Parent–offspring recognition in thick-billed murres (Aves: Alcidae)

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Abstract. Using field experiments, we investigated the development of parent–offspring recognition in the thick-billed murre, Uria lomvia. Cross-fostering experiments (N = 73) showed that the likelihood of parents accepting a foreign chick decreased with chick age. Simultaneous-choice playback experiments demonstrated that chicks discriminate between the calls of their parents and both strange and familiar adult conspecifics from as early as 3 days old. In presentation experiments with chicks of fledging age (≥ 14 days), adults responded more strongly to the calls of their own chicks than to other familiar chicks from the same breeding ledge. Results are consistent with those of earlier studies of parent–offspring recognition in the congeneric and ecologically similar common murre, U. aalge, which were among the first to suggest that parent birds and their chicks can identify each other’s calls.

Parent–offspring recognition is particularly important in breeding colonies, where the potential for confusion is maximized due to the proximity of nesting sites and the risk of intermingling young. Such recognition is well developed in colonial bird species, where its development coincides with the onset of brood mobility (Falls 1982; for example alcids: Tschanz & Hirsbrunner–Scharf 1975; Jones et al. 1987; gulls: Beer 1969; Evans 1970; penguins: Jouventin 1982; Davis & McCaffrey 1989; Proft & M Cleen 1991; Seddon & Van Heezik 1993; swallows: Beecher 1981, 1985, 1986; Beecher 1991).

Tschanz (1959, 1968) first documented individual recognition in colonial birds with his studies of parent–offspring interactions in common murres, Uria aalge. His studies centred on four main experiments.

1. When he flushed all parents from a nesting ledge, chicks aged 4 days and older (N = 23) reunited with the correct parent on their return (Tschanz 1959).

2. When he placed chicks in bags (N = 13), parents called in response to the chicks’ calling, and in some cases tucked the entire bag under their wing (Tschanz 1959).

3. He also played both natural and artificially generated adult (but not parental) calls to eggs being incubated in a laboratory. In a simultaneous-choice test conducted after hatching, most chicks (N = 99) approached only the call they had heard from the egg (Tschanz 1968).

4. When he played either parent or stranger calls from a single speaker to chicks of fledging age (N = 21), they approached the speaker more often when he played the parental call (Tschanz 1968).

Based on these results and other anecdotal observations, Tschanz concluded that parents and chicks could recognize each other’s calls.

Tschanz’s pioneering studies of vocal recognition paved the way for subsequent work on vocal communication in colonial birds. There were some weaknesses in his experimental design, however. His finding that chicks responded to parental
calls and vice versa could have been simply a response to conspecific calls and is thus not clear evidence for parent–offspring recognition. The most powerful test would compare the response to calls of different individuals presented simultaneously (Falls 1982), requiring a forced choice by the test subject (Beecher 1991). The difference that T'shanz found in chick response to parent versus stranger calls could also have resulted from discrimination between familiar and unfamiliar calls instead of true recognition between parent and offspring (Beer 1969; Falls 1982).

We investigated parent–offspring recognition in the thick-billed murre, U. lomvia, a species ecologically similar to the common murre except that thick-billed murres tend to breed on narrower ledges (Harris & Birkhead 1985). The calls of both chicks and adults are to some extent individually distinctive in this species (Fig. 1: K. Lefevre, unpublished data), which could provide a physical basis for recognition. Behavioural observations suggested that parent–offspring recognition does occur; for example, banded parents and their chicks correctly reunited after disturbance by predatory gulls or human observers (A. J. Gaston & K. Lefevre, personal observations). Chicks would also benefit by recognizing their parents at about 21 days of age, when they glide to the ocean from ledges up to 1000 m high and reunite with their male parent (Gaston & Nettleship 1981). Breeding ledges, where there is often a high chance of chicks intermingling, create an obvious selection pressure for offspring to develop recognition abilities before they become mobile.

We experimentally tested three hypotheses about parent–offspring recognition.

(1) Using a cross-fostering experiment, we tested the hypothesis that parent–offspring recognition develops soon after hatching, before chicks become mobile and can intermingle with other chicks.

(2) We predicted that chicks would respond to parents more than to either strangers or neighbours. Since murres sometimes provide alloparental care to neighbouring chicks (Birkhead & Nettleship 1984; A. J. Gaston & K. Lefevre, personal observations), we also predicted that chick response to neighbours would be greater than their response to strangers.

(3) We predicted that parents would respond more strongly to their own offspring than to other familiar chicks.

**GENERAL METHODS**

**Study Site**

We conducted experiments at the western subsection of the only thick-billed murre colony on Coats Island, Northwest Territories, Canada (62°56’N, 81°56’W) in northern Hudson Bay, from 22 July to 17 August 1995. We conducted preliminary observations that formed the basis for this work during the 1994 breeding season. Approximately 30 000 breeding pairs of thick-billed murres nest on 75-m high cliffs at this colony,
which is the site of a long-term demographic study (Gaston et al. 1993, 1994).

