



Sex-biased aggression and male-only care at sea in Brünnich's Guillemots *Uria lomvia* and Razorbills *Alca torda*

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In several groups in the order Charadriiformes, biparental care is followed by a period of male-only care. Several hypotheses attempting to explain extended male parental care in shorebirds do not fit the Alcini. In a previous study of Brünnich's Guillemots *Uria lomvia* and Razorbills *Alca torda*, we did not find support for female-biased parental effort at the breeding site that would lead to males being in better condition to care for chicks at sea. However, in both species, males spent more off-duty time at the breeding site than females, suggesting greater involvement in the defence of egg or chick, breeding site and mate. We predicted that there would be a male bias in size and aggressive behaviour associated with parental roles. To test this, body size and aggression of attending male and female Brünnich's Guillemots and Razorbills were measured during incubation and brooding on the Gannet Islands, Labrador. Parental aggression was measured using natural observations of all agonistic interactions and, in Razorbills only, *in situ* responses to presentations of a predator model. In both species, males were significantly larger than females in culmen and gape length. Guillemot males initiated agonistic interactions more frequently than females during incubation. In contrast, female Guillemots were subjected to aggression more frequently than males and as a result were involved in more fights. In addition, the few chicks that were seen to die were being attended by single females. During the brooding period, Razorbill males responded aggressively to intruders more frequently than females, made more aggressive responses than females, and responded aggressively more frequently and more intensely than females to a predator model. In both species there was a similar male bias in morphology and behaviour that is consistent with male parents being more capable of protecting their chick, a probable advantage to chick survival during the uniparental care phase of some Charadriiformes.

Keywords: aggression, Alcini, offspring defence, parental roles, sex, sexual size dimorphism.

In a number of species in the order Charadriiformes (Scopalcids, Charadrii, Alcids), biparental care is followed by a period of male- or female-only care. The reasons for this two-phase pattern are poorly understood. Attempts to explain it have mostly focused on shorebirds where biparental care (incubation and sometimes early brooding) and male-only care (Howe 1982, Pierce 1997, Currie *et al.*

2001) are sometimes accompanied by sequential polyandry (Lenington 1984, Nethersole-Thompson 1986, Székely & Lessens 1993). In the Alcini, which comprise Brünnich's Guillemot *Uria lomvia*, Common Guillemot *Uria aalge*, Razorbill *Alca torda* and Little Auk *Alle alle*, both parents take care of a single offspring at the breeding site for 2–4 weeks, followed by male-only care of the partially grown chick for the subsequent 3–4 weeks at sea (Harris & Birkhead 1985, Stempniewicz 1995, Gaston & Jones 1998, Harding *et al.* 2004, Paredes

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et al. 2006). Although female-only care can occur (Tuck 1960) it is rare and likely to be accidental (Harris & Birkhead 1985, Scott 1990). There are several proposed explanations for the 'intermediate' chick development and departure strategy shown by the Alcini (Cody 1971, Ydenberg 1989, Houston *et al.* 1996, Gaston & Jones 1998). However, there is no evolutionary, ecological, behavioural or physiological explanation for why it is the male sex that usually accompanies the chick at sea.

In shorebirds with biparental care, there are two leading hypotheses for why males stay at the nest and care for the brood while females desert: re-mating opportunity and differential parental capacity. Under the re-mating opportunity hypothesis, females gain greater reproductive success from deserting than males (Oring 1986). The hypothesis is not applicable to the Alcini because females do not have time to raise a second offspring after males depart with the first chick. In addition, based on evidence of high year-to-year mate fidelity, Harris and Wanless (2003) concluded that while Guillemot males depart with chicks, females stay behind at the colony to retain ownership of high-quality breeding sites rather than to assess the potential of future mates.

Under the differential parental capacity hypothesis, female desertion and male care are explained by the decrease in female body condition associated with the production of eggs (Erckmann 1983). This could be particularly important for female shorebirds and Alcids because they lay large eggs relative to their body size (Rahn *et al.* 1975). However, female investment in additional or larger eggs could potentially be recovered rapidly during the post-laying period, or at least within the same breeding attempt, by increasing food intake (Williams 2005). Supporting this conclusion, body mass and body composition as well as energetic costs during incubation did not differ between sexes in Kentish Plovers *Charadrius alexandrinus* (Amat *et al.* 2000). This holds true for at least one of the Alcini; body mass of Common Guillemots did not differ between sexes during late incubation or through the chick-rearing period (Wilhelm 2004). Thus, it does not appear that either the benefits of re-mating or the costs associated with egg production explain the two-phase care of the Alcini.

Because these two explanations do not appear to explain the two-phase parental care pattern in the Alcini, a third hypothesis was suggested: the

differential parental effort hypothesis (Paredes *et al.* 2006, 2008). An extension of the differential parental capacity hypothesis, this explanation takes into account all factors affecting male or female condition during breeding: mate and site defence, egg production, brooding, provisioning, and offspring defence (intra- and interspecific). The sex that ultimately takes sole care of the chick is predicted to be the one with the least parental effort and consequently is in the best condition when the transition to at-sea care occurs. However, our results with Common Guillemots and Razorbills (Paredes *et al.* 2006, 2008) did not support this explanation of male extended care. The parental effort allocation of males was equal to or greater than that of females. Although males fed chicks less often, they spent more time brooding and defending the breeding site and chick (off-duty time), had longer foraging trips and dived deep more frequently than females. Similar daily mass loss rates between sexes in Brünnich's Guillemots (Paredes *et al.* 2005) and Common Guillemots (Cameron-MacMillan *et al.* 2007) suggest that the condition of males and females were similar during chick-rearing. Likewise, body mass did not differ between sexes in Common Guillemots at the end of the chick-rearing period (Wilhelm 2004).

Common Guillemot and Razorbill males spend more off-duty time (time spent by the non-attending parent) at the breeding site than females, suggesting greater involvement in the defence of egg or chick, breeding site and mate (Paredes *et al.* 2006). This suggested that the male-only phase of a two-phase parental care system might relate to differences between the sexes in their abilities to defend their offspring from either predators or conspecifics. This could be viewed as part of Orings' (1986) parental quality hypothesis; male care and female desertion could spread in a population if males caring for their offspring on their own achieve higher reproductive success than single caring females. Adult removal experiments in Kentish Plovers indicated that male parents were more capable of raising offspring in high-density colonies (Székely 1996, Székely *et al.* 2006). During the transition from biparental care to male-only care, chicks are able to move out of the nest and follow the parent(s) to feeding areas; however, full or partial provisioning and protection against predators or conspecifics is required. Parental aggression in the form of defence or protection of offspring increases parental fitness by reducing the

likelihood of offspring mortality. But there are also costs for the parent that shows aggressive behaviour during reproduction, including risk to self, energy expended and time invested. In theory, optimal nest/offspring defence should maximize net fitness benefits of the aggressive parent (Montgomerie & Weatherhead 1988).

