Sex differences in razorbill *Alca torda* parent–offspring vocal recognition

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Summary

We investigated differences in parent–offspring vocal recognition between males and females in a natural population of razorbills *Alca torda*, a long-lived and highly social species of auk (Family: *Alcidae*). Razorbills provide biparental care to their chicks while at the nest site, after which the male is the sole caregiver for an additional period at sea. Parent–offspring recognition in razorbills is most challenging once the chick becomes mobile, leaves the nest site and goes to sea with the male parent. It is during this period when selection pressure acting on recognition behaviour is expected to be strongest. As a result, we predicted that parent–offspring recognition would be better developed in the male parent, that is, show a paternal bias. To test this prediction we used vocal playback experiments conducted on breeding razorbills at the Gannet Islands, Labrador, Canada. We found (1) most positive responses to playbacks (vocal and phonotactic) occurred close to fledging, (2) males responded more to calls from their chicks than to calls from strange chicks, (3) females responded indifferently to calls from their own or strange chicks and (4) chicks responded more to calls from their male parent than to calls from other adult males. The results provide clear evidence of mutual vocal recognition between the male parent and the chick but not between the female parent and the chick, supporting the prediction that parent–offspring recognition is male biased in this species. Such a bias could have important social implications for a variety of behavioural and basic life history traits such as cooperation and sex-biased dispersal.

Key words: razorbill, *Alca torda*, parent–offspring vocal recognition, sex difference, behaviour, monogamous, seabird, auk, Alcidae.

Introduction

Individual recognition is a complex and variable phenotypic trait with implications for animal social behaviour ranging from cooperation and parental care to patterns of social organization (Beer, 1982; Falls, 1982; Colgan, 1983; Stoddard, 1996; Sherman et al., 1997). Comparing the variability of recognition behaviour within and among species can show how selective pressures shape such a complex behavioural phenotype. For instance, intraspecific comparisons across age and sex classes have shown clear patterns in recognition behaviour that agree with the predicted strength of selective pressures (e.g. Searcy and Brenowitz, 1988; Insley, 2001). The aim of the present study was to investigate sex differences in parent–offspring vocal recognition in razorbills *Alca torda* where, owing to a particular pattern of parental care, males appear to have a far more demanding recognition task than females.

The auk family is a diverse group of long-lived and socially monogamous seabirds that exhibit a high degree of natal philopatry and a variety of chick developmental patterns (Bédard, 1985; Strauch, 1985; Freison et al., 1996; Gaston and Jones, 1998). Most species are very social and vocal communication is well developed (Tschanz, 1968; Ingold,

1973; Birkhead, 1978; Wagner, 1992, 1997; Lefevre et al., 1998). While birds in most other families have a single developmental pattern, the auks include species with three modes of chick rearing (Sealy, 1973; Gaston, 1998; Ydenberg, 2001). Guillemots (*Cepphus* sp.), *Brachyramphus* murrelets, puffins (*Fratercula* sp.), and auklets have semi-precocial young that are cared for at the nest site until they are close to adult size, and then fledge unaccompanied by their parents. *Synthliboramphus* murrelets have precocial young that depart the colony at only 2 days of age accompanied by both parents, who provide extended care at sea. Razorbills and murres (*Uria* sp.) have 'intermediate' young that receive biparental care at the nest site until they are about 30% of adult body mass, followed by a period of male only care at sea (Wanless and Harris, 1986; Gaston and Jones, 1998; Hipfner and Chapdelaine, 2002). For more detailed descriptions of fledging behaviour and natural history, see Gaston and Jones (1998) and Hipfner and Chapdelaine (2002). These different developmental patterns are likely to result in distinct selective pressures acting on the ontogeny of parent–offspring recognition.