**Capture, Marking and Measuring**

We studied breeding sites that were safely accessible with basic climbing gear. We captured chicks with our hands or simple nooses; adult birds were not captured, but some bore unique bands from previous work. Chicks were immediately identified with coloured felt marker on the breast, a metal band, a red colour band and a toe clip in case bands fell off. Adults were similarly marked on the breast. We measured wing chord (to the nearest mm) and mass (to the nearest g). Based on approximate hatch dates (±2 days), wing chord length, feather development and/or degree of mobility (Tuck 1961), we categorized chicks into three stages of development that roughly correspond to those used by Tschanz (1959): 'early' (downy and not very mobile, wing length 26–30.5 mm, 1–5 days old), 'middle' (downy and mobile, wing length 35–56 mm, 6–13 days old) and 'late' (fully feathered, gave calls used prior to colony departure (K. Lefevre, unpublished data), wing length >56 mm, 14–22 days old).

**Statistical Analysis**

We used parametric tests for data that were normally distributed or could be so transformed; otherwise we used non-parametric analyses. Two-tailed P-values are reported unless stated otherwise; when a priori, directional predictions were made, one-tailed tests were used. Whenever two or more related tests were performed simultaneously on the same data, we used the sequential Bonferroni method (Rice 1989) to correct the type-I error rate; such tests are reported as significant when tablewide \( \alpha \leq 0.05 \).

**EXPERIMENT 1: PRESENCE AND DEVELOPMENT OF RECOGNITION**

**Methods**

To investigate the occurrence and ontogeny of recognition, we performed a cross-fostering experiment. Since apparent recognition may be due to the behaviour of either parents or offspring, or both, the purpose of this experiment was simply to determine whether and when recognition occurred. To minimize the possibility that foster parents and chicks would be familiar with each other’s calls, we exchanged chicks between two areas of the colony ('exchange areas') that were separated by approximately 20 m. Half of the exchanges were 'swaps' (experimental group); that is, two chicks of a similar age were exchanged between sites. The rest were 'shams' (control group), in which chicks were treated with the same handling procedure as swaps, but were returned to their original sites.

Suitable breeding sites were chosen so that we had a clear view of the site for observing parent and chick behaviour. We used chicks of all three age classes in both control and experimental exchanges (total=six treatment groups). We aimed for a minimum sample size of 10 chicks per group; each chick and parent was used in only one exchange.

To minimize the effects of disturbance, we tried to avoid flushing parents from their ledges during chick capture, although some did leave. Normally one or two chicks were taken from an exchange area at one time; in one case, it was possible to take four chicks in close proximity from each exchange area. Two observers communicating by portable radio selected chicks of similar ages from the two exchange areas. We took chicks to a location half-way between the two sites for processing. We matched chicks to swap between sites based on mass and wing chord length (mean discrepancy based on size of smaller chick=7.5% in mass, 7.1% in wing length). We attempted to use chicks of similar sizes in swap and sham treatments. Chicks were usually placed at breeding sites within 45 min of initial removal.

After chick transfer, we observed the sites for 30 min. To compare post-exchange acceptance between swap and sham treatments, we noted the general response of parents and chicks to each other and we measured the total time that adults brooded chicks. We re-measured chicks that were still present 4 days after the transfer.

We used three measures of acceptance.

1. We classified chicks as accepted or rejected based on the per cent change in mass between weighings. When thick-billed murre chicks are fed by their parents on the ledge, they almost always gain mass every day; for example, during the early stage of development, chicks on Prince Leopold Island, Northwest Territories, gained about 10 g/day (Gaston & Nettleship 1981). Thus, a swapped
chick was considered accepted if the chick grew, or if the mass had not decreased by more than 1%, since a loss of mass over a 4-day period clearly indicates that a chick is not being fed. If no second mass was available, we scored fates based on qualitative observations; for example, chicks that were pecked off the ledge by a parent were clearly rejected. We made all classifications blind to the treatment group of chicks.

(2) We tested for changes in chick mass both within individuals and between swap and sham treatments.

(3) Between treatments, we compared the total time that chicks were brooded after transfers.

Results

We studied 73 chicks: 38 experimental swaps (14 early, 14 middle, 10 late) and 35 sham controls (13 early, 11 middle, 11 late). Sample sizes for each analysis do not total 73 because the data were not complete for each trial; for example, not all chicks were present for a second weighing. Three trials were also eliminated from analysis due to fox predation or because we were not confident that the chick had been returned to the correct breeding site (murres have no physical nest and, in the absence of adults, nest sites can be difficult to locate).