The ability to defend offspring often manifests itself in aggressive behaviour, but because aggressive behaviour has a number of functions it can be influenced by many different selective forces. Male-biased aggressive behaviour has been associated primarily with intra-sexual (male–male) competition, especially in species where the intensity of aggression is higher during the courtship and laying periods (Butler & Janes-Butler 1983, Moreno *et al.* 1995). Nonetheless, males play a major role in nest defence throughout the chick-rearing period in many other bird species, suggesting that male-biased aggressive behaviour also has a parental in addition to just a sexual function (Regelmann & Curio 1983, Winkler 1992). Studies of Crested Auklets *Aethia cristatella* have shown that the two sources of selection for male-biased aggression, male–male competition and offspring defence, are not mutually exclusive (Jones & Hunter 1999, Fraser *et al.* 2002).

One way to assess whether aggressive behaviour is directed toward the protection of the offspring is by measuring the aggressive response of the attending bird to threats in the absence of its mate. Other studies on aggressive behaviour in Alcids (Birkhead 1978, Creelman & Storey 1991) and between sexes (Kober & Gaston 2003) have measured the frequency and/or duration of interactions, usually with off-duty birds. This approach may not be an effective means of detecting differences in protective aggression between the sexes because the behaviour of an off-duty bird is likely to be influenced by the mate's presence. In addition, it is often difficult to assess whether the off-duty bird is protecting its on-duty mate or the chick. In contrast, although the behaviour of attending birds is likely to be less extreme (Birkhead 1978), it is a less ambiguous means of detecting and comparing protective aggressive behaviour in defence of the egg or chick. The extent to which a bird responds to a threat and whether it is the initiator or the receiver in an agonistic encounter while on-duty are important variables for determining differences in ability to defend the offspring. For instance, higher predation rates of eggs

and chicks have been found in species and individuals that failed to respond to aerial predator attacks (Gilchrist & Gaston 1997a, Yorio & Quintana 1997, Olendorf & Robinson 2000). Among conspecifics, the initiator of an aggressive encounter usually wins and the receiver usually loses (Jackson 1991, Burton & Evans 2001). These behaviours can potentially affect chick survival; Common Guillemots that failed to give threat displays to potential intruders more often ended up fighting (Birkhead 1978), thus exposing their chicks to potential dislocation.

This study aimed to assess sex differences in parental aggressive behaviour and sexual size dimorphism in Brünnich's Guillemots and Razorbills. Our approach first involved taking a standard suite of morphological measures; the Alcini are known to be slightly sexually dimorphic in some measurements (Gaston & Jones 1998, Gaston & Hipfner 2000, Ainley *et al.* 2002, Hipfner & Chappelaine 2002). We then conducted observational and experimental measures of parental aggression, measuring the frequency and intensity of aggressive/protective responses of attending individuals to potential intruders using opportunistic observations of aggressive interactions between con- and heterospecifics, and experimental observations of aggressive behaviour resulting from the presentation of a predator model. In addition, we assessed whether chick loss occurs during aggressive encounters of attending females and males. We predicted that there would be a male bias in both size and parental aggression that might explain the male bias in extended care in these species. Specifically, if attending males are the more aggressive and protective sex, then we would expect them to respond to and initiate threat displays to potential intruders (con- and heterospecifics) more frequently and more intensely than females.

METHODS

Study site

The study was undertaken at a mixed colony of Brünnich's Guillemots and Razorbills located at GC4, one of the six islets of the Gannet Islands, Labrador (53°56'N, 56°32'W), during June–August 2001 and 2002. Fledgling success was relatively high for both species during these years; 93–97% of chicks survived (Paredes *et al.* 2006). Both species lay eggs in early June and both parents

incubate the single egg for approximately 30–34 days. Eggs lost early in the season are usually replaced. Chicks hatch in July and both sexes take care of the offspring for 15–20 days. Males then depart with their chicks for 3–4 weeks at sea (Gaston & Jones 1998). Although both sexes participate in all parental activities (Gaston & Hipfner 2000, Hipfner & Chapdelaine 2002), females are more involved in chick provisioning and males in chick care and breeding site defence (Paredes *et al.* 2006).

Brünnich's Guillemots breed in dense groups (side-by-side neighbours) on bare cliff ledges, usually the uppermost ledges. Razorbills on the Gannet Islands, as elsewhere, breed in lower density groups (0.75–1 m apart) on open nests and crevices located on cliff slopes and beaches. A few breeding pairs of Common Guillemots, Black-legged Kittiwakes *Rissa tridactyla* and Atlantic Puffins *Fratercula arctica* were located in the same areas. The principal predator of chicks of both species, and to a lesser degree of adults, was the Great Black-backed Gull *Larus marinus*; 25 pairs nest on the Gannet Islands (Robertson & Elliot 2002). Other occasional predators observed were Peregrine Falcon *Falco peregrinus*, Northern Raven *Corvus corax* and Herring Gull *Larus argentatus*.

Individual identification and body measurements

Individuals were identified by temporary marks of picric acid (yellow) or fluorescent paint (green, pink and orange) delivered from a 10-mL open-top container attached to the tip of a 4-m graphite pole. This method allowed birds to be marked without disturbing the colony. Individual mark patterns and other life-history information were recorded on ID cards for quick reference. In addition, one member of each pair was captured during the chick-rearing period for permanent marking (ringing with stainless steel and plastic colour leg bands), measuring and sex determination. An extendable 7-m noose pole was used to capture birds. Razorbills were also captured with small noose-carpets or noose-strings, positioned on the cliff ledges that were frequented by the birds. Body mass was measured to ± 5 g with a Pesola balance, and wing cord and tail length (tail-tip to where feathers join the skin under the uropygial gland) were measured with a steel ruler to ± 1 mm. Measurements of the culmen length (bill tip to where

feathers meet the top of the bill), bill depth at gonys and gape length (bill-tip to where mandibles join) were taken with vernier calipers to ± 0.1 mm. Blood samples (0.5 mL) were taken from the tarsal vein and stored in 95% ethanol for later sex determination using molecular DNA analysis (Fridolfsson & Ellegren 1999). In addition, six Razorbills were opportunistically sexed by behavioural observations; males were seen leaving the colony with the chick. The results of sexing were obtained after the field season, so observations were made without the researchers knowing the sexes of the birds.

Aggressive interactions

Observations of Brünnich's Guillemot aggressive behaviour were conducted in 2001, on 21 days (378 h) during their incubation period. Razorbills were observed in 2002, on 30 days (540 h) of the incubation period, and 12 days (192 h) of the brooding period. Frequency and intensity of agonistic interactions of attending birds during the incubation and brooding period and responses of brooding Razorbills to the presentation of a model predator were recorded.

