Voice variance may signify ongoing divergence among black-legged kittiwake populations

HERVE MULARD[1,2*,†], THIERRY AUBIN[3], JOËL F. WHITE[1,2,4‡], RICHARD H. WAGNER[2] and ÉTIENNE DANCHIN[4]

[1]*Laboratoire d'Écologie, UMR 7625, Université Pierre et Marie Curie, 7 Quai Saint-Bernard, Case 237, 75005 Paris, France*
[2]*Konrad Lorenz Institute for Ethology, Austrian Academy of Science, Savoyenstrasse 1a, 1160 Vienna, Austria*
[3]*Laboratoire Mécanismes de Communication, NAMC CNRS UMR 8620, Université Paris-Sud, Bât. 446, 91405 Orsay cedex, France*
[4]*Evolution et Diversité biologique (EDB), UMR 5174 CNRS-UPS, Université de Toulouse, 118 Route de Narbonne, 31062 Toulouse Cedex 9, France*

Acoustic features are important for individual and species recognition. However, while dialectal variations in song characteristics have been described in many songbirds, geographical divergence in vocal features across populations has seldom been studied in birds that are not thought to have song-learning abilities. Here, we document marked differences in the vocal structure of calls of two populations of black-legged kittiwakes (*Rissa tridactyla*), a seabird whose call is considered as not being learned from other individuals. We found that calls vary both within and between populations. Within-population variation may convey individual identity, whereas the marked differences in frequency and temporal parameters observed between the two populations may reveal ongoing divergence among kittiwake populations. Moreover, we were unable to detect any sex signature in adult calls in a Pacific population (Middleton, Alaska), while these were detected in an Atlantic population (Hornøya, Norway), potentially affecting sexual behaviours. Despite the fact that these calls seemed to change over the reproductive season and across years, the individual signature remained fairly stable. Such vocal differences suggest that Pacific and Atlantic populations may be undergoing behavioural divergences that may reveal early stages of speciation, as is suggested by molecular data. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **97**, 289–297.

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INTRODUCTION

Songbirds usually learn songs from other adults, song characteristics thereby being inherited by vocal imitative learning (Nelson & Marler, 1994). Errors in social learning may accumulate and cause divergences between populations (Chilton & Lein, 1996; Irwin, 2000; Ellers & Slabbekoorn, 2003). Song learning is thus thought to generate geographic song variations, or dialects (Chilton & Lein, 1996; Searcy *et al.*, 2002), that have been proposed to result from divergent cultural selection or drift (Danchin *et al.*, 2004; reviewed in Kroodsma & Miller, 1996). Evolutionary changes in song characteristics may, for instance, result from the overproduction of previously memorized song, as well as the counter-selection of those that fail to match the general dialect of the population

(Nelson & Marler, 1994). Evolutionary changes in song may also result from differences in transmission linked to structural differences of the environment (the habitat selection hypothesis, Slabbekoorn & Smith, 2002; Van Dongen & Mulder, 2006). In the long term, such song divergence driven by divergent social inheritance may potentially lead to speciation (Grant & Grant, 1997; Irwin, 2000; Slabbekoorn & Smith, 2002; Danchin *et al.*, 2004).

Like songbirds, seabirds widely use acoustic signals in pair formation, nest relief and parent–offspring interactions (e.g. Tinbergen, 1953; Evans, 1970; Ingold, 1973; Danchin, 1991; Aubin & Jouventin, 1998; Lengagne, Lauga & Aubin, 2001). Most seabirds are sexually monomorphic and breed in large and dense colonies, which creates risks of misidentification (Slabbekoorn, 2004). Vocal displays may thus play a major role in mate and parent–offspring recognition (Falls, 1982), as has been shown, for instance, in penguins (Aubin & Jouventin, 2002; Aubin, 2004) and in Larids (Hutchinson, Stevenson & Thorpe, 1968; Beer, 1969; Evans, 1970; Charrier *et al.*, 2001; Mathevon, Charrier & Jouventin, 2003). Contrary to songbirds, the different types of calls in seabirds are usually considered as not learned from adults, therefore acoustic features of these calls are assumed to be fixed and thus implicitly under strong genetic control (review in Kroodsma, 2004). As acoustic signals, like all heritable features, may change gradually over time as a result of mutations, selection and drift (West-Eberhard, 1983; Seddon & Tobias, 2007), two genetically different populations are likely to also have distinct acoustic features. However, this hypothesis has mostly been addressed in songbirds (e.g. Seddon & Tobias, 2007) and studies in non-oscines are lacking.