Both swap (92%) and sham (92%) chicks were accepted in early exchanges, but only sham chicks were accepted in the middle and late age periods (Table I). The difference in acceptance rate between middle swap (36%) and sham (80%) exchanges was significant (Fisher’s exact test, $P = 0.02$). Late swap chicks were completely rejected; the difference in the acceptance rates of swaps (0%) and shams (89%) was highly significant ($P = 0.0004$). There was no difference in the acceptance rates of sham chicks of different ages (contingency table, G-test, $G^2 = 0.78$, $P > 0.5$), but the rate of acceptance of swap chicks significantly decreased as age increased ($G^2 = 24.30$, $P < 0.0001$; Fig. 2).

Post-exchange growth patterns also varied among treatments (Table I). Based on changes in the mass of individual chicks, early exchanges in both treatments were accepted by parents; the growth of both early swap and sham chicks was significant (mean = +73.2% and +73.6%, respectively; Table II). Although sham chicks of the middle period grew significantly, the mass of swap chicks decreased (mean = +9% and −2%, respectively; Fig. 3). We were able to re-weigh only one late swap chick, since most chicks in this treatment were quickly rejected by the foster parents, but this chick’s mass decreased by 21%. On average, the masses of late sham chicks increased slightly (mean = +3.5%) but not significantly. There was no significant difference in the overall per cent change in chick mass between the swap and sham treatment groups within each age class (Mann-Whitney U-tests, $P > 0.05$ for early, middle and late; Fig. 3).

The pattern of adult brooding times was similar to that of chick mass changes, but these trends were not significant (Table I). Early chicks of both groups were brooded for almost the entire post-exchange period, but sham chicks were brooded more than swap chicks in both the middle and late groups (Fig. 4). In fact, late swap chicks were not brooded at all by their foster parents (0/10), but most sham chicks (7/11) were brooded for some portion of the observation period.

### Table I. Fates of chicks after cross-fostering experiments

<table>
<thead>
<tr>
<th>Age class</th>
<th>Treatment</th>
<th>Accepted</th>
<th>Rejected</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>Swap</td>
<td>11</td>
<td>1</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>Sham</td>
<td>12</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Middle</td>
<td>Swap</td>
<td>5</td>
<td>9</td>
<td>0.02*</td>
</tr>
<tr>
<td></td>
<td>Sham</td>
<td>8</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Late</td>
<td>Swap</td>
<td>0</td>
<td>10</td>
<td>0.0004*</td>
</tr>
<tr>
<td></td>
<td>Sham</td>
<td>8</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

$P$-values are one-tailed, from Fisher’s exact tests for each age group.

*Significant at tablewide $\alpha = 0.05$.

![Figure 2](image-url) Acceptance rates of thick-billed murre chicks in a cross-fostering experiment.
These results indicate that early swaps were highly successful, some middle swaps were accepted, but all late swaps were rejected. In contrast, most shams of all ages were accepted. This evidence indicates that recognition in thick-billed murres develops during or just prior to the middle stage of development when chicks are 6–13 days old.

**EXPERIMENT 2: DO CHICKS RECOGNIZE PARENT CALLS?**

**Methods**

We conducted simultaneous-choice playback experiments in an outdoor enclosure with chicks of different ages to test whether murre chicks recognize the calls of their parents soon after hatching. We used actual parent calls instead of the natural and synthesized calls of non-parents used by Tschanz (1968). For playbacks, we used the crowing call, a parental vocalization used to communicate with the chick (Cramp 1985; K. Lefevre, unpublished data; equivalent to the common murre luring call described in Tschanz 1968).

Accessible breeding sites were haphazardly chosen for study, and were monitored daily from June to August 1995 to determine hatch dates. Chicks younger than 3 days old were not used, since they have limited mobility and are relatively fragile.

**Recordings and playback tapes**

The chick and parent at each site studied were individually coloured with felt markers. We used

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**Table II. Changes in mass between weighings (before and 4 days after exchanges) and differences in time brooded of swap and sham-exchanged chicks**

<table>
<thead>
<tr>
<th>Age</th>
<th>Treatment</th>
<th>Chicks growth? (one-tailed P; N)†</th>
<th>Mass change (mean ± sd %)</th>
<th>Difference in treatments? (P)‡</th>
<th>Time brooded (min (± sd; N))</th>
<th>Difference in treatments? (P)‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>Swap</td>
<td>Yes (&lt;0.01*; 10)</td>
<td>+73.2 (56.9)</td>
<td>23.5 (11.7; 11)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sham</td>
<td>Yes (&lt;0.01*; 12)</td>
<td>+73.6 (21.2)</td>
<td>N o (0.74)</td>
<td>25.0 (9.1; 12)</td>
<td>N o (0.25)</td>
</tr>
<tr>
<td>Middle</td>
<td>Swap</td>
<td>N o (0.37; 12)</td>
<td>−2.0 (24.3)</td>
<td>8.4 (12.1; 12)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sham</td>
<td>Yes (&lt;0.01*; 10)</td>
<td>+9.0 (11.2)</td>
<td>N o (0.24)</td>
<td>16.5 (12.4; 10)</td>
<td>N o (0.04)§</td>
</tr>
<tr>
<td>Late</td>
<td>Swap</td>
<td>N o (1)</td>
<td>−21.5</td>
<td></td>
<td>0.0 (0; 3)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sham</td>
<td>N o (0.12; 6)</td>
<td>+3.6 (6.3)</td>
<td></td>
<td>8.0 (9.4; 7)</td>
<td>N o (0.03)§</td>
</tr>
</tbody>
</table>