Frequency and intensity of aggressive interactions

Observations were made from a hide, using a 20–60 \times /60-mm spotting scope and 10 \times 50 mm binoculars. Focal individuals were chosen from a group of pairs (Brünnich's Guillemots $n = 30$; Razorbills $n = 31$) that were thereafter observed continuously. During the incubation period, opportunistic agonistic interaction data were recorded continuously, concurrent with breeding-site attendance observations (04:00–23:00 h). This was feasible because, in comparison with the brooding period, other parental activities were less frequent (i.e. incubation shifts) or absent (i.e. feedings). During the brooding period, we conducted the same observations during two 4-h focal blocks each day (04:00–08:00, 08:00–12:00, 12:00–16:00 and 16:00–20:00 h) so that a full day of observation was completed every 2 days.

During each session, we recorded the encounters of marked subjects while they were attending eggs or chicks. These observations were made while their mates were absent in order to avoid confounding results. By focusing on attending birds

when the mate was not present, we ensured that aggressive behaviour was protective of the offspring as opposed to the mate. Observations included interactions between neighbours (mostly Brünnich's Guillemots), but in these cases we only analysed encounters between the on-duty individual (focal bird) and the off-duty neighbour (intruder). Encounters between two focal birds (incubating–incubating or brooding–brooding) were not recorded to maintain independence of variables.

Once the presence of a potential intruder (birds that landed or walked close to the breeding site) was detected near to a focal nest, the agonistic response of the attending individual was recorded together with the identity of the initiator and recipient of any threat displays. Response escalations were recorded as well as obvious effects on the chick (i.e. displacement and/or loss); agonistic interactions tend to escalate to fights when birds fail to show a threat display (Birkhead 1978), which can result in chick loss. We also made opportunistic records of fights, chick/egg loss and gull predation events of known-sex birds that were part of a concurrent study on parental care (Paredes *et al.* 2006).

Because Brünnich's Guillemots breed in dense colonies in close proximity to their neighbours, it was not possible to assess whether a bird transgressed a boundary (potential intruder) unless a threat display was given (e.g. the 'stretch away' display). As a result, it was not possible to measure the frequency of responses to potential intruders in Brünnich's Guillemots. Instead we recorded the initiator and the recipient of the aggression. Various studies have shown that initiators of aggressive encounters usually win (e.g. Jackson 1991, Burton & Evans 2001), and consequently the frequency that a bird initiates aggression may also be a reasonable metric of its ability to protect the offspring. During the incubation and brooding periods, on-duty Razorbills mostly responded to the presence of potential intruders by giving threat displays (i.e. initiating aggression). Occasionally they did not respond to a potential intruder, and very infrequently they were recipients of overt aggressions. As a result, comparing how often birds initiated or received aggression (as done with Guillemots) was not informative. How frequently birds responded to intrusions was recorded instead.

Two forms of aggressive behaviour were recorded: threat displays and physical interactions.

Threat displays included: (i) bill-gaping, in which opponents expose the bright-yellow lining of their mouths, usually accompanied by a low-pitched growling (in Razorbills); (ii) stretch-away (Birkhead 1978), a lunge with the bill towards the opponent; (iii) standing facing the opponent; and (iv) chasing. Chasing in Razorbills involves the nest owner rushing towards the opponent with wings raised and opened, head plumage held erect while giving an attack call (Bédard 1969). Physical behaviour included: (i) jabbing and pecking with the bill and (ii) fight, including grappling and twisting opponents with the bill (bill-grappling) and slapping with the wings (Cramp 1985). We also recorded whether there was no apparent response or a submissive response to the presence of a potential intruder (mostly to gulls), which included: (i) movement away from the intruder but remaining near egg/chick or (ii) temporary abandonment of the breeding site. Ordinal scores were assigned according to the subjectively escalating degree of the encounter. Behavioural responses were scored as follows: -2 = breeding site abandonment; -1 = move away from breeding site; 0 = no response; 1 = bill-gaping and stretch-away; 2 = jabbing & pecking (≥ 1 ; not moving from the egg/chick); 3 = standing facing the opponent and chasing (moving from the egg/chick); and 4 = fighting.

Model presentation

Focal nests for the model experiment were chosen from different groups of Razorbills. No more than two focal pairs in any group of birds were used; focal nests from the same group of birds were not in visual contact to avoid possible effects of habituation to the predator model. We presented a model predator, a taxidermy mount of a Great Black-backed Gull, to 17 pairs of brooding Razorbills with chicks 9–12 days old. The model was attached to a 2-m wooden pole and presented on the ground with wings folded as if it were walking toward the breeding site. The model was presented from a hidden site to each sex of a breeding pair when their mates were absent. During each session, the model was presented first at 3 m distance for 3 min, and then moved to a second position, 1 m away from the breeding site, for another 3 min. We scored the model trials using the same methods and values used to score the observations of agonistic interactions (detailed above).

Additional non-aggressive protective responses observed and recorded only during the predator model trials included: (i) move toward the chick and (ii) place the chick under the wings. Response scores were compared between sexes. Responses of Razorbills to the predator model were also compared with actual gull predation attempts.

Data analysis

As explained above, it was not possible to measure response frequencies to intruders as a measure of aggressive behaviour in Brünnich's Guillemots. Instead, we compared frequencies of events and aggression intensity scores where the attending bird was either the initiator or the recipient of the aggression. In Razorbills, we compared the frequency (presence/absence) and intensity of responses to the presence of an intruder (con- and heterospecific) between the sexes. Initiator vs. recipient categories were not used because the focal Razorbills initiated aggressive responses to intruders in almost all encounters (incubation: 667/672 interactions; brooding: 171/171 interactions). All threat displays and physical attacks performed by the attending adult were recorded during each interaction, but only the highest score was used for the analysis. In the case of the predator model, we compared the frequency of protective behaviour displays performed between male and female Razorbills.

We used the highest agonistics scores for the analysis of the intensity of aggression between sexes. Individual scores were first averaged to avoid autocorrelation or pseudoreplication problems. The only place this was not done was during the frequency analyses. In these cases, diad interactions involved multiple individuals on different dates, many with one non-identified bird, making individual standardization of data problematic.

To control for distance effects on responses of Razorbills to intruders, we estimated distances between the two using the maximum width of a Razorbill's body (approximately 0.15 m) as a reference. The estimated distance between the breeding site owner and the potential intruder varied between 0 and 3 m. The average distance that produced an aggressive reaction from the incubating Razorbill was 0.21 ± 0.01 m. When there was no aggressive response from the Razorbills, sexes did not differ in their average distance to the potential intruder during incubation (Student's

t-test: $t_{1,62} = 0.632$, $P = 0.529$). There were very few non-responses of Razorbills (four females and two males) during brooding for comparison between sexes. Therefore, we used all non-responses of males and females for the analysis.

Statistical analyses used SPSS version 11.5. We used parametric tests (independent *t*-test, paired *t*-test) to compare groups when data were normally distributed and variances were approximately equal, and non-parametric tests when they were not. The chi-square test and Fisher's exact test were used to compare proportions when sample sizes were large and small, respectively. Means are expressed as \pm se unless otherwise indicated. All comparisons were two-tailed and differences were considered significant when $P \leq 0.05$.