The development of parent–offspring recognition in various

taxa is usually related to the timing and probability of misidentification. For example, in many species of birds, the onset of parental recognition coincides with offspring mobility, i.e. fledging (Beer, 1982; Falls, 1982; Beecher, 1991). Before chicks are mobile they can often be reliably identified by geographic cues alone, such as the nest site. Similar patterns have been reported for some mammal species (Holmes, 1990; Charrier et al., 2001). The exceptions are those species that are colonial nesters with poorly defined nest sites (e.g. murres and gulls), where chicks may be confused earlier in life (Beer, 1982; Falls, 1982). Razorbills, although colonial, have distinct and separate nest sites (1–5 m apart) and chicks generally do not move from these sites prior to fledging (Birkhead, 1977; Hipfner and Chapdelaine, 2002). As a result, geographic cues alone should be sufficient for identification of razorbill chicks while at the nest site. The crucial period for parent–offspring individual recognition in razorbills is during the chick's mobile stage at sea, when only the male parent is providing care. We would then expect the onset of individual recognition to coincide with the fledging period, and furthermore, if the pressure to recognize were restricted to the male parent, parent–offspring recognition would be likely to develop a paternal bias.

Aspects of individual vocal recognition between parents and offspring have been investigated experimentally in four species of auk, each study providing information about recognition onset. Common murre (*Uria aalge*) chicks recognize their parent's calls that they have heard only from within the egg (Tschanz, 1968). Thick-billed murre (*Uria lomvia*) parent–offspring recognition is mutual, with chicks recognizing their parent's calls as early as 3 days post-hatching (Lefevre et al., 1998). Ancient murrelets (*Synthliboramphus antiquus*) also have mutual parent–offspring recognition, developing within 2 days of hatching (Jones et al., 1987). In razorbills, Ingold (1973) reported that parents (of unknown sex) recognized their chick's calls at 10 days but not 4 days after hatching (razorbill chicks fledge in approximately 15 days; Gaston and Jones, 1998; Hipfner and Chapdelaine, 2002). Ingold's (1973) findings are consistent with the development of parent–offspring recognition in razorbills coinciding with the transition to mobility, but whether there is a sex bias in recognition remains untested. The primary goal of this study was to test whether there is a paternal bias in razorbill vocal recognition by comparing the responses of male and female parents to playback experiments of chick calls.

Materials and methods

Study site

Our research was carried out at the Gannet Islands in Labrador, Canada (53°56′N, 56°32′W), between June and August, 2001. These islands support the largest and most diverse seabird colony in Labrador, with large numbers of breeding common and thick-billed murres, razorbills and Atlantic puffins *Fratercula arctica*, and smaller numbers of black guillemots *Cepphus grille*, northern fulmars *Fulmarus glacialis*, leach's storm-petrels *Oceanodroma luecorhoa*, black-legged kittiwakes *Rissa tridactyla* and great black-backed gulls *Larus marinus* (Lock et al., 1994). The breeding population of razorbills was estimated at 6420 pairs in the 1980s (Lock et al., 1994). Geologically, the Gannet Islands are a low-lying cluster of glaciated rocky islands. As such, individual nests are much more accessible for recording and playback than the steep cliffs upon which these species are often found. All work was conducted on GC4, one of the six Gannet Islands. Here, recordings of chick and adult calls were made at 60 different nest sites in seven study areas. Six blinds were available for working with breeding razorbills. The use of these blinds, in addition to numerous natural hides, enabled us to get close enough (i.e. 1–10 m) to accomplish the necessary observations, recordings and playback experiments without disturbing the birds.

Individual and sex identification of birds

Accurate individual and sex identification of razorbills *Alca torda* L. was accomplished using existing metal/colour leg bands (numbers visible by scope) or applied temporary marks. Additional banding of focal birds was not feasible because capture sensitized subjects to our presence, precluding close observation. Two methods were used for marking. A one-time site-sweep was made soon after chicks hatched, at which time a small quantity (approx. 50 ml) of brown or red hair dye was placed on each nest site. When birds settled back into the nests (usually within 5–10 min), they were marked by the dye. The second method used picric acid (non-toxic dye that turns yellow upon contact with feathers) delivered *via* a 100 mm syringe. The second method was delivered while hidden so that the target birds would react as though they had been hit by falling guano (a constant occurrence). Both of these methods resulted in unique individually identifiable shapes that withstood daily diving behavior. The dye patterns, along with variations of natural markings and life history information, were recorded on individual ID cards.