*Significant differences after sequential Bonferroni corrections (tablewide α = 0.05).
†Based on paired masses of individual chicks; paired t-test within each treatment group.
‡One-tailed Mann-Whitney U-test within each age group.
§Not significant after Bonferroni corrections.

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**Figure 3.** Comparison of per cent change in mass from day 1 to day 5 (day 4 for late chicks) between swap (□) and sham (○) treatments. Sample sizes are given above each box. Differences were not significant (Mann-Whitney U-tests, P > 0.05), but the mass increase was always higher for shams. Box plots show the 10th, 25th, 50th, 75th and 90th percentiles and all data points outside this range.

**Figure 4.** Duration (min) that swap (□) chicks were brooded by foster parents after exchange compared to the duration that sham (○) chicks were brooded by their own parents after exchange. Box plots as in Fig. 3. Sample sizes are given above each box.
a Sony Professional Walkman (WM D6) tape-recorder, Sony UX cassette tapes and an Audio-technica model AT815a directional microphone to record the crowing call of the brooding parent and the same call of the nearest neighbour breeding within 1 m. Adult calls were recorded from approximately 1 m away, during natural interactions with the chick when possible; otherwise, we stimulated the parent to call by nudging the chick with a pole or noosing the chick with a 1-m long noose pole and immediately returning it to the site. We recorded several calls from each individual. Crowing calls of four adults from different areas of the colony out of hearing range of the focal birds (>50 m) were recorded, to use as a pool of stranger calls for playback experiments. Since this species is sexually monomorphic, the sex of most birds recorded was unknown (the sexes of some banded birds were known from previous observations of copulations or egg laying). Parents of both sexes were probably represented in the sample, but most recordings were made from 0900 to 2100 hours and thus were probably of male parents, since this is the time of day when most brooding parents are males (A.J. Gaston, personal observations). Both sexes contribute approximately equally to parental care on the ledges (Gaston & Nettleship 1981), so chicks should be able to recognize both parents. Recordings were made only in relatively calm weather conditions to minimize ambient noise.

For each parent studied, recordings of clear calls with minimum background noise were chosen for playback. Using a second Sony Walkman tape-recorder, we dubbed one to two calls onto a 20-s answering machine loop tape until the loop was filled. The loop was recorded continuously for 90 s to a new cassette tape to create a playback tape of the individual parent (P). A similar playback tape was created for the corresponding neighbour (N), and for each of the four strangers (S).

**Experimental protocol: playbacks**

The experimental enclosure for playbacks was an oval, 60-cm high chicken wire fence stapled to a 2.6 × 1.3-m plywood base; it was designed to roughly simulate a breeding ledge (Fig. 5). We anchored the base into a natural alcove on a sod ledge above the colony, parallel to the cliff. One observer sat at each end on natural, raised areas; the observers were positioned greater than 1 m above the enclosure, and thus were not visible at a chick’s eye level. Marks were drawn on the base at 10-cm intervals, and were numbered from 0, the centre, to 10, where Aiwa SC-A8 speakers were positioned 1 m from the centre at each end. Semicircles (radius 30 cm) denoted goal areas around the two speakers. We connected each speaker to a separate Sony Walkman tape-recorder; one observer controlled all playback equipment (Fig. 5).

Playbacks were conducted on fair days with little wind, as soon as possible after recordings were made. Most experiments (23/26) took place...
within 3 days of recording, but two were run 5
days later and one was 8 days later due to poor
weather conditions. Each experiment consisted of
calls presented in three simultaneous-choice trials
with the same chick, always in the same sequence:
(1) parents versus stranger, (2) parents versus
neighbour, and (3) neighbour versus stranger. The
north observer randomly chose the stranger for
each experiment and the starting location (north/ south) of the parent call for trial 1. The south
observer was blind to this information and
recorded all behavioural observations. At the start
of each trial, the chick was placed in the centre of
the enclosure and allowed to habituate to the
enclosure for 90 s (pre-playback period).

