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

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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.

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

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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