Razorbills, as is the case for most auks, are sexually monomorphic, making it difficult to determine the sex of birds observed in the field. Sexing birds was accomplished by three on-site behavioral methods while a fourth laboratory method was used for confirming the accuracy of the behavioral methods. First, when copulations were observed, the mounting bird (i.e. dorsal position) is reliably a male (Wagner, 1996). Although the bird being mounted is likely female, Wagner (1996) observed a number of male–male mountings and so mounting was not used as a definitive method for sexing the ventral bird. Second, when chicks fledge, they depart with the male parent (Wanless and Harris, 1986; Gaston and Jones, 1998) and thus observation of a fledging event was sufficient to identify the putative male. Third, despite male and chick having departed, females would return to the empty nest site, usually at dawn with food for the chick, and stay at the nest site. Although the third method is not entirely independent of the second, together the three methods were sufficient to sex all subjects. Accuracy of the behavioural sexing criteria was
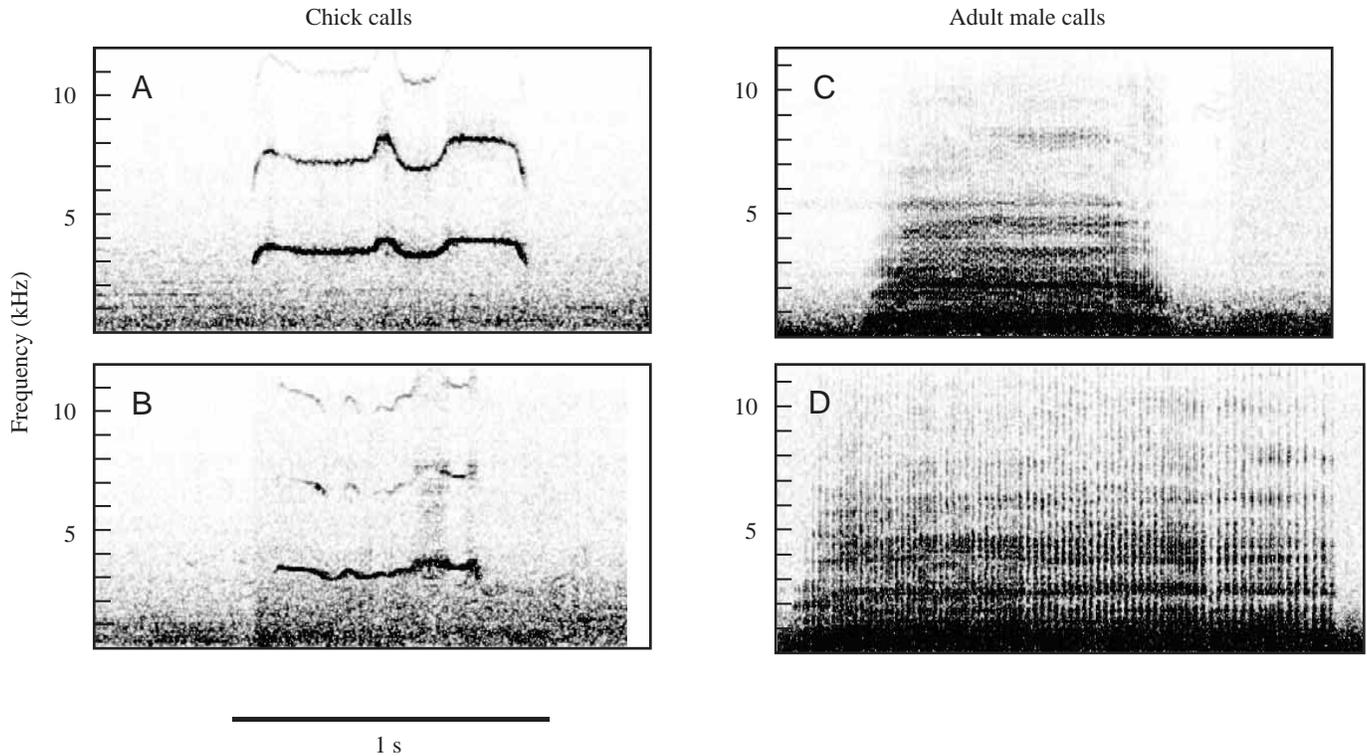
Chick calls Adult male calls