We then placed the chick under a plastic 750-ml
cup in the middle of the enclosure, allowed it to
acclimatize for 30 s, and then raised the cup with a
long pole. To create a forced choice, we simul-
taneously played recordings for 90 s during each
trial. All recordings had been made in similar
conditions at the same recording level, and vol-
umes were further equalized by ear prior to the
trial. We recorded time to first movement and
vocalization by the chick and its position on the
grid every 15 s. The leads from the speakers were
switched after trial 1 to change the location of the
parent call in trial 2, but we left the neighbour call
in the same position for trials 2 and 3. After each
trial, we observed the chick for 30 s with no
stimulus played. Between successive trials, the
chick was held in a cloth bag for 3 min, and gently
rotated three times before replacement in the
enclosure, to minimize any bias in movement from
the previous trial. The entire testing process for
one experiment (three trials) lasted 19.5 min, at
which time the chick was marked, measured
and returned to its site within 40 min of initial
removal.

Chick response

For each chick, we calculated an index of
response to each of the three playbacks as follows.
To obtain measures of the chick’s location in
the enclosure every 15 s during a 90-s trial, we
assigned a positive sign to positions in the pre-
dicted side of the enclosure and a negative sign for
the opposite side (predicted direction: trials 1 and
2=parent (P); trial 3=neighbour (N)). From these
six measures, we summed only those in the goal
areas (i.e. within 30 cm of a speaker) to minimize
the effects of random wandering by the chick in
the enclosure. This sum, a measure of movement
toward the playback calls, was used as an index of
chick response. A positive response score repre-
sented a net movement to the predicted goal, and
a negative score represented a net movement to
the opposite goal.

We used randomization tests (Simon 1995) to
determine whether the mean score for each of
the three tests was in the predicted direction. For
each test, we ran 1000 iterations, sampling with
replacement. If the resulting probability was less
than 0.001, the test was repeated with 10 000
iterations. We used one-tailed tests for parent
versus stranger (S) and parent versus neighbour
comparisons because chicks of many colonial
bird species distinguish between the vocalizations
of their parents and other conspecific adults
(Catchpole & Slater 1995). To determine whether
the order of playback presentations affected our
results, we derived a score of total movement for
each chick in response to the playbacks of each
trial by summing the absolute values of the six
measures of location in the enclosure for each
chick. We then tested for a significant differ-
ce in total movement between the trials.

Results

Chick orientation in enclosure

We tested nine early aged, seven middle-aged
and 10 late-aged chicks. During pre-playback
periods, young chicks tended to move to the back
of the artificial ledge and face inland toward the
cliff (direction of movement: N =13 cliff, 7 sea, 7
neither). In contrast, older chicks moved more
often toward the outer edge of the enclosure and
faced the sea (N =4 cliff, 10 sea, 16 neither). This
difference in the movement of young and old
chicks was significant (Fisher’s exact test, N =34,
one-tailed P =0.04, excluding chicks that made no
choice). Thus, the general orientation of chicks to
the sea or cliff side of the enclosure was related to
their age, which is similar to natural behaviour on
the ledges.

Once we ceased to broadcast calls, chicks gen-
erally remained within 20 cm of their position at
the end of playback. Hence, playback calls stimu-
lated movement, which ceased when these adult
calls stopped. This trend was found in all three
trials (binomial tests for departure from random
movement after playbacks, P versus S trials: 22
remained in place, four moved, \( P < 0.001 \); \( P \) versus \( N \) trials: 21 remained, five moved, \( P < 0.01 \); \( N \) versus \( S \) trials: 20 remained, six moved, \( P < 0.01 \).

**Figure 6.** Median latency (s) to first (a) movement and (b) vocalization in pre-playback and playback periods of the Parent/Stranger experiment (trial 1). The same 26 chicks are represented in each box plot. Box plots as in Fig. 3.

...chicks...}

**Trial 1: parent versus stranger calls**

Pre-playback periods indicated no inherent bias in chick movement; the majority of chicks favoured neither side, and the ratio of chicks that moved north versus south (four north, seven south; 15 neither) was not significantly different from 1:1 (binomial test, \( N = 11, P = 0.39 \)). The latency to both movement (Wilcoxon signed-ranks test, \( T = 64, N = 26, P = 0.005 \); Fig. 6a) and vocalization (\( T = 3, N = 26, P = 0.016 \); Fig. 6b) of chicks was significantly less during playback than in the pre-playback period.

There was no significant correlation between the response scores of chicks and their wing lengths (for each trial, \( r = 0.1, N = 26, P > 0.5 \)). Since response scores did not increase significantly with age (Fig. 7), we combined the three age classes for analysis of each trial. Chicks moved significantly closer to parent calls than to stranger...