RESULTS

In Brünnich's Guillemots, we recorded 162 encounters (females $n = 98$ and males $n = 64$) between attending individuals and potential intruders (0.43 encounters per hour) in which incubating birds initiated or responded to a threat display. In Razorbills, we recorded 672 encounters of incubating birds (females $n = 340$ and males $n = 332$; 1.24 encounters per hour), and 171 encounters (females $n = 68$ and males $n = 103$; 0.89 encounters per hour) of brooding birds responding or not to the presence of an intruder.

Body measurements

In both species, males had on average 3% longer gape and 3–5% longer culmen than females. Male Brünnich's Guillemots were significantly heavier than females, and male Razorbills had a 2% greater bill depth (Tables 1 & 2).

Aggression: Brünnich's Guillemots

Most of the agonistic interactions of incubating Brünnich's Guillemots occurred between conspecifics (90%, $n = 162$). The majority of heterospecific interactions (15 of a total of 16) involved neighbouring Common Guillemots. Very few gull predation attempts were observed among focal birds. About 46% of the agonistic interactions between conspecifics occurred between neighbours (i.e. on-duty bird with an off-duty neighbour) and 54% between unknown adults. Brünnich's Guillemot nests were too closely spaced to detect

Table 1. Body measurements of male and female Brünnich's Guillemots captured at the Gannet Islands, Labrador, during the 2000–2002 breeding seasons.

Trait	Females			Males			Difference	
	<i>n</i>	Mean ± sd	95% CL	<i>n</i>	Mean ± sd	95% CL	<i>t</i>	<i>P</i>
Body mass (g)	44	906 ± 58.47	888.0–923.5	39	950 ± 70.11	949.8–950.2	–3.073	0.003
Culmen (mm)	45	33.2 ± 0.20	32.9–33.06	39	34.8 ± 0.22	34.7–34.9	–3.443	0.001
Bill depth (mm)	45	14.0 ± 0.10	13.7–14.3	39	14.2 ± 0.05	14.2–14.2	–1.507	0.136
Gape (mm)	45	58.9 ± 0.32	58.8–58.9	39	60.9 ± 0.35	60.8 ± 61.0	–2.723	0.008
Wing cord (mm)	45	211.2 ± 0.53	211.1–211.4	38	213 ± 0.57	212.8 ± 213.2	–1.193	0.236
Tail (mm)	43	64.0 ± 0.53	63.8–64.2	34	64.7 ± 0.59	64.5 ± 64.9	–0.609	0.544

t, *t*-tests for independent samples (two-tailed); CL, 95% confidence limits.

Table 2. Body measurements of male and female Razorbills captured at the Gannet Islands, Labrador, during the 2000–2003 breeding seasons.

Trait	Females			Males			Difference	
	<i>n</i>	Mean ± sd	95% CL	<i>n</i>	Mean ± sd	95% CL	<i>t</i>	<i>P</i>
Body mass (g)	27	705 ± 43.9	687.6–722.4	29	705 ± 37.6	690.7–719.3	0.046	0.963
Culmen (mm)	26	32.9 ± 0.10	32.8–32.9	26	33.9 ± 0.15	33.8–33.9	–2.760	0.008
Bill depth (mm)	26	22.8 ± 0.06	22.7–22.8	26	23.3 ± 0.07	23.3–23.4	–2.551	0.014
Gape (mm)	26	52.2 ± 0.29	52.1–52.3	26	54.0 ± 0.22	53.9–54.1	–2.552	0.014
Wing cord (mm)	26	205 ± 0.49	204.8–205.2	26	204 ± 0.63	204.7–205.2	0.562	0.576

t, *t*-tests for independent samples (two-tailed); CL, 95% confidence limits.

whether a potential intruder had crossed an on-duty bird's boundaries, unless the on-duty bird initiated a threat display. Thus, instead of frequency of responses to intruders, we used initiator vs. recipient as a parameter for measuring differences in aggression between sexes. We recorded a total of 162 agonistic interactions of attending Guillemots involving threat displays or physical aggression from con- and heterospecifics. In 107 of these cases the attending birds were initiators and in 55 cases they were recipients. Most initiators of aggressive behaviour were males (78% vs. 56%) and most recipients of aggressions were females (44% vs. 22%; $\chi^2_1 = 6.888$, $P < 0.01$). Aggressions were nearly always responded to (males 99.4%, females 99%) with no sex difference. The same results were found when only conspecific interactions were analysed. Males (78% vs. 58%) initiated agonistic interactions more often than females; and females received aggressions (42% vs. 22%) more often than males ($\chi^2_1 = 5.529$, $P = 0.019$; Fig. 1).

The intensity of aggression exhibited by Brünnich's Guillemots during incubation did not differ between sexes (Mann–Whitney *U*-test:

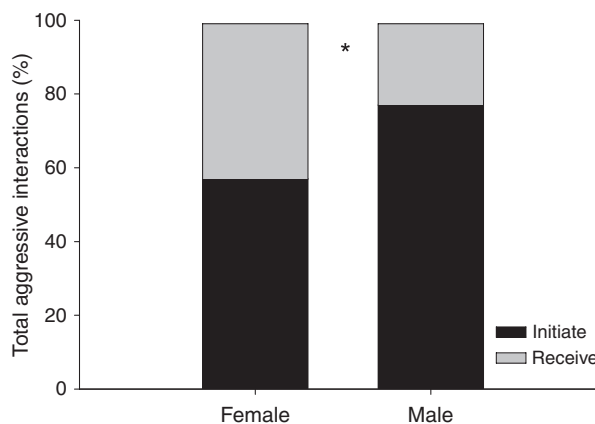


Figure 1. Frequency of conspecific agonistic interactions initiated or received by female and male Brünnich's Guillemots during the incubation period. *Chi-square test, $P = 0.019$.

$U = 553.0$, $P = 0.073$). However, the marginal *P*-value indicated a tendency towards higher male aggressive behaviour. Despite the many agonistic interactions, there were few actual fights in the focal birds (all between conspecifics) and none that caused a chick dislocation. As expected, most

fight (four of five) involved recipient females and one involved a male initiating. Three chicks were lost during observations of another group of known-sex adults in the same colony; all chicks were lost by attending females (one during a fight).

Aggression: Razorbills

During incubation, most of the agonistic interactions involved conspecifics (91%, $n = 672$). Only a small number of the conspecific interactions involved neighbours (2%, $n = 613$); most involved unknown Razorbills. Most of the heterospecific interactions involved Brünnich's Guillemots (69%, $n = 59$), followed by Puffins (19%) and gulls (12%). There were no sex differences in frequency of all aggressive responses (female: 89%, $n = 340$; male: 90%, $n = 332$; $\chi^2_1 = 0.272$, $P = 0.301$). The same results were found when only the conspecific interactions were analysed; no differences were found in the frequency of aggressive behaviour between sexes ($\chi^2_1 = 0.015$, $P = 0.452$; Fig. 2). The intensity of aggression for incubating Razorbills also showed no significant differences between sexes for interactions involving either conspecifics (Mann-Whitney U -test: $U = 203.0$, $P = 0.668$; Fig. 2) or heterospecifics (Mann-Whitney U -test: $U = 86.00$, $P = 0.942$).