Here, we compare the acoustic features and the potential for vocal recognition among individuals and between sexes in two distant populations of adult black-legged kittiwakes, *Rissa tridactyla*, a subarctic gull breeding in dense, vertical colonies. Aubin *et al.* (2007) have documented individual and sex signatures in kittiwake long-calls in an Atlantic population (Hornøya, Barents Sea, Norway). We tested whether vocal sexual differences also exist in a Pacific kittiwake population (Middleton, Gulf of Alaska, USA). Furthermore, as Wooller (1978) suggested that long-calls may change within and between reproductive seasons, we recorded long-calls at different stages of the breeding season and in two consecutive years to test for temporal changes in long-call characteristics. We also expected to detect significant differences in long-calls between Atlantic and Pacific kittiwakes because these populations differ genetically and morphologically (McCoy, Boulinier & Tirard, 2005).

MATERIAL AND METHODS

STUDIED POPULATIONS

Middleton Island (north-central Gulf of Alaska, 58°25′N, 146°19′W) supports a large population of black-legged kittiwakes (25 000 individuals in 1999, Gill & Hatch, 2002). We studied kittiwakes nesting on sites on an abandoned US Air Force radar tower which has been modified to enable close observations and easy captures (Gill & Hatch, 2002). Hornøya Island (Barents Sea, Norway, 70°21′N, 31°02′E) supports a population of more than 10 000 breeding pairs (for further details, see Aubin *et al.*, 2007). In both colonies, tape recordings focused mainly on ringed adults of known sex.

RECORDINGS

Long-calls (also named 'kittiwake' calls; Tinbergen, 1953; Cullen, 1956; Wooller, 1978; Danchin, 1987) are usually emitted as individuals land on their nest and by pair members when they greet each other on the nest. At the Middleton population, a AKG D770 microphone (connected to a Marantz PMD670 digital recorder, sampling frequency 48 kHz) was placed directly on the nest and calls were recorded from a distance of less than 30 cm. Adults were recorded in May and early June (corresponding to the pre-laying period) and again in late July and August (corresponding to the chick rearing period) in 2005 and 2006. On Hornøya, individuals were not as easily accessible as on Middleton and they were thus recorded from a distance of 10–20 m with a SEN-NHEISER ME 64 microphone equipped with a 60-cm TELLINGA parabola (connected also to a Marantz PMD670 with a sampling frequency of 48 kHz, Aubin *et al.* (2007). These slight methodological differences between the two studies may affect variables linked to energy repartition (i.e. the different quartiles, see below and Table 1), but cannot affect temporal parameters and fundamental frequencies measures.

LONG-CALL ANALYSES

We used the SASLab software (Avisoft) for call measurements (Fig. 1). Measured parameters were the same as in Aubin *et al.* (2007; Table 1). Depending on the individual, some calls have a break in frequency inside the 'wake' part; for such calls, we therefore distinguished two parts within the 'wake'. We refer to this kind of call as 'first class calls', and refer to calls without frequency break (and for which the variables linked to the second part of the 'wake' could not be estimated) as 'second class calls'.

STATISTICAL ANALYSES

Statistical analyses were carried out using the SAS® package (SAS Institute, 1999). Following Aubin *et al.*