**Figure 7.** Response scores of thick-billed murre chicks to adult calls in a playback experiment. Each bar represents the mean response of chicks to two simultaneous calls (predicted and opposite response). The same 26 chicks (ages: nine early, seven middle, 10 late) were tested in each trial (see Methods). □, Early chicks; □, middle chicks; ■, late chicks.
calls (randomization test, \(N = 26\), one-tailed \(P = 0.0002\)). The median score for this trial was +39.5 (Fig. 8) compared to a possible range from +60 (entire time in parent goal) to −60 (entire time in opposite goal). A similar result was obtained when we considered just the direction of response; significantly more chicks chose the parent goal than the stranger goal (binomial test, \(N = 18\), \(P = 0.005\); three chose both or neither). Chicks frequently ran immediately to the parent speaker, moving around it and calling repeatedly and insistently. Some chicks touched the speaker with their beaks and breasts, similar to their behaviour while being brooded.

**Trial 2: parent versus neighbour calls**

The movement of chicks in the pre-playback period did not differ significantly from random, since there was no bias in favour of the parent's position from trial 1 (binomial test, \(N = 10\) parent side from trial 1, 15 other side, 1 neither; \(P = 0.21\)). As in trial 1, chicks responded to playback calls in general; latency to movement was significantly less during playback than pre-playback (\(T = 13\), \(N = 26\), \(P = 0.0001\); Table III). Chicks also called sooner during playback than pre-playback, but this trend was not significant (\(T = 59.5\), \(N = 26\), \(P = 0.26\); Table III).

Chicks moved closer to parental calls than to neighbour calls (median response score=+29; Fig. 8), but not significantly so (randomization test, \(N = 26\), one-tailed \(P = 0.07\)). When direction rather than strength of response is considered, the result is similar; chicks apparently preferred the calls of their parents, choosing them twice as often as neighbours, but this trend was not significant (binomial test, \(N = 15\), \(8\), \(3\) both or neither, one-tailed \(P = 0.11\)).

**Trial 3: neighbour versus stranger calls**

As in trial 2, the movement of chicks in the pre-playback period of this trial did not differ from random, since there was no significant bias toward the position of the parent's call from trial 2 (binomial test, \(N = 9\) parent side from trial 2, 12 other side, 5 neither; \(P = 0.33\)). There was no significant difference in latency to movement in playback compared to pre-playback (\(T = 84\), \(N = 26\), \(P = 0.10\)) unlike the two trials with parent calls. Overall as the three trials progressed, the time to first movement decreased during pre-playback period but increased during playback (Table III), but this trend was not significant (Kruskal-Wallis test, \(H = 2.90\), \(N = 78\), \(P = 0.23\)). Similarly, there was no significant difference in vocal latency between the playback and pre-playback periods (\(T = 59.5\), \(N = 26\), \(P = 0.42\)), and latency decreased in the pre-playback period but increased in the playback period as testing progressed (Table III), but this trend was not quite significant (\(H = 5.43\), \(N = 78\), \(P = 0.07\)).

Chick response to neighbours was not significantly different from the response to strangers (randomization test, \(N = 26\), \(P = 0.62\)). Generally, chicks preferred neither neighbours nor strangers. Chicks did not simply respond less to these playbacks than they did in trials 1 and 2, however; although 18/26 chicks still chose one goal over the other, this result was equally split between the neighbour (\(N = 9\)) and stranger (\(N = 9\)) calls (median response=0; Fig. 8).
Order effects

There was no significant difference in the total movement scores of chicks across the three trials (H = 1.16, N = 78, P = 0.56). Responses did not decrease among the three trials, suggesting that the overall response of chicks to playback calls did not diminish as testing progressed.

**Experiment 3: Do Parents Recognize Chick Calls?**

**Methods**

To test Tschanz’s (1959) suggestion that murre parents can recognize their own chick’s calls, we designed an experiment to measure the response of parents to their own chick versus other chicks on the same breeding ledge. We used only late-aged chicks in this experiment. On each of three study ledges, chicks and parents were uniquely marked for identification of families; parents were colour-marked and chicks were banded.

At the start of this experiment, all marked chicks on a ledge were removed and held in a cloth bag. One observer then chose a chick for presentation to the parents and recorded its band number. The chick was then presented in a cardboard box (25 × 20 × 15 cm) with an 8 × 10-cm hole cut into the top and covered with wire mesh. From a position 3.5 m back from the ledge, the first observer placed the box 0.5 m from the cliff edge, half-way along the ledge, using a long pole. A second observer was also 3.5 m from the ledge, approximately 5 m from the first observer. The second observer recorded all behavioural observations and was blind to the identity of the chick presented. Once the box was in place, we recorded the response of all parents each time the chick called (0: no response; 1: adult called in response; 2: adult called and moved toward the box). We ran the experiment until the chick called four times, or until 6 min passed with no calls from the chick.

The response of a parent to its own chick was defined as the mean score in response to the four calls of the chick. For each adult, the mean score in response to each of the chicks except its own was also determined, and the mean of these scores was defined as the response of an adult to familiar chicks. This score was based on an adult’s response to one to three familiar chicks, depending on the ledge in question.