Fig. 1. Examples (256-point FFT sound spectrograms) of contact calls given by two different razorbill chicks (A,B) to their parents and two different adult males (C,D) to their chicks.

tested by applying it to 10 subjects of a concurrent study (sex differences in parental investment; R. Paredes, unpublished data) from which 0.5 ml blood samples were taken and used for determination of sex using molecular markers (Fridolfsson and Ellegrin, 1999). We purposely avoided capturing the subjects of the study reported here so that these birds would more readily habituate to our presence. The sex for each of these 10 birds had been determined with at least two of the three behavioural criteria. In each case the sex determined with the behavioural criteria agreed with the molecular technique (R. Paredes, unpublished data). The results of the current study indicate that vocal behaviour, in addition to the behavioural methods listed above, can also be used as a reliable indicator of sex for breeding adult razorbills.

Audio recordings

Audio recordings of razorbill vocal behavior were made with an AKG (AKG Acoustics, Vienna, Austria) ultra-directional (shotgun) microphone, through a Sennheiser (Wennebostel, Germany) power supply and into a Sony (Sony Corp., Tokyo, Japan) TCD D10 Pro II DAT recorder, a Sony Pro-Walkman cassette recorder, or direct-to-disk. Direct-to-disk recording was converted at 16 bits using Syrinx software (Burt, 1999) using a Fujitsu (Fujitsu Ltd., Tokyo, Japan) laptop platform (600 MHz processor, 20 GB hard drive and 256 MB RAM). Playback experiments were run from the same computer through an Acoustic Research (Lake Mary, FL, USA) speaker-amplifier (±5 dB frequency response between

50 Hz–20 kHz). All playback experiments were videotaped with a Sony Hi8 camcorder. Power for all equipment was supplied by a portable (5 A) solar panel connected to two 12 V collection batteries, from which individual rechargeable batteries (Ni–Cd or Li) were recharged as needed.

Initially, all accessible razorbill nests (approximately 120) on the island were scouted for recording, observation and playback potential. Focal nests were chosen (60 nests in seven areas), adults were marked (see above), and a rotation was established to record vocalizations from as many birds at different sites as possible. Recording site selection was determined by weather (i.e. wind and rain direction and severity) and background noise (mostly surf and other birds, con- and heterospecific), in addition to what recordings were needed. The vocalizations targeted and used for all playback experiments were those between the chick and attending adult given while on or near the nest. Examples of these chick and adult contact calls are provided in Fig. 1. These calls correspond to Bédard's (1969; from Hipfner and Chapdelaine, 2002) 'Lure Call' made by adult males and 'Departure Call' made by chicks.

Playback experiments

A total of 89 playback experiments were conducted to 42 individual birds at 19 different nests. Four different types of playbacks were conducted: (1) chick calls played to male pair-members (i.e. putative fathers, herein referred to as males or male parent; N=29 playbacks to 14 males); (2) chick