Table 1. Parameters measured on black-legged kittiwakes' long-calls on Middleton

Parameter name	Significance
Time parameters	
DurKi	Duration of the 'ki' part
DurKiTi	Duration between the end of the 'ki' and the beginning of the 'ti' part
DurTi	Duration of the 'ti' part
DurTiWk	Duration between the end of the 'ti' and the beginning of the 'wake' part
DurWake	Duration of the 'wake' part
DurWakeBeg	Duration of the first part of the 'wake' part when existing
DurIntKi	Duration between two consecutive 'ki'. On Middleton Island, we measured for some calls the DurIntKi and the duration between two consecutive 'wake' (used for Hornøya population, Aubin *et al.*, 2007), and found no significant difference between both measures, thus, as DurIntKi is easier to record on Middleton, we will use that one in this paper.
Frequency parameters	
F0KiBeg	Fundamental frequency of the beginning of the 'ki' part
F0KiMax	Maximum fundamental frequency of the 'ki' part
F0KiEnd	Fundamental frequency of the end of the 'ki' part
F0TiBeg	Fundamental frequency of the beginning of the 'ti' part
F0TiEnd	Fundamental frequency of the end of the 'ti' part
F0WakeBeg	Fundamental frequency of the beginning of the 'wake' part
F0Wake	General fundamental frequency of the 'wake' part, or of the first part of the 'wake' when this one is spliced in two
Q25, Q50 and Q75	First, second and third quartile of the 'wake' part, or of the first part of the 'wake' when this one is split in two parts
F0WakeB	Fundamental frequency of the second part of the 'wake' part, when existing
Q25B, Q50B, Q75B	First, second and third quartile of the second part of the 'wake' part
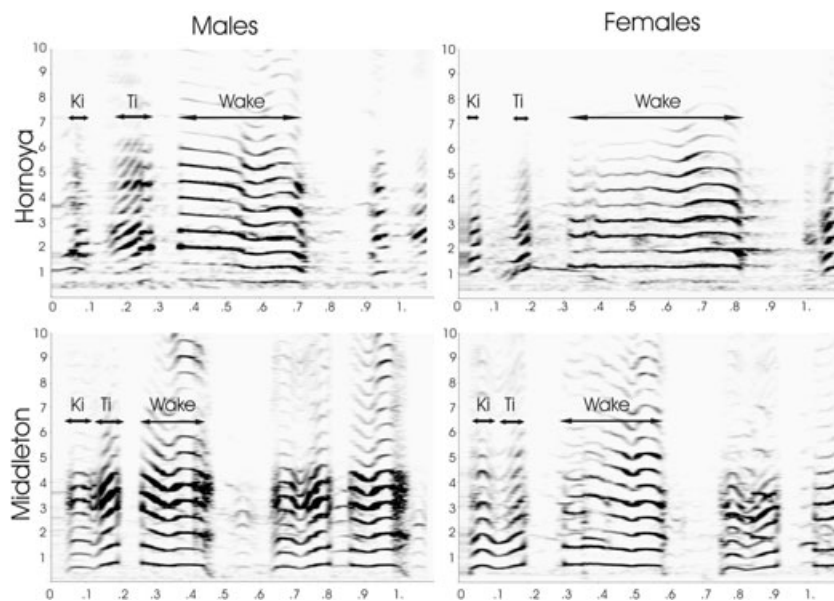
Figure 1. Spectrograms of the long-calls in the two populations. Each panel represents the same amount of time (1.1 s) and the same frequency domain (0–10 000 Hz), with a tick every 0.1 s on the x-axis and every 1000 Hz on the y-axis.

(2007), we defined the potential for individual coding (PIC) as the among-individual coefficient of variation divided by the intra-individual coefficient of variation. Similarly, the potential for sex coding (PSC) and the potential for population coding (PPC) were the coefficient of variation between sexes (or populations) divided by the intra-sex (or intra-population) coefficient of variation. PSC and PPC were calculated over the means per individual for each parameter. The significance of PIC, PSC and PPC were estimated using Kruskal–Wallis tests. When not stated otherwise, discriminating analyses were performed using the principal components of the selected variables calculated over all available long-calls of individuals for which at least four calls were recorded. For discrimination between sexes or between populations, we also tested the efficiency of the discriminating analyses using χ^2-tests between the number of errors made by the analysis and the number of errors expected from a random sorting.

RESULTS

INDIVIDUAL SIGNATURE ON MIDDLETON

We calculated the coefficient of variation and the PIC on 760 calls produced by 78 individuals (35 females, 41 males and two unsexed adults). Eighteen individuals gave only second class calls and thus the variables for the second part of the 'wake' were assessed for the remaining 60 individuals only. All variables were found to potentially code for individuality (all Kruskal–Wallis tests were highly significant; Table 2).