**Results**

Adults responded significantly more to their own chick’s calls than to the calls of other chicks ($T = 0$, $N = 10$, one-tailed $P = 0.02$; Fig. 9). Parents generally called in response to the calls of their own chicks (median response=1.0), but some adults also called in response to other familiar chicks (mean response=0.3). One adult in particular was very vocal and called to all chicks that were presented; due to the small sample size, this may result in an overestimate of the general adult response to chicks that are not their own. Results of this experiment suggest that parents can recognize the calls of their own chicks prior to fledging.

**Discussion**

The results of this study confirm Tschanz’s (1959, 1968) original findings that murre parents and chicks can use vocalizations for mutual recognition. Our cross-fostering study indicated that the likelihood that foreign chicks will be adopted by potential foster parents decreases with chick age (Fig. 2). Although swap and sham chicks were accepted in early exchanges, many middle and all late swap chicks were rejected. The results of the two subsequent vocalization experiments confirmed that recognition does occur and allow us to make conclusions about recognition by both parents and offspring in murres.
Response of Murre Adults to Chicks

When presented with late-aged chicks prior to fledging (experiment 3), parents discriminated between the calls of their own and other chicks (Fig. 9). Most adults called only in response to the calls of their own chick. A better test of the ability of parents to recognize the calls of their chicks would be a simultaneous-choice playback experiment using chicks of different ages, similar to our test of chicks.

Response of Murre Chicks to Adults

Chicks responded to the calls of adult conspecifics since they were quicker to move and vocalize when calls were broadcast than when they were not. In addition, chicks tended to stop moving once calls ceased, indicating that they moved in response to playbacks. A mere response to sound, tapes or speakers in general would have resulted in random movement of chicks between the speakers, yet chicks significantly favoured the side to which parental calls were randomly assigned.

Playbacks showed that chicks discriminated between parent and stranger calls (Fig. 8); even the youngest chicks tested (age 3 days, N = 2) responded strongly to the calls of their parents. Chicks also responded to parents more than neighbours (Fig. 8). A positive response (of some degree) to neighbours is understandable since breeding murres often brood neighbouring chicks (Birkhead & Nettleship 1984; K. Lefevre, personal observations). We did not expect chicks to move preferentially towards neighbours over parents as they sometimes did (8/26 trials). Some response to neighbours was possibly due to the position of the parent call in trial 1, which became the neighbour speaker when the leads were switched for trial 2, but there was no significant bias in the pre-playback period of this trial.

The response of chicks to neighbours and strangers was equal (9 N versus 9 S; Fig. 8), contrary to our prediction. A gain, we expected chicks to respond more to familiar neighbours, since alloparental care and, less frequently, actual adoption occur in this species (Gaston et al. 1995). We also expected chicks generally to avoid stranger calls since (1) chicks may be killed by other adults during colony departure, either pecked ofI ledges when moving through adjacent territories to approach the cliff edge, or drowned by aggressive mobs of adults after failure to reunite with the male parent on the ocean after fledging (Gilchrist & Gaston 1997). Although more chicks avoided the goals in this trial (6/26) than in the others (2/26 in each of trials 1 and 2), nine chicks did move into the stranger goal. This puzzling result was not due to a diminishing response towards the calls; response scores decreased as the trials progressed (Fig. 7), but the difference in total movement between the trials was not significant, and the majority of chicks (18/26) still moved into a goal area. Thus, chicks showed less choice between the calls with time, not less response. The most likely explanation for the willingness of chicks to approach strangers' calls is that chicks became confused after being tested three times in 30 min and hearing parent calls played from both ends of the enclosure by trial 3. Thus, we cannot conclude whether the equal response to neighbours and strangers is based on an order effect or represents the natural behaviour of chicks. On the basis of general observations, however, we suspect that chicks avoid the calls of unfamiliar conspecifics under natural conditions. Speirs & Davis (1991) showed that male Adélie penguins, Pygoscelis adeliae, discriminate between playback of neighbour and stranger calls, and future tests of this hypothesis in colonial seabirds are warranted.

Although it was not logistically feasible for us to test the same chick on three successive days (due to weather conditions in the Arctic, the time constraint of accessing sites with climbing gear, and predation by arctic foxes, Alopex lagopus, and glaucous gulls, Larus hyperboreus), a future design could involve using each chick for only one trial. To use more chicks and make more playback tapes is labour and time intensive, a limiting factor in the short Arctic breeding season, but this approach would eliminate effects of the order of playbacks.