calls played to female pair-members (i.e. putative mothers, herein referred to as females or female parent; N=28 playbacks to 13 females); (3) male calls played to chicks (N=15 playbacks to 12 chicks); and (4) male calls played to their female mates (N=17 playbacks to 10 females). Each subject was only sampled once during data analysis for each type of playback experiment (i.e. samples are independent; see below for criteria). The experiments tested whether (1) males and (2) females recognize their chicks, and (3) whether chicks recognize their male parent. The goal of the fourth playback experiment, testing whether females recognize their mates, was to demonstrate that females would respond to the procedure. It was not possible to playback female calls to their chicks and to their mates because females rarely called, except when male and female parents reunited on their nests, but these call sequences tended to be highly overlapped and therefore unreliable to extract only female calls. Playback experiments were serial presentations of control- and test-call treatments and then repeated in opposite order (for a fuller treatment of playback design issues, see McGregor, 1992). Test treatments consisted of four different calls (to control for psuedoreplication; Kroodsma, 1989) from the focal individual's parent or offspring. Control treatments were four different calls from a non-parent or non-offspring from the same area (i.e. within audible range) except for two subjects that had isolated nests. Starting orders (control or test treatment) were randomly determined by a coin toss and then alternated for all subsequent playbacks during that session (i.e. until the equipment was moved to a different location).

Experiments began by setting up speakers within 5 m of each nest. Playbacks followed shortly thereafter if this had been accomplished without being detected by the birds. If the birds were disturbed (i.e. moved off their nests), the area was vacated for 1–4 h to allow normal behaviour to resume before initiating a playback. All playbacks occurred when chicks were between 11–18 days old. Although adults and chicks were vocal prior to fledging, clear counter-calling (i.e. bidirectional, repeated calling) between parent and chick only began once the chick began showing signs of mobility. It was only after this point in time that parents and chicks clearly responded to the playbacks of each other's calls. At the same time, the amplitude of chick calls increased substantially, which greatly facilitated recording. Consequently, most of the playback experiments (i.e. 57 of 89) occurred within 48 h of fledging and we were thus able to restrict the comparative analyses to this time period (see below). Finally, because the playbacks occurred *in situ*, the chick was usually with one parent during most experiments. In order to control for the problem of response interference by a non-focal bird, any such overt response (i.e. calling or movement) during the playback sequence terminated the experiment.

Responses to playbacks were measured *in situ* based on the number of calls given, orientation behavior (presence/absence), and phonotaxis (i.e. movement towards the broadcast sound source; presence/absence and distance). Subjective accounts of response strength and any additional information were also made at the same time. Videotaped accounts of playbacks were used to verify scores in the laboratory. If a subject gave no apparent response to a playback using the *in situ* criteria then the experiment was repeated at a later time. Analyses of response frequencies include all responses to all playback data (i.e. test or control conditions) and any repeated measures on the same subject were averaged before combining data across subjects. The analyses involving treatment comparisons (i.e. test *versus* control) used only the data from within 48 h of fledging (with the exception of playbacks to two males that gave clear responses 72 h prior to fledging), to ensure that female–chick tests were not conducted systematically earlier than male–chick tests. If a subject had received multiple playbacks for these tests, the analyses included only the first playbacks to which subjects gave any category of response. The final analyses summarized the playbacks with two methods: (1) the mean number of calls or distance moved (the best indicators for most conditions being ratio data and unambiguous in nature) and (2) a composite score combining measurements of the three categories of bivariate data: Call?, Orient? and Taxis? (ordinal data). Untransformed ratio data (i.e. number of calls; distance moved) were tested with parametric statistics after being screened for departures from normality. Ordinal (i.e. the composite response) and bivariate data (i.e. response rates) were analyzed using nonparametric comparisons. All comparisons were two-tailed and paired within individuals. Sample sizes (N or degrees of freedom, d.f.) always refer to different individual birds and are given as subscripts with the test statistic.

Results

Response rates of the three classes of subjects (i.e. males, females and chicks) to each of the four playback experiments using three measurement assays are given in Fig. 2. Adult males and chicks responded vocally to playback experiments while females did so very infrequently (Fig. 2). The comparison between males and females was of specific interest; males responded by calling significantly more than females (Chi-squared test: χ^2_1=19.58, P<0.0001). Orienting responses to playbacks were frequent from all three classes of subjects but also during all treatments, so was of limited value as an experimental assay alone. As a result, these responses were used only as part of the composite variable combined with the presence/absence of calling and taxis. Taxis responses were consistently low in frequency across all classes. The exception was during the playbacks of male calls to females and so this was the only analysis where these responses were considered separately (see below). All vocal and taxis responses occurred within 48 h of fledging, with the exception of two males who responded vocally to their chick's calls approximately 72 h prior to fledging.