Using a discriminating analysis on principal components calculated for all variables except those of the second part of the 'wake', we assigned the correct owner to 75% of the calls (760 calls coming from 78 individuals recorded at least four times, 16 variables), indicating that calls were individually distinct. With the 21 variables estimated on first class calls, we reached a correct discrimination of 88% of the calls according to individual (538 calls coming from 60 individuals with at least four recorded first class calls, 21 variables). Using principal components calculated from temporal variables only (seven variables), we obtained a correct discrimination of 58%, and with frequency variables only (14 variables), we obtained a correct discrimination of 57% of these calls, which is still significantly different from random sorting (assuming a random sorting probability of 1/60, $\chi^2_2 = 398$, $P < 0.0001$).

SEXUAL DIMORPHISM ON MIDDLETON LONG-CALLS

We first tested whether males were more likely to give first class calls than females. Among the 35 recorded females, 13 gave only first class calls, nine

Table 2. Individual signature in the long-call in the Middleton kittiwake population

Parameters	CVbet	CVind	PIC	KW
DurKi (78)	20.9	15.2	1.37	**335.7**
DurKiTi (78)	222.8	185.8	1.20	**414.7**
DurTi (78)	26.2	19.5	1.34	**429.7**
DurTiWk (78)	44.8	25.6	1.75	**517.7**
DurWake (78)	20.3	11.7	1.74	**513.8**
DurWakeBeg (60)	28.4	18.0	1.58	**340.5**
DurIntKi (78)	10.5	6.4	1.65	**506.9**
F0KiBeg (78)	11.5	8.7	1.32	**343.8**
F0KiMax (78)	11.2	8.6	1.30	**363.6**
F0KiEnd (78)	17.4	11.0	1.57	**445.1**
F0TiBeg (78)	18.3	12.1	1.51	**425.5**
F0TiEnd (78)	10.1	8.4	1.21	**282.0**
F0WakeBeg (78)	10.1	8.1	1.24	**291.8**
F0Wake (78)	10.5	7.4	1.41	**373.1**
Q25 (78)	18.9	16.4	1.15	**232.4**
Q50 (78)	12.5	10.2	1.22	**250.8**
Q75 (78)	19.7	15.7	1.26	**205.4**
F0WakeB (60)	34.0	25.9	1.31	**233.6**
Q25B (60)	22.5	19.0	1.18	**193.3**
Q50B (60)	18.0	13.6	1.32	**121.0**
Q75B (60)	34.0	27.1	1.25	**184.2**

For each parameter, the number of observations is given by the number in brackets (we only kept the individuals with at least four recorded calls).
Potential of individual coding (PIC) is the quotient of the among-individual coefficient of variation (CVbet) by the within-individual coefficient of variation (CVind). Its significance was tested by a Kruskal–Wallis test (the 'KW' column giving the χ^2 with significant results in bold; P-values were all below 0.0001).

gave only second class calls and 13 gave both. Among the 41 males, 21 gave only first class calls, nine gave second class calls and 11 gave both. Thus, there was no difference between males and females in the general structure of the calls ($\chi^2_1 = 1.58$, $P = 0.45$, $N = 76$).

We then looked for a sexual signature in the different recorded variables. The duration of the first part of the wake (when present) and four frequency variables differed significantly between males and females: the fundamental frequencies of the beginning of the 'ki' and 'wake' part, of the end of the 'ti' part, of the first and the second part of the 'wake' (see Table 3). After Bonferoni correction for multiple tests, F0KiBeg and F0TiEnd were no longer significant. Using only the variables that may code for a sexual signature, we obtained a correct discrimination of the sex for only 58% of the 750 recorded calls (with four variable: F0WakeBeg, F0Wake, F0KiBeg and F0TiEnd) and 62% of the 528 first class calls (with the