During the brooding period, male Razorbills responded aggressively more frequently to the presence of intruders than did females but differences were only marginally significant (90% vs. 98%; Fisher's Exact test: $P = 0.05$; Fig. 2). Most of the agonistic interactions during brooding involved

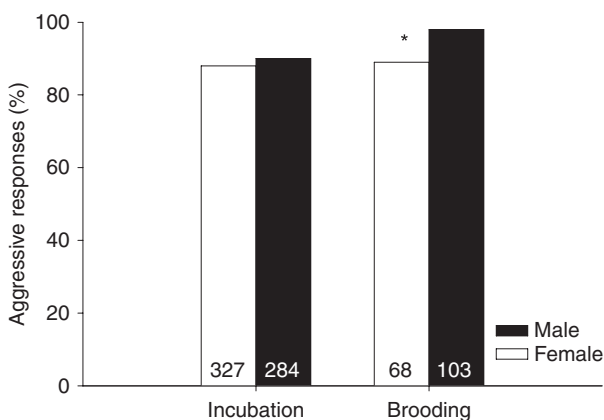


Figure 2. Frequency of responses to a potential conspecific intruder by female and male Razorbills during incubation and brooding periods. *Fisher's Exact test, $P = 0.05$.

conspecifics (87%, $n = 171$). The remaining heterospecific interactions (13%, $n = 171$) involved mostly Brünnich's Guillemots (55%) and Puffins (41%). Similarly, although males responded more often than females to encounters with conspecifics ($n = 152$), these differences were not significant (98% vs. 90%; Fisher's Exact test, $P = 0.07$). However, the marginal P -value indicated a tendency towards higher male aggressive behaviour. The intensity of aggression for brooding Razorbills showed no significant differences between the sexes for interactions involving either conspecifics (Mann-Whitney U -test: $U = 69.0$, $P = 0.302$) or heterospecifics (Mann-Whitney U -test: $U = 19.50$, $P = 0.699$). However, males performed most of the interactions with the highest aggression scores (67%, 4 = chase). Only one fight was recorded and it was between a male Razorbill and a Brünnich's Guillemot.

Over the course of a breeding season, higher aggression intensity scores were found during brooding (median: 2, range: 1–4) compared with incubation (median: 2, range: 0–4; Mann-Whitney U -test: $U = 842.5$, $P < 0.0005$). These differences were found in both Razorbill males (Mann-Whitney U -test: $U = 241.5$, $P = 0.003$) and Razorbill females (Mann-Whitney U -test: $U = 181.5$, $P = 0.039$).

Model predator presentation

Nearly all model predator (gull) presentations resulted in measurable responses from subjects (59/68, or 87%). Of the nine presentations with no response, seven (78%) occurred at the greater distance (3 m). The frequency and type of responses to the model predator differed significantly between sexes (Fig. 3a). At both distances from which the gull model was presented, males responded with aggressive displays significantly more than females, whereas females showed no response or responded with self-protective behaviours (e.g. leave the chick alone temporarily) more than males (3 m: $\chi^2_2 = 4.371$, $P = 0.019$; 1 m: $\chi^2_2 = 6.585$, $P = 0.005$; Fig. 3a). Male responses were also more intense than female responses at both model presentation distances (3 m: Mann-Whitney U -test: $U = 82.5$, $P = 0.031$; 1 m: Mann-Whitney U -test: $U = 73.00$, $P = 0.013$; Fig. 3b). In addition, more males than females showed protective behaviour (i.e. moved toward and/or covered the chick) at both model presentation distances

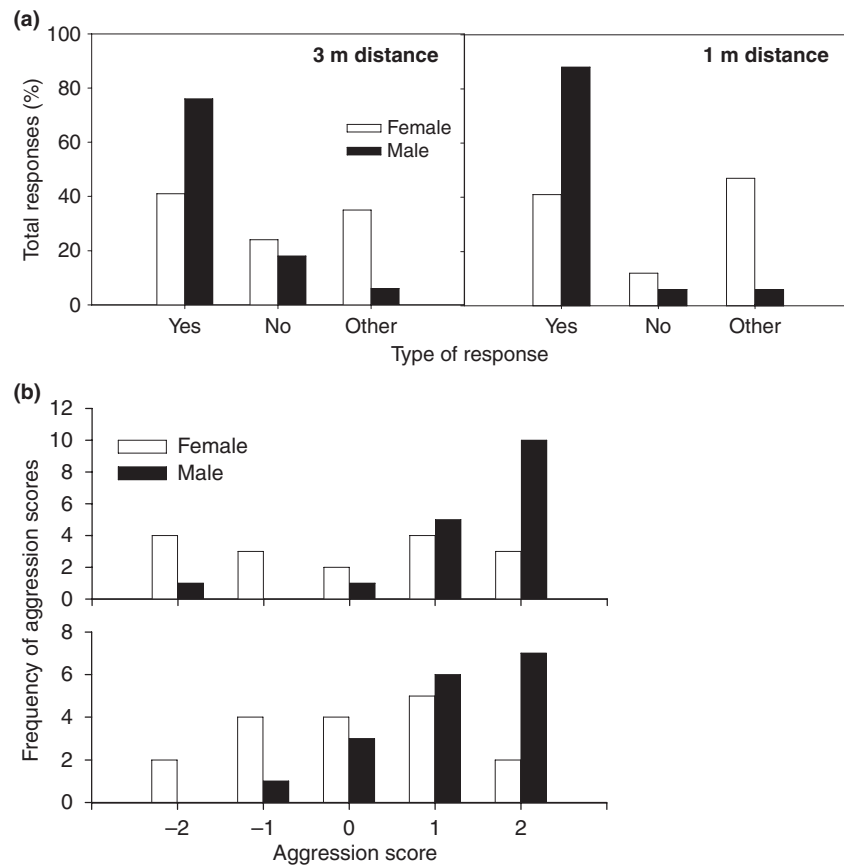


Figure 3. (a) Frequency of responses: yes (1 & 2), no (0), other (-1 & -2) and (b) intensity scores of female and male Razorbills to the presentation of a predator (Great Black-backed Gull) model at two distances (1 m and 3 m). Response scores: -2 = Breeding site abandonment; -1 = Move away from breeding site; 0 = No response; 1 = Bill-gaping and Stretch-away; 2 = Jabbing & pecking.

(3 m: 8 vs. 1; Fisher's Exact test, $P = 0.017$; two-tailed; 1 m: 7 vs. 0; Fisher's Exact test, $P = 0.003$).