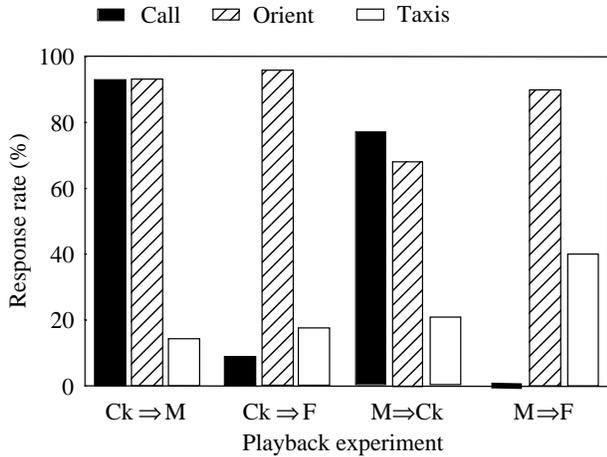Males (putative fathers) responded more to the calls of their

Fig. 2. Response rates of razorbills to each of the four types of playback experiments (Ck→M, chick calls played to adult males; Ck→F, chick calls played to adult females; M→Ck, adult male calls played to chicks; and M→F, adult males played to adult females) for each of the three assay categories (call, orient and taxis). Response rates include all responses to all playback data (i.e. test and control conditions) and averaged any repeated measures on the same subject before combining data across subjects. Vocal responses were frequent from males and chicks but not from females. Orienting responses were frequent in all classes. Taxis or movement responses were consistently low, except from females receiving male calls.

chicks than to those of strange chicks, indicating paternal vocal recognition (Fig. 3A,B). Both call and the composite assay indicated significant differences between test and control treatments (paired t-test for variable calls: $t_{13}=4.38$, $P=0.0008$; Wilcoxon signed-ranks test for composite score variable: $T=4$, $N=14$, $P=0.0166$).

Females (putative mothers) did not respond more to the calls of their chicks than to those of strange chicks (Fig. 3C,D). Neither calling or movement responses analyzed separately nor the composite assay indicated significant differences between test and control treatments (paired t-test for variable calls: $t_{12}=0$, $P=1.0$; paired t-test for variable distance moved: $t_{12}=0.955$, $P=0.3613$; Wilcoxon signed-ranks test for composite score variable: $T=9$, $N=13$, $P=0.753$).

Chicks responded more to the calls of their male parent than to those of strange adult males, indicating mutual paternal vocal recognition (Fig. 3E,F). Both call and the composite assay indicated significant differences between test and control treatments (paired t-test for variable calls: $t_{11}=4.33$, $P=0.0012$; Wilcoxon signed-ranks test for composite score variable: $T=0$, $N=12$, $P=0.0431$).