Table 3. Sexual signature in the long-call in Middleton kittiwakes

Parameters	Females	Males	CVb	CVw	PSC	KW	P-value
DurKi (ms) (35–41)	72 ± 11 (42–111)	73 ± 10 (40–94)	14.5	14.6	0.99	0.001	0.98
DurKiTi (ms) (35–41)	11 ± 17 (0–72)	10 ± 14 (0–51)	149.2	150.0	0.99	0.096	0.76
DurTi (ms) (35–41)	67 ± 13 (43–99)	67 ± 15 (34–96)	20.8	20.8	1.00	0.62	0.43
DurTiWk (ms) (35–41)	85 ± 32 (0–148)	90 ± 36 (0–179)	39.4	39.5	1.00	0.09	0.76
DurWake (ms) (35–41)	183 ± 38 (126–294)	181 ± 26 (133–229)	17.7	17.8	0.99	0.26	0.61
DurWakeBeg (ms) (27–31)	123 ± 28 (76–173)	115 ± 26 (57–171)	22.9	22.9	1.00	**4.7**	0.03
DurIntKi (ms) (35–41)	578 ± 54 (488–747)	572 ± 47 (446–684)	8.74	8.83	0.99	1.01	0.32
F0KiBeg (Hz) (35–41)	510 ± 50 (423–635)	496 ± 36 (418–596)	8.64	8.59	1.01	**5.79**	0.02
F0KiMax (Hz) (35–41)	582 ± 55 (498–705)	569 ± 37 (495–646)	8.15	8.10	1.01	1.73	0.19
F0KiEnd (Hz) (35–41)	473 ± 76 (371–619)	467 ± 52 (374–594)	13.6	13.7	1.00	1.64	0.20
F0TiBeg (Hz) (35–41)	482 ± 80 (371–642)	475 ± 63 (372–624)	14.9	15.0	0.99	0.28	0.60
F0TiEnd (Hz) (35–41)	709 ± 57 (612–825)	689 ± 41 (616–797)	7.14	7.05	1.01	**4.36**	0.04
F0WakeBeg (Hz) (35–41)	683 ± 53 (539–777)	656 ± 41 (553–747)	7.27	7.03	1.03	**23.3**	< 0.0001
F0Wake (Hz) (35–41)	638 ± 55 (525–754)	620 ± 50 (521–763)	8.44	8.40	1.00	**14.8**	0.0001
Q25 (Hz) (35–41)	2496 ± 273 (1761–3068)	2451 ± 294 (1593–3042)	11.5	11.5	1.00	2.25	0.13
Q50 (Hz) (35–41)	3397 ± 260 (2920–3893)	3419 ± 295 (2355–3950)	8.18	8.20	1.00	0.023	0.88
Q75 (Hz) (35–41)	4799 ± 500 (3725–6321)	4809 ± 411 (3913–5630)	9.42	9.55	0.99	0.27	0.61
F0WakeB (Hz) (27–31)	1217 ± 310 (801–1760)	1394 ± 282 (830–1845)	23.4	23.1	1.02	**24.6**	< 0.0001
Q25B (Hz) (27–31)	2850 ± 400 (1868–3542)	2818 ± 429 (1728–3630)	14.6	14.8	0.99	0.22	0.64
Q50B (Hz) (27–31)	3674 ± 297 (3116–4700)	3666 ± 291 (2954–4392)	7.98	8.09	0.99	0.017	0.90
Q75B (Hz) (27–31)	5920 ± 1121 (3560–8598)	6295 ± 1223 (3981–8750)	19.4	19.3	1.00	2.90	0.09

For each parameter, the number of observations is given in parentheses (females–males; we only kept in the analyses the individuals with at least four recorded calls). We give the mean ± SD (minimum–maximum) for the mean per individual of each parameter.

Potential of sex coding (PSC) is the ratio of the between-sex coefficient of variation (CVb) to the intra-sex coefficient of variation (CVw). Its significance was tested by a Kruskal–Wallis test over all calls (the 'KW' column giving the χ^2 and significance of the test following, with significant results in bold).

four previous variables, DurWakeBeg and F0WakeB). With all variables, we obtained a correct discrimination of the sex for only 68% of the 750 recorded calls (16 variables) and 69% of the 528 first class calls (21 variables). These figures differ from random sorting ($\chi^2_1 = 41$, $P < 0.0001$), but are far from the 100% of discrimination found in Hornøya (Aubin *et al.*, 2007). Furthermore, most PSCs were very close to 1 in Middleton, indicating also that the recorded variables were unlikely to code for sex.

CHANGES OF THE LONG-CALL DURING THE SEASON AND BETWEEN YEARS ON MIDDLETON ISLAND

Analyses presented in the following lines were made with all calls without taking into account variables calculated from this second part of the 'wake'. In 2005 and 2006, 11 birds (133 calls) were recorded both in the pre-incubation and chick-rearing periods (seven males and four females with a minimum of three calls/individual/period). In this subsample, we correctly discriminated 93% of the calls according to individual only. To test whether calls change during the reproductive season, we created a new variable concatenating the individual and the recording period. On the basis of a discriminating analysis using principal components calculated for all variables, we were able to correctly classify 86% of the calls according to this variable. Among the 18 misclassified calls, eight were still correctly classified according to individual. This analysis took into account the fact that calls may change differently from one individual to the next. Indeed, the variables that differed between the two recorded periods differed among the 11 tested individuals.