Few actual attempts of gull predation of known birds with eggs or chicks were observed, precluding sex comparisons. Responses were mainly threat displays in both species. Two male Guillemots responded with stretch-away displays and pecking; and two male and two female Razorbills responded with threat displays similar to those recorded with the predator model.

DISCUSSION

Monomorphic seabirds, being monogamous and practising biparental care, are expected to exhibit little specialization in their parental roles (Ligon 1999). In this light, the parental specialization in the Alcini, in which males are solely responsible for chick care at sea, appears to be anomalous and thus difficult to explain. In a related study of

parental care of Razorbills and Brünnich's Guillemots, two Alcini species with no apparent dimorphism in body size, we demonstrated clear sex differences in parental roles (Paredes *et al.* 2006). We have also shown sex differences or specializations in other aspects of the behavioural ecology of these two species that are relevant to parental care (foraging ecology: Paredes *et al.* 2008, parent-offspring recognition: Insley *et al.* 2003). In addition, an increasing body of evidence supports the contention that sexual differences in parental behaviour are widespread among seabirds (Nelson 1978, Burger 1981, Wanless & Harris 1986, Creelman & Storey 1991, Fasola & Saino 1995 and references therein, Fraser *et al.* 2002, Cameron-MacMillan *et al.* 2007, Thaxter *et al.* 2009). In particular, we suspect that in many apparently monomorphic seabirds, males will be better equipped, physiologically, behaviourally and morphologically, to handle aggressive encounters. In

this light, the extended male-only care practised by seabirds in the Alcini tribe may not be such an anomaly, but instead merely an extension of a pre-existing trait. Males are more capable of defending chicks, as shown in this study, and thus are more likely to be successful caring for chicks at sea.

Sexual dimorphism

Sexual selection (via either male–male competition or female choice) is the main process proposed to explain sexual size dimorphism (SSD) in birds (reviewed by Jehl & Murray 1986, Székely *et al.* 2007). Although relatively low levels of mate competition are expected for truly monogamous birds, a range of SSD in some morphological traits has been found in seabirds. A recent phylogenetic study testing the three major processes proposed to explain SSD in seabirds found support for the sexual selection as opposed to the fecundity selection or differential niche utilization hypothesis (Serrano-Meneses & Székely 2006). Consistent with other studies (e.g. Székely *et al.* 2000 and references therein), males tended to be larger relative to females in species where competition for mates as well as courtship displays and fights occur on the ground. Body mass does not appear to be a reliable measure of SSD, probably because it can change over time (Croxall 1995); we found sex differences in body mass only for Brünnich's Guillemots, in contrast to other studies (Grecian *et al.* 2003, Kober & Gaston 2003).

In several bird species, inter-sexual divergence in morphology is accompanied by the evolution of large differences in bill length (Jehl & Murray 1986). In Alcids (with ground displays and fights), slight SSD has been found in bill and head morphology (Corkhill 1972, Nelson 1981, Jones 1993, Niizuma *et al.* 1999, Jakubas & Wojczulanis 2007, Berzins *et al.* 2009). Our results support these studies and previous studies of Razorbills and Brünnich's Guillemots (Stewart 1993, Wagner 1999, Gaston & Hipfner 2000, Grecian *et al.* 2003); males had slightly greater (3–5%) culmen and gape than females at the Gannet Islands. It has been proposed that positive assortative mating for bill morphology in Least Auklets *Aethia pusilla* (Jones & Montgomerie 1991), Razorbills and Atlantic Puffins (Wagner 1999) may reflect mate choice for ornaments. In species with non-ornamented bills such as guillemots, sex differences in bill size are thought not to be the result of mate

choice; no evidence of assortative mating based upon body size was found in related Black Guillemots *Cephus grylle* (Berzins *et al.* 2009). On the other hand, SSD in bill size in Brünnich's Guillemots and Razorbills could not be explained by differences in foraging behaviour during the breeding (Paredes *et al.* 2008) or winter seasons (Moody & Hobson 2007). An alternative mechanism underlying SSD in bill size of guillemots is mate and territorial defence (Stewart 1993, Berzins *et al.* 2009), probably related to differences in aggressive behaviour. Concurrently, larger bills may also confer upon males an increased ability to defend and protect offspring, and be related to the significant involvement of males in brooding and breeding site defence roles (Fraser *et al.* 2002, Paredes *et al.* 2006).

Aggression

Although sexes are not expected to differ in levels of self-protection aggression unless there is sex-biased predator pressure, there is often specialization in defensive aggression (e.g. protecting the offspring) by one sex (Archer 1988). SSD in bill traits was accompanied by sex differences in defensive aggression by attending individuals (incubating or brooding) in both species; these were stronger in response to conspecifics for Brünnich's Guillemots than for Razorbills.

Parental investment theory predicts that nest defence should increase with the fitness value of the nest content, from egg to chick (Montgomerie & Weatherhead 1988). Agreeing with this trend, we found higher levels of aggression in Razorbills during brooding than during incubation. Similar trends have been reported for Brünnich's Guillemots elsewhere, where aggressive interactions increased at the time of hatching (Kober & Gaston 2003). Alternatively, in Guillemots lower levels of aggressive behaviour during incubation compared with brooding may also result from eggs being more easily dislocated from narrow ledges during fights (Gaston & Nettleship 1981).

When interpreting agonistic interactions, the direction of such actions is clearly important (Jackson 1991, Burton & Evans 2001) and was sexually skewed in our results. Although incubating Guillemot females were involved in more such interactions than males, males were more often the initiators. Most fights (three of four) involved females that did not initiate the aggression but

were recipients of threat displays or physical aggression. Although chick mortality was low during the study years (93–97% of hatched chicks survived) for both species, the three Brünnich's Guillemot chick separations observed all occurred while being brooded by single females (Paredes *et al.* 2006). Other studies have found no sex differences in aggression (e.g. Guillemots at Coat Island, Maine; Kober & Gaston 2003), perhaps because only the total number of aggressive events was measured and not its directionality. That Brünnich's Guillemot females were more often targets of aggressions and males were more often initiators implies that eggs or offspring may be safer with attending males.

Razorbill nests are more dispersed and consequently the relevant aggression metric was not who initiated the agonistic behaviour but whether one sex responded more often and more vigorously to the presence of a potential intruder. In Razorbills, sex differences in aggressive behaviour were found only during the brooding period. Male Razorbills showed higher frequencies of aggressive responses to the presence of intruders (con- or heterospecific) than females, but these differences were weak. Both sexes responded with similar intensity to the presence of intruders. Nevertheless, males were more likely to be the sex that performed the most intense aggressive behaviours (i.e. pecking and chase). Higher aggressiveness in female Razorbills relative to female Brünnich's Guillemots may result from female–female competition; female Razorbills actively defend their mates from other females in arenas (Wagner 1992). When males go to sea with the chicks, female Brünnich's Guillemots stay behind, possibly to defend the nest (Harris & Wanless 2003), although it is unknown if high female–female aggressions occurs.