Finally, male calls were played back to their female mates as a supplemental test of whether or not females would respond to the procedure. The problem being confronted was whether the lack of discrimination shown by females to their chick's
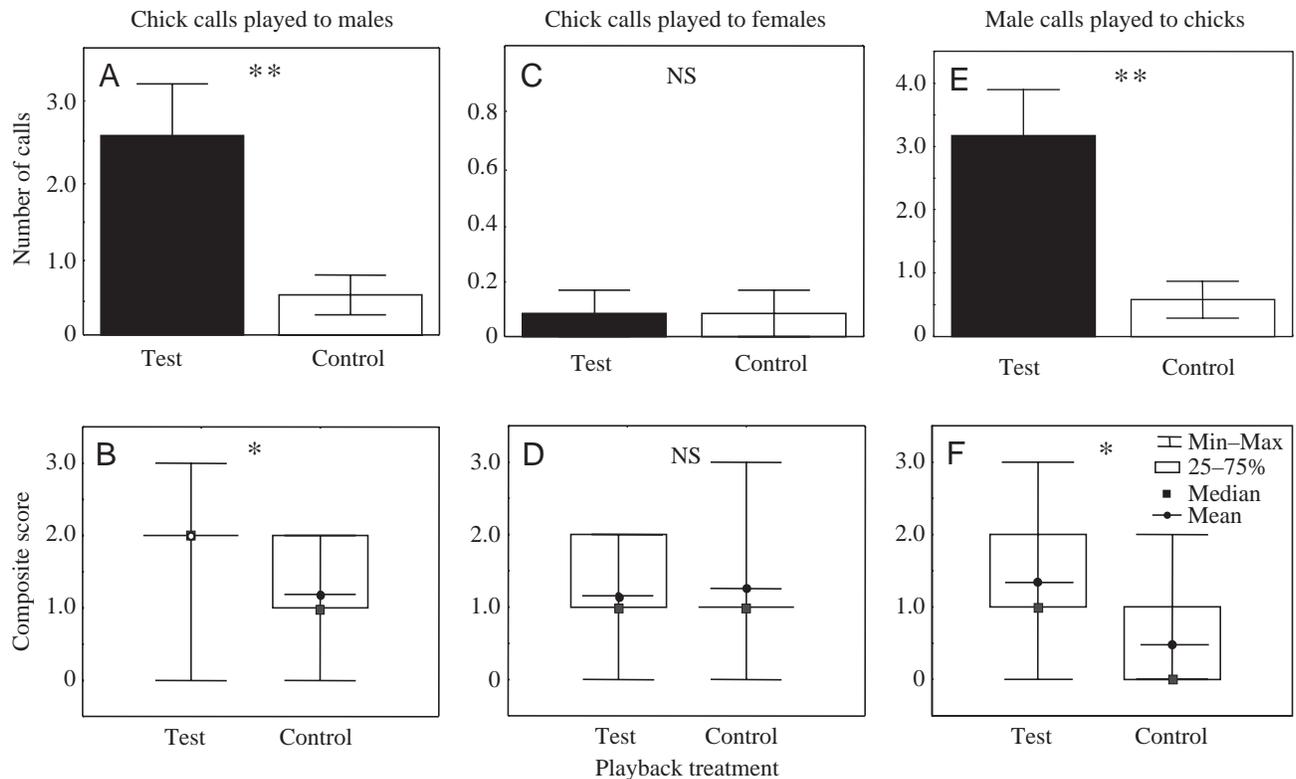

Fig. 3. Responses of razorbill adult males (A,B), adult females (C,D), and chicks (E,F) to playback experiments. The upper row (A,C,E) shows scores of the number of calls given in response to playbacks (mean ± S.E.M.). Note the different scales. The lower row (B,D,F) shows boxplots (mean, median, 25th–75th percentile, and minimum/maximum; refer to key in F) of the composite scores (combination of call, orient and taxis) in response to playbacks. $*P<0.05$, $**P<0.01$, NS, not significant.

calls truly indicated a lack of recognition (Fig. 3C,D) or if females were simply not responding to the experimental procedure. Females, as previously, did not respond vocally, but they approached the speaker only during playbacks of their mates' calls and did not respond to the calls of other males. However, the data only bordered statistical significance at the 5% level using a two-tailed test (paired t-test for variable distance moved: t_8=1.58, P=0.1529; Wilcoxon signed-ranks test for composite score variable: T=0, N=10, P=0.1088), probably because of low statistical power caused by an unavoidably small sample size (i.e. 18.2 and 18.5% for the two tests, respectively). As a result, the test is suggestive of mate recognition but not conclusive. The main reason for conducting the mate recognition playbacks, however, was to ascertain whether females would respond to the procedure and clearly they did respond.