Twenty-one individuals (253 calls from fourteen males and seven females with a minimum of three calls/individual/year) were recorded during the pre-incubation period in both 2005 and 2006. We correctly discriminated 88% of the calls according to individual only. To test whether calls change over years, we created a new variable concatenating the individual and the recording year. We were able to classify 86% of the calls according to this variable and, among the 39 misclassified calls, 18 were at least correctly classified according to individual. Thus, among-year variation in long-call variation exists but is not strong enough to iron out individual signature. The sample

Table 4. Long-call differences between Hornøya and Middleton kittiwakes

Parameters	Hornøya	Middleton Island	CVb	CVw	PPC	KW	P-value
DurKi (ms) (21–58)	42 ± 15 (24–91)	73 ± 13 (40–111)	29.4	27.0	1.09	**172.3**	< 0.0001
DurKiTi (ms) (21–58)	51 ± 15 (30–91)	10 ± 17 (0–72)	115.2	95.9	1.20	**224.9**	< 0.0001
DurTi (ms) (22–58)	88 ± 15 (62–122)	66 ± 13 (34–93)	23.3	18.9	1.23	**111.5**	< 0.0001
DurTiWk (ms) (22–58)	121 ± 65 (60–355)	91 ± 36 (0–189)	47.9	47.2	1.01	**18.1**	< 0.0001
DurWake (ms) (22–58)	450 ± 94 (230–564)	176 ± 29 (109–226)	53.5	18.7	2.86	**253.1**	< 0.0001
DurWakeBeg (ms) (6–46)	328 ± 102 (194–424)	114 ± 28 (56–173)	57.9	28.3	2.04	**79.0**	< 0.0001
DurIntKi (ms) (22–58)	926 ± 97 (723–1062)	570 ± 48 (446–693)	25.9	9.5	2.72	**241.0**	< 0.0001
F0WakeBeg (Hz) (22–58)	606 ± 85 (462–750)	654 ± 48 (521–757)	10.0	10.8	0.92	**33.6**	< 0.0001
F0Wake (Hz) (22–58)	586 ± 64 (499–739)	616 ± 53 (503–763)	9.5	9.9	0.96	**15.1**	< 0.0001
Q25 (Hz) (22–58)	2085 ± 351 (1179–2659)	2456 ± 275 (1719–3042)	14.4	14.1	1.02	**54.3**	< 0.0001
Q50 (Hz) (22–58)	3193 ± 337 (2396–3756)	3397 ± 261 (2645–3950)	9.8	10.0	0.99	**22.8**	< 0.0001
Q75 (Hz) (22–58)	4759 ± 432 (3822–5427)	4797 ± 544 (3725–6778)	10.8	10.3	1.05	2.07	0.15
F0WakeB (Hz) (6–46)	1659 ± 165 (1359–1827)	1326 ± 316 (604–1845)	23.5	17.2	1.37	**14.8**	0.0001
Q25B (Hz) (6–46)	2783 ± 311 (2278–3173)	2789 ± 416 (1620–3630)	14.8	13.8	1.08	1.72	0.19
Q50B (Hz) (6–46)	3731 ± 419 (3225–4353)	3609 ± 252 (3116–4503)	7.6	9.4	0.81	0.001	0.98
Q75B (Hz) (6–46)	5851 ± 1158 (4608–7773)	6159 ± 1170 (3560–9120)	23.7	21.4	1.11	0.29	0.59

For each parameter, the number of individuals is given in parenthesis (first number for Hornøya, second for Middleton; we only kept in the analyses the individuals with at least three recorded calls). For each population, we give the mean ± SD (minimum–maximum) of the mean per individual of each parameter.

Potential of population coding (PPC) is the ratio of the between-population coefficient of variation (CVb) to the intra-population coefficient of variation (CVw). Its significance was tested by a Kruskal–Wallis test over all calls (the 'KW' column giving the χ^2 and significance of the test following, with significant results in bold).

size was too small to test for a change between calls recorded in the 2005 and 2006 rearing periods.