Predators represent a more serious threat for the egg/chick and potentially also for adult survival (Patterson *et al.* 1980, Margalida & Bertran 2005, Stenhouse *et al.* 2005), so we expected stronger responses to predators than to conspecifics or non-predator intruders. Responses of Brünnich's Guillemots and Razorbills to actual gull predation attempts were more frequent (almost always responded) but less intense (low-scored threat displays) than to conspecifics. Our simulated predator experiment used the most common avian predator at the Gannet Islands, the Great Black-backed Gull, presented in a natural manner. The results

showed clear and significant differences between male and female Razorbill responses to its presence. Males responded aggressively more often and more intensely than females to the model at both distances (3 m and 1 m). These differences were mainly due to the higher frequency of self-defence responses (i.e. move away from or abandon chick) or lack of apparent responses by females. In contrast to conspecific intruders, there were no high-scored aggressive responses (e.g. chase and fight) orientated to the predator model by either sex. In addition to the aggressive responses, Razorbills also performed chick protective behaviours (i.e. moved towards chick and/or accommodated chick under wings); these behaviours were mostly performed by males.

Attending (brooding or incubating) Brünnich's Guillemot and Razorbill males: (i) more often avoided fights (and the subsequent dislocation danger posed to chicks) with conspecifics either by responding more often to intruders or by showing initial threat displays; (ii) responded more aggressively to predator model presentations; and (iii) lost or were separated from their chicks less often than females. Altogether, our results suggest that males of both species were more capable of protecting the offspring than females.

Sex-biased aggression and male-only care at sea

Male-biased aggressive behaviour and SSD in bill size in Guillemots and Razorbills is consistent with their roles in defending the breeding site (Paredes *et al.* 2006). These results hold true for other Alcids (Creelman & Storey 1991, Fraser *et al.* 2002, Table 3). However, sex differences in breeding site defence were not found in Little Auks (Welcker *et al.* 2009). Whether this indicates equal levels of aggressive behaviour between sexes requires further investigation. If Alcids males are generally more aggressive and better equipped (i.e. larger bills) than females, then it follows that males would be the more effective parent to accompany the chick at sea. When Guillemot and Razorbill chicks depart their breeding sites, they typically call, walk towards the edge of the cliff, jump and attempt to fly/glide to the ocean below. They may be accompanied by the parent or a group of adults, or be alone. Chick mortality occurs as a result of injuries from the jump, failure of parent–offspring reunification, predation and attacks from groups of

Table 3. Sex differences in bill dimensions and territory and nest defence in shorebirds and Alcids with emphasis on species with biparental care and male-only care.

	Parental care duration	Culmen size	Territory/nest defence incubation	Territory/nest defence brooding	References ^a		
					Parental care	Bill size	Nest defence
Shorebirds							
American Avocet (<i>Recurvirostra americana</i>)	M ≥ F	M > F	M > F ²	–	13, 2	1	2
Black-necked Stilt (<i>Himantopus mexicanus</i>)	M ≥ F	M = F	M > F ²	–	6, 2	1	2
Eurasian Lapwing (<i>Vanellus vanellus</i>)	M ≥ F F ≥ M	M = F	M > F ¹	M > F ¹	4, 6	6	5, 23
Eurasian Curlew (<i>Numenius arquata</i>)	M ≥ F	F ≥ M	–	M = F ²	3, 21	21, 6	22
Kentish Plover (<i>Charadrius alexandrinus</i>)	M > F	M = F	–	M > F ^{2,3}	15	6	8 ^b
Greater Golden Plover (<i>Pluvialis apricaria</i>)	M > F	M = F	–	M > F ¹	4	6	22
Purple Sandpiper (<i>Calidris maritima</i>)	M > F	F ≥ M	M > F ¹	n/a	16, 12	6, 16	12
Killdeer (<i>Charadrius vociferus</i>)	M > F	M = F	M > F ¹	M > F ^{1,2}	17, 10	6	18
Eastern Willet (<i>Catoptrophorus semipalmatus</i>)	M > F	M = F	–	M > F ¹	19	6	19
Malasian Plover (<i>Charadrius peronii</i>)	M = F	–	M > F ¹	M = F ¹	20	–	20
Black-tailed Godwit (<i>Limosa limosa</i>)	M = F	M = F	M > F	M > F	14, 6	6	5
Alcids							
Brünnich's Guillemot (<i>Uria lomvia</i>)	M > F	M > F	M > F ¹	–	7	28, This study	This study
Razorbill (<i>Alca torda</i>)	M > F	M > F	M = F ¹	M > F ^{1,2}	7	29, This study	This study
Little Auk (<i>Alle alle</i>)	M > F	M > F	–	M = F ⁴	24	25	26
Crested Auklet (<i>Aethia cristatella</i>)	M = F	M > F	–	M > F	7	23	11
Atlantic Puffin (<i>Fratercula arctica</i>)	M = F	M > F	M > F ¹	M > F ¹	7	7	9
Black Guillemot (<i>Cephus grylle</i>)	M = F	M > F	–	–	7	27	–

Parental care duration: M ≥ F: biparental or biparental plus male-only care; M = F: biparental care; F ≥ M: biparental care or biparental plus female-only care.

¹Observations, ²Predator-model experiments, ³Mate removal experiments (measure of chick survival), ⁴Radiotelemetry.

n/a, not applicable because females desert the nest right after hatching.

^aReferences: 1, Hamilton (1975); 2, Sordahl (1990); 3, Reynolds and Székely (1997); 4, Nethersole-Thompson (1986); 5, Hehgy and Sasvari (1998); 6, Johnsgard (1981); 7, Gaston and Jones (1998); 8, Székely (1996); 9, Creelman and Storey (1991); 10, Brunton (1988); 11, Fraser *et al.* (2002); 12, Pierce (1997); 13, Gibson (1971); 14, Lind (1961); 15, Székely and Lessens (1993); 16, Cramp and Simmons (1983); 17, Lenington (1984); 18, Brunton (1990); 19, Howe (1982); 20, Yasué and Dearden (2007); 21, Currie *et al.* (2001); 22, Byrkjedal (1987); 23, Jones (1993); 24, Harding *et al.* (2004); 25, Jakubas and Wojczulanis (2007); 26, Welcker *et al.* (2009); 27, Berzins *et al.* (2009); 28, Stewart (1993); 29, Grecian *et al.* (2003).

^bHigh-density colony (no sex differences in chick survival in low-density areas; Székely *et al.* 2006).

conspecifics (Gilchrist & Gaston 1997b). The timing of chick departures, usually late evening, is believed to have evolved in response to terrestrial and avian predator pressure (Tuck 1960). Gull and fox predation seems to be the main cause of fledging failure of Brünnich's Guillemots and Razorbill chicks crossing beaches or rock slopes to reach the sea (Hipfner & Chapdelaine 2002). At colonies where chicks are able to jump directly into the sea, attacks from conspecifics attracted by chick calls are a major cause of departure failure (Gilchrist & Gaston 1997a,b). In either case, defence of the chick during departure and while at sea appears to be crucial for its survival and consequently for parental fitness. In several shorebirds, where males take care of the chick after female desertion, males are also more aggressive than females during the

incubation and/or brooding period and several are also larger in body size (Table 3). Thus, sex-biased aggressive behaviour aiding offspring protection appears to be an important factor for understanding the division of parental roles in Alcids, shorebirds and possibly other seabird species.