Parent-offspring Recognition in Murres

Based on these three experiments, we conclude that mutual parent-offspring recognition of calls occurs in thick-billed murres. The dense breeding ledges of murres are an ideal place for
parent–offspring recognition to be favoured by selection. Indeed, thick-billed murre chicks discriminate between the calls of parents and other adults within 2 days after hatching. We also demonstrated that parents recognize the calls of their chicks before fledging, but we did not test the ability of parents to recognize chicks younger than 14 days of age. Our cross-fostering study showed that young chicks are readily accepted by foster-parents, and the likelihood of acceptance declines with chick age. This type of study, however, does not control for the behaviour of chicks towards parents. We suggest that although chicks learn parent calls while in the egg (Tschanz 1968), parents probably learn their chick’s call during the first few days post-hatching while brooding is frequent (Tuck 1961). The total dependence of chicks on adults for food, warmth and protection could explain why chicks are willing to be adopted by neighbours even though they can recognize their parents’ calls. An additional explanation of this outcome is that parents may disregard any potential signature cues provided by young chicks because of the high likelihood that any early chick at the site is indeed theirs; the cost of rejecting their own chick is high and intruding chicks at this stage are rare (Beecher 1991).

Our conclusions correspond to findings from studies of the congeneric common murre (Tschanz 1959, 1968). Our findings support and add to this work by demonstrating that murres not only respond to familiar conspecific calls, but parents and offspring clearly respond to each other’s calls when provided with the simultaneous choice of another familiar call. Our study also shows that (1) beyond being able to learn adult calls in the laboratory, murre chicks do learn the calls of their parents in their natural environment, and (2) chicks not only recognize the call of their parent by the time of departure, they identify this call in nature at least by the age of 3 days.

**Parent–offspring Recognition in Other Colonial Birds**

The development of parent–offspring recognition in thick-billed murres supports the pattern that emerges from comparative studies of swallows, gulls, terns, penguins and colonial birds in general (reviews by Beecher 1981; Falls 1982; Catchpole & Slater 1995); recognition is most developed in species with an intermingling of young and when a high risk of misidentification exists.

Similar studies of alcids with different modes of development (Sealy 1973) also suggest that recognition develops when spatial cues are insufficient to prevent misidentification by both parents and young. Semi-precocial common puffins, Fratercula arctica, are alcids that rear their chicks in a burrow, the discrete location of which should be an adequate identification cue for the parent. Parent–offspring recognition does not appear to exist in this species; for example, puffins continue to feed foster chicks that are 8–10 days younger than their own (Hudson 1979; Harris 1983). By the time chicks fledge at age 34 days or older, they are independent of their parents (Harris & Birkhead 1985) and would have no need to recognize their calls. An example of the opposite extreme within the Alcidae is the ancient murrelet, Synthliboramphus antiquus, which is highly precocious and shows mutual parent–offspring recognition (Jones et al. 1987). Chicks recognize parental calls during the relatively early departure from burrows at 2 days of age, and parents preferentially approach their own calling chicks at this time (Jones et al. 1987). Although thick-billed murre chicks depart their sites later (at 21 days) than ancient murrelets, they still require the ability to recognize parental calls soon after hatching due to the likelihood of intermingling on murre ledges.

Along with murres, razorbills, Alca torda, represent an intermediate stage of chick development among the alcids (Sealy 1973); chicks depart when partly grown, by 28 days of age. Razorbills also lay a single egg on bare rock in colonies, but not in direct physical contact; most breeding sites are partially or fully enclosed in crevices or by scree (Harris & Birkhead 1985). Since razorbill breeding sites are more discrete and less dense than murre sites, the risk of chicks intermingling is relatively low. There is a need for recognition during fledging, however, because razorbills have the same departure strategy as murres. As predicted based on this breeding ecology, artificially incubated, young razorbill chicks are less able to discriminate between control and training calls than common murres (Tschanz & Hirsbrunner-Scharf 1975). Also, adults do not recognize their own chick’s call at age 4 days but they do at age 10 days (Ingold 1973).
A large body of comprehensive evidence has accumulated since the time of Tschanz’s early work to show that parent-offspring recognition of bird vocalizations is an adaptation to living in dense groups (e.g. Beecher 1981; Medvin & Beecher 1986). Further research in the area of parent-offspring recognition would benefit from the investigation of related questions. For example, most studies of vocal recognition are based upon social learning and the assumptions that birds are monogamous and that chicks that hatch at a nest are the genetic offspring of the attending adults. Given the overwhelming genetic evidence that this is not the case (Birkhead & Møller 1992), the genetic basis for recognition should be explored. Dense seabird colonies provide ample opportunities for extra-pair copulations (Birkhead et al. 1985); accordingly, we suspect that vocal recognition is based more on social than genetic relationships. There is some evidence for the existence of kin groups in murre colonies (Birkhead et al. 1980; Friesen et al. 1996); studies that combine investigations of relatedness and genetic parentage with analyses of the actual cues used in individual recognition pose an exciting direction for future research in the area of kin recognition.

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