ACOUSTIC DIFFERENCES BETWEEN MIDDLETON AND HORNØYA

On Hornøya, birds were recorded only during the pre-incubation period (Aubin *et al.*, 2007). We thus compared them to calls coming from that period on Middleton (2005 and 2006 combined).

Except for the 'ki', all temporal parameters were significantly shorter in Middleton individuals (cf. Table 4 and Fig. 1). Middleton individuals distribute vocal energy in higher frequencies (Q25, Q50 and Q25B were significantly higher) and start the 'wake' at a significantly higher frequency than Hornøya birds. Using principal components calculated with these significant variables (nine variables without the variables of the second part of the 'wake'), we were able to classify 98% of the calls correctly (22 individuals from Hornøya, 58 from Middleton). Using temporal variables only, we still classified 98% of the calls correctly (six variables). The discrimination dropped to 73% using frequency variables only (five variables), which still differ from random sorting ($\chi^2_1 = 79.7$, $P < 0.0001$, $N = 688$).

F0Wake and F0WakeBeg were found to differ between sexes in Hornøya (Aubin *et al.*, 2007) with
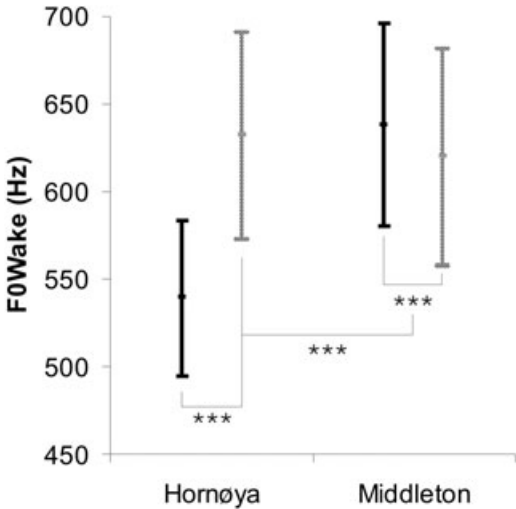

Figure 2. Differences in the fundamental frequency of the 'wake' part between males and females from the two populations. Black, females; grey, males (±SD). All *P*-values were below 0.001 (***).

males calling higher than females. Surprisingly, these variables appeared sufficient to correctly discriminate the sexes on Hornøya but not on Middleton (see above and Fig. 2).

DISCUSSION

Our acoustic analyses demonstrated the existence of a clear individual signature in the long-call in Middleton Island black-legged kittiwakes. This is consistent with Aubin *et al.* (2007), who found that 93.04% of Hornøya kittiwakes' long-calls were individually distinct. Our discriminating analyses further showed that acoustic features may change slightly over the season and across years. Interestingly, most misclassified calls were closer to calls of the same individual at a different time period than to calls of any other individual. Although calls may change slightly over time, the individual signature was still clearly detectable, confirming a previous study carried out over six consecutive years (cited in Wooller, 1978).

Surprisingly, and contrary to results of Aubin *et al.* (2007) on Hornøya, sexual dimorphism was weak in the long-call on Middleton. As sex assessment by calls is likely to be important in monomorphic species, we expected the strong sexual differences found in Hornøya to be a common feature of kittiwake populations. Our results suggest that Middleton adults either rely on other parameters of the long-call or use other clues (Baird, 1994; Jodice *et al.*, 2000; Chardine, 2002) to distinguish potential mates from sexual competitors. However, sex assessment based exclusively on visual features may be problematic in certain circumstances (e.g. in foggy weather) and morphological variables overlap noticeably between males and females (Jodice *et al.*, 2000; Chardine, 2002). Thus, parameters used by Middleton kittiwakes to differentiate sexes remain unclear.

In addition to the absence of sexual dimorphism in Middleton long-calls, many variables also differed sharply between the two populations. Long-calls were noticeably shorter on Middleton and some frequency variables also differed. Most of theses differences are unlikely to result from the slight differences in recording procedures, allowing us to conclude that Hornøya and Middleton populations have different long-calls.