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REFERENCES

- Ainley, D.G., Nettleship, D.N., Carter, H.R. & Storey, A.E.** 2002. Common Murre (*Uria aalge*). In Poole, A. & Gill, F. (eds) *The Birds of North America*, no. 666. Philadelphia, PA: Academy of Natural Sciences and Washington, DC: American Ornithologists' Union.
- Amat, J.A., Henk Visser, G., Pérez-Hurtado, A. & Arroyo, G.M.** 2000. Brood desertion by female shorebirds: a test of the differential parental capacity hypothesis on Kentish plovers. *Proc. R. Soc. Lond. B Biol. Sci.* **267**: 2171–2176.
- Archer, J.** 1988. *The Behavioural Biology of Aggression*. Cambridge Studies of Behavioural Biology. Cambridge: Cambridge University Press.
- Bédard, J.** 1969. Histoire naturelle du Gode, *Alca torda*, L., dans le golfe Saint-Laurent, Province de Québec, Canada. *Étude Serv. Can. de la Faune* no. 7, Ottawa, Ontario.
- Berzins, L.L., Gilchrist, H.G. & Burness, G.** 2009. No assortative mating for body size in Black Guillemots breeding in the Canadian Arctic. *Waterbirds* **32**: 459–463.
- Birkhead, T.R.** 1978. Behavioral adaptations to high density nesting site in the Common Guillemot (*Uria aalge*). *Anim. Behav.* **26**: 321–331.
- Brunton, D.H.** 1988. Energy expenditure in reproductive effort: the reproductive strategies of male and female Killdeer (*Charadrius vociferus*). *Auk* **105**: 553–564.
- Brunton, D.H.** 1990. The effects of nesting stage, sex, and type of predator on parental defense by Killdeer (*Charadrius vociferus*): testing models of avian parental defense. *Behav. Ecol. Sociobiol.* **26**: 181–190.
- Burger, J.** 1981. Sexual differences in parental activities in breeding Black Skimmers. *Am. Nat.* **117**: 975–984.
- Burton, N.H.K. & Evans, P.R.** 2001. Aggressive behaviour and correlates of dominance in Purple Sandpipers *Calidris maritima* at a communal winter roost. *Ibis* **143**: 248–254.
- Butler, R.G. & Janes-Butler, S.** 1983. Sexual differences in the behavior of adult Great Black-backed Gulls, *Larus marinus*, during the pre- and post-hatch periods. *Auk* **100**: 63–75.
- Byrkjedal, I.** 1987. Antipredator behaviour and breeding success in Greater Golden-plover and Eurasian Dotterel. *Condor* **89**: 40–47.
- Cameron-MacMillan, M.L., Walsh, C.J., Wilhelm, S.I. & Storey, A.E.** 2007. Male chicks are more costly to rear than females in a monogamous seabird, the Common Murre. *Behav. Ecol.* **18**: 81–85.
- Cody, M.L.** 1971. Ecological aspects of reproduction. In Farner, D.S. & King, J.R. (eds) *Avian Biology*: 461–512. New York: Academic Press.
- Corkhill, P.** 1972. Measurements of puffins as criteria of sex and age. *Bird Study* **19**: 193–201.
- Cramp, S.** 1985. *The Birds of the Western Palearctic: Terns to Woodpeckers*, Vol. 4. Oxford: Oxford University Press.
- Cramp, S. & Simmons, K.E.L. (eds)** 1983. *The Birds of the Western Palearctic*, Vol. 3. Oxford: Oxford University Press.
- Creelman, E. & Storey, A.E.** 1991. Sex differences in reproductive behavior of Atlantic Puffins. *Condor* **93**: 390–398.
- Croxall, J.P.** 1995. Sexual size dimorphism in seabirds. *Oikos* **73**: 399–403.
- Currie, D., Valkama, J., Ber, A., Boschert, M., Norrdahl, K., Hännine, M., Korpomäki, E., Pöyri, V. & Hemminki, O.** 2001. Sex roles, parental effort and offspring desertion in the monogamous Eurasian Curlew *Numenius arquata*. *Ibis* **143**: 642–650.
- Erckmann, W.J.** 1983. The evolution of polyandry in shorebirds: an evaluation of hypothesis. In Waser, S.K. (ed.) *Social Behaviour of Female Vertebrates*: 113–168. New York: Academic Press.
- Fasola, M. & Saino, N.** 1995. Sex-biased parental-care allocation in three tern species (Laridae, Aves). *Can. J. Zool.* **73**: 1461–1467.
- Fraser, G.S., Jones, I.L. & Hunter, F.M.** 2002. Male–female differences in parental care in monogamous Crested Auklets. *Condor* **104**: 413–423.
- Fridolfsson, A.-K. & Ellegren, H.** 1999. A simple and universal method for molecular sexing of non-ratite birds. *J. Avian Biol.* **30**: 116–121.
- Gaston, A.J. & Hipfner, M.J.** 2000. Thick-billed Murre (*Uria lomvia*). In Poole, A. & Gill, F. (eds) *The Birds of North America*, no. 497. Philadelphia, PA: Academy of Natural Sciences and Washington, DC: American Ornithologists' Union.
- Gaston, A.J. & Jones, I.L.** 1998. *The Auks*. Oxford: Oxford University Press.
- Gaston, A.J. & Nettleship, D.N.** 1981. The Thick-billed Murres of Prince Leopold Island. *Can. Wildl. Serv. Monogr.*, no. 6. Ottawa: Canadian Wildlife Service.
- Gibson, F.** 1971. The breeding biology of the American Avocet *Recurvirostra americana* in Central Oregon. *Condor* **73**: 444–454.
- Gilchrist, H.G. & Gaston, A.J.** 1997a. Effects of murre nest site characteristics and wind condition on predation by Glaucous Gulls. *Can. J. Zool.* **75**: 518–524.
- Gilchrist, H.G. & Gaston, A.J.** 1997b. Factors affecting the success of colony departure by Thick-billed Murre chicks. *Condor* **99**: 345–352.
- Grecian, V.D., Diamond, A.W. & Chardine, J.W.** 2003. Sexing Razorbills *Alca torda* breeding at Machias Seal Island, New Brunswick, Canada, using discriminant function analysis. *Atlantic Seabirds* **5**: 73–80.
- Hamilton, R.B.** 1975. Comparative behavior of the American Avocet and the Black-necked Stilt (*Recurvirostridae*). *Ornithol. Monogr.*, no. 17. Washington, DC: American Ