$) which revealed that chicks reacted more strongly to their father's calls containing only the 'ki-tti' part (Table 1) than to unknown calls. Overall, 10 chicks reacted to the father's 'ki-tti' call, six to the father's 'wake' call (four responding to all their father's incomplete calls), four to the mother's 'ki-tti' call and four to the mother's 'wake' call (two responding to all their mother's incomplete calls). Thus, the father's calls containing only the 'wake' part and the mother's calls containing either the 'ki-tti' or the 'wake' part (Table 1) were not sufficient to trigger a significantly higher reaction than unknown individual calls.

Vocal Recognition of Mates

Adults never reacted to unknown or to close neighbours, while one (3%) of 29 tested breeders moved its head in response to its own complete call and nine (31%) responded to their mate's complete call, seven (24%) of them calling back in response (Table 2). Thus, individuals reacted significantly more to their mate's complete calls than to those of other individuals (Table 2). There was no difference between males and females, as four of 13 females and five of 16 males responded to their mate's complete calls ($\chi^2_1 = 0.0008$, $N = 29$, $P = 0.98$).

One individual was not tested with its mate's incomplete calls. Among the 28 remaining birds, two reacted to their mate's incomplete calls, although these birds did not react to complete calls. Four (14%, one female and three males) reacted to the 'kitti' part of the call. One of them called back in response. Two birds (7%, one male and one female) reacted and called back to the 'wake' part. However, even when adults reacted more to their mate's than to their own incomplete calls, this was not significant (Table 2).

DISCUSSION

Chicks reacted significantly more to their parents than to other adults. To our knowledge, this is the first study to document parent recognition by young kittiwake chicks. Despite the possibility of experimentally induced stress, about a third of the chicks reacted as early as 20 days of age, and these responses were repeatable. This relatively weak response rate may reflect the effects of experimental stress or weak selection pressure for parent recognition in the chicks of this species. Most kittiwakes in the study population rear only one chick to fledging (Roberts & Hatch 1993; Gill et al. 2002). Beyond about 10 days after hatching, most chicks do not have to compete with siblings for food and parental care; thus there may be little to gain by reacting immediately to their parents' landing. Alternatively, because parental attendance remains high before chicks are 20–25 days old (Roberts & Hatch 1993), the selection pressure on chicks to recognize their parents may apply only later. However, the fact that 21% of the chicks reacted to their parents' complete calls at 20 days of age, and that this percentage did not increase significantly over time, argues against the latter explanation.

Our results further indicate that chicks can recognize their parents' calls when they hear only half of the call (and particularly the 'ki-tti' part). This suggests that the first part of the call may convey some individual cue. However, although the effect was not significant, some birds also reacted to the 'wake' part, and some reacted to both parts of parental calls. This suggests that the identity cues may vary from one individual to another, and perhaps that the signature is coded in different ways throughout the signal. This is also consistent with the fact that multiple repetitions of the long call are needed to elicit a response. Previous studies (Aubin et al. 2007) suggested that an individual signature is probably not encoded in one particular acoustic parameter, but is rather multiparametric. This may facilitate detection in the noisy environment of a bird colony (Danchin & Nelson 1991; Aubin & Jouventin 2002).

Our results also confirm that adults of both sexes are able to recognize their mates according to vocal cues (Wooller 1978). As for chicks, only a part of the call may be sufficient to elicit recognition, but only a third of the tested adults reacted noticeably. This low proportion is consistent with the observation that most birds called back to their mates' prelanding calls less than 1 s before

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Table 2. Adult maximal responses observed for each of the calls

Stimulus call		Number of adults reacting by			Total number of observations	McNemar's *S*	*P*
Origin	Type	Moving the head	Calling back	Total			
Unknown adult	Complete	0	0	0	142 (29 birds tested)		
Neighbour	Complete	0	0	0	57 (24 birds tested)		
Mate	Complete	9	7	9	29	6.4	0.01
	'Ki-tti'	4	1	4	28	1.8	NS
	'Wake'	2	2	2	28	2.07*	NS
Own	Complete	1	0	1	27		
	'Ki-tti'	1	0	1	29		
	'Wake'	0	0	0	28		

McNemar's chi-square test associated with the paired comparison, for a given type of call, between response to own call (used as reference) and to the mate's call.
*Simple chi-square test, since no adults react to their own 'wake'.

the actual landing, that is, when the mate was already very close (personal observation). Only a small proportion of adults called back well ahead of the landing of their mate, indicating that in most instances, vocal cues alone may be insufficient to elicit a detectable response. Visual cues may also convey information about the identity of the incoming adult. After landing in the presence of their mate, individuals perform complex displays including vocalizations and head movements (Heath et al. 1982; Danchin 1987; Baird 1994) that may help confirm identity visually and acoustically. Interactions with intruders also involve numerous vocalizations (calls, bow and moan, choking) that presumably have a role in individual recognition and site defence. Wooller (1978) reported that adults did not react when calls were broadcast from inside the warehouse colony, suggesting that directional orientation of the sound matters. The location of loudspeakers (ca. 20 m beneath and 40 m distant from nest ledges) may have contributed to the weak response of adult kittiwakes in our study. Furthermore, a breeder's reaction to the voice of its mate might be more evident during pair formation than during chick rearing. Wooller (1979) found a peak of vocalizing at the beginning of the breeding season, suggesting vocalizations are important for individual recognition in that early stage. This is consistent with the fact that pair formation in kittiwakes conspicuously involves repeated arrivals and departures at the nest site (Danchin & Nelson 1991). Finally, the absence of response does not necessarily imply lack of recognition.

We were unable to detect any vocal recognition among neighbours; neither adults nor chicks reacted differently to calls of close neighbours and calls from more distant adults. Many social interactions assume individual recognition between neighbours, and it would be surprising if individuals of a highly social species such as the kittiwake could not recognize at least some immediate neighbours. Some observations in natural conditions strongly suggest that breeders do recognize their neighbours. For example, adults often chase prospectors on neighbouring nests, which implies that they do recognize unestablished birds. However, prospectors usually land silently on nests (Danchin 1987; Danchin et al. 1998) and neighbours may thus identify such adults as foreigners by their behaviour, not by their vocal signature. Alternatively, we speculate that adults may recognize their neighbours but have no reason to react in a detectable way. Indeed, only squatters (individuals temporarily occupying a nest occupied by a pair, Monnat et al. 1990) are a problem for established breeders, as they often provoke high levels of disturbance (fights, harassment, Cadiou et al. 1994). Thus, while breeders generally do not react conspicuously to their neighbours' calls, one should stress again that the absence of response does not necessarily mean absence of recognition.

The level of response to vocal cues in black-legged kittiwakes appears to be among the lowest of any larid, which is probably a derived trait associated with the species' cliff-nesting habit. For example, Mathevon et al. (2003) showed that individual recognition of chicks by adults is less developed in the nidicolous black-headed gull than in the nidifugous slender-billed gull. Most larids studied have an acute ability to recognize their mate (e.g. little terns, *Sterna albifrons*: Moseley 1979) or parents (e.g. black-headed gulls: Charrier et al. 2001; laughing gulls: Beer 1969, 1970). In some species, there is also a change in individual recognition with age, chicks being able to recognize their parents only after fledging (e.g. black-billed gulls: Evans 1970). In black-legged kittiwakes, chick movements are highly constrained, and the low outward response to the vocal environment may thus be caused by relaxed selection pressure for individual recognition.

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