The question of whether these differences reveal the existence of true 'dialects' remains entirely open, the term dialect being usually restricted to geographic variation arising from social learning (Chilton & Lein, 1996). In songbirds, dialectical divergences among populations are usually considered as arising from social learning errors accumulated over generations (Grant & Grant, 1996). In the kittiwake long-call we may speculate that differences result from errors during a hypothetical 'cryptic learning' phase, with young learning and imitating the call of neighbouring conspecifics. However, there is no evidence of such processes in this part of the avian phylogeny, but this may just result from the lack of studies.

Alternatively, observed acoustic divergences may result from either genetic drift or natural selection, such as that imposed by the sound transmission properties in two different habitats (Slabbekoorn & Smith, 2002; Slabbekoorn, 2004). Differences in vocal signals between two distant populations have been suggested to provide the first clue of genetic differentiation (Kroodsma, 2004). Atlantic and Pacific kittiwakes are genetically divergent (McCoy *et al.*, 2005), revealing the occurrence of genetic differentiation between these populations. Kittiwake colonies extend across the Arctic coast of both North America and Asia and North Atlantic populations are thought to have been established only during the past 10 000 years (Stein, Nam & Schubert, 1994). What remains unclear is whether there is a distinct genetic and acoustic separation between the different populations along the Bering Strait or if there is a genetic cline from one ocean to the other (McCoy *et al.*, 2005). Differences in acoustic characteristics may also reveal differences in selective pressures imposed by differences in the transmission properties of the environments. Variations in songbird songs have been found to match differences in environmental resonance capacity (e.g. Van Dongen & Mulder, 2006). However, there is no indication that environments differ significantly as the two studied populations live in similar open coastal areas. The differences reported here are therefore more likely to have evolved by drift than by habitat-dependent selection.

In non-oscine birds, the role of learning in call development is thought to be minimal and acoustic features are generally seen as fixed. Acoustic divergences between Atlantic and Pacific populations could therefore be linked to morphological constraints and reflect some differences in the vocal apparatus. Pacific kittiwakes are on average heavier and have a longer culmen and wing than Atlantic kittiwakes (Sluys, 1982; Chardine, 2002). This may result in differences in resonance patterns and syringal membrane lengths that may explain a part of the differences in vocal features, particularly in frequency. This is, however, difficult to predict, as differences in size do not systematically correlate with differences in acoustic features (e.g. Slabbekoorn & Smith, 2000). Furthermore, differences in temporal variables are unlikely to result from differences in the vocal apparatus and may potentially be an indication of a cryptic, yet-to-be-discovered, learning process. For example, Madden & Davies (2006) have recently shown that cuckoo (*Cuculus canorus*) nestlings develop their begging call through experience, underlining that call learning may exist in non-oscine birds. Cross-fostering experiments are therefore needed to tell apart genetic from social learning inheritance.

Previous studies on kin recognition have shown that kittiwakes use the long-call to recognize mates (Wooller, 1978) and parents (Mulard & Danchin, 2008; Mulard *et al.*, 2008). However, the level of response to kin calls is low in comparison with other Larids (Mulard *et al.*, 2008). This may be because, in kittiwakes, selection is weaker during rearing, either on the individual discrimination or on the acoustic parameters of the long-call. Calls may therefore evolve freely by genetic (and potentially cultural) drift, rapidly leading to differentiation. Interestingly, differences in wingtip patterns seem to change from Arctic Canada anticlockwise around the Arctic to the Pacific (Chardine, 2002). Here, we document acoustic differences between two distant populations along this gradient, but further studies are needed to test whether closer populations are also distinguishable on acoustic features and how vocal divergence matches genetic divergence along the Arctic Ocean. Future studies should also focus on populations at the boundary between Atlantic and Pacific black-legged kittiwakes (i.e. on the Arctic coast of North America and Eastern Siberia) to see whether long-call divergence promotes isolation and limits gene flow between the two populations (Seddon & Tobias, 2007). Temporal changes in long-calls found on Middleton may reveal some plasticity in a non-oscine bird, which may also generate divergence. As no clear genetic differences have been found in close populations in the Atlantic Ocean (McCoy *et al.*, 2005), this context provides an interesting area to test whether other factors (such as morphology, behaviour and acoustics) may evolve faster than genetics, leading to divergence, and potentially speciation, between seabird populations.

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