Discussion

The patterns, underlying mechanisms, and ultimate implications of sex differences in communication abilities are of considerable interest to studies in animal communication (Balaban, 1994; Ratcliffe and Otter, 1996; Yamaguchi, 2001). Few studies, however, have directly tested adult animals in nature for sex differences in recognition behaviour (Searcy and Brenowitz, 1988; Brown, 1998), a fundamental aspect of communication that could initiate a cascade of social effects such as sex-biased cooperative interactions or dispersal (Holmes, 1990; Clutton-Brock, 1991; Emlen, 1997).

In this study, the pattern of parental care of razorbills appears to interact with the ontogeny of individual recognition, resulting in a male gender bias in parent–offspring recognition. Our results agree with those of Ingold (1973), supporting the prediction that recognition onset in razorbills develops during the end of the nestling stage as the chick becomes increasingly mobile and ready to fledge. Our results also agree with several studies that show parent–offspring vocal recognition can be bi-directional or mutual with alcids (Tschanz, 1968; Ingold, 1973; Jones et al., 1987; Lefevre et al., 1998). Our results are unique, however, in that we show that mutual parent–offspring recognition in razorbills appears to be limited to the male parent, despite a significant period of biparental care. Specifically, males responded preferentially to their own chick's calls and chicks responded preferentially to the calls of their male parent. In contrast, the playback experiments were not able to show any evidence of recognition between razorbill female parents and their offspring. Females responded infrequently to their chick's calls and indifferently to the calls of strange chicks. Finally, we found that females only rarely vocalized to their chicks, hampering our efforts to test the chick's ability to recognize their female parents (this vocal bias did, however, prove to be a reliable means of sexing breeding razorbills). Our attempts to test whether chicks recognized the calls made by their female parent that were relatively infrequent and directed elsewhere (e.g. mate counter-calls) were not successful. Thus, chicks may recognize their female parents *via* these less frequent vocal cues or *via* other modalities (e.g. visually). These possibilities remain to be tested.

While our data suggest that female razorbill parents do not recognize their chicks' calls, a lack of response cannot be equated to a lack of vocal recognition. Our observations are strengthened by additional non-vocal behavioural assays (i.e. orienting and phonotaxis) that similarly showed a lack of discrimination between control and test treatments by females. In addition, playback experiments between mates (i.e. adult male to adult female) demonstrate that females respond to the procedure but not selectively to their chick's calls, supporting the conclusion that female–chick vocal recognition is nonfunctional and possibly absent. It remains possible, however, that females recognize their chicks using vocalizations or another sensory mechanism, but do not respond to them at the nest because it is inappropriate or unnecessary. Male parents gave their strongest responses to playbacks close to the time of fledging, when they were off the nest attempting to counter-call with their chick. In contrast, females were never observed counter-calling with their chicks either on or off the nest. Because females rarely interact vocally with their chicks, there is little opportunity for chicks to learn their female parents' calls. It would thus appear that regardless of whether or not female parents recognize their chicks' calls, their lack of functional response to their chicks would decrease if not negate any future benefit (e.g. nepotism) that vocal recognition might provide (Holmes, 1990; Sherman et al., 1997). Ultimately, this needs to be tested by observing interactions between adult females and their mature offspring (e.g. Insley, 2000).

To sum, evolutionary pressures do not act solely on the finished product (the breeding adult) but also upon every stage of an animal's life history. In the present study with razorbills, a particular behavioural phenotype (i.e. male biased parent–offspring vocal recognition) appears to result from the interaction of two primary factors. First, razorbills follow a life history strategy of biparental care until chick mobility, after which a period of paternal-only care ensues (Sealy, 1973; Wanless and Harris, 1986; Gaston, 1998; Gaston and Jones 1998; Ydenberg, 2001). Second, the developmental onset pattern of vocal recognition commonly occurs during a neonate's transition to mobility when other cues such as location are no longer available (Beer, 1982; Falls, 1982; Beecher, 1991). The final result is a sex-bias in recognition behaviour, an ability that is fundamental to many social interactions. Such a result in the context of a long life span combined with natal philopatry could play a decisive role in driving other higher order social phenomena within this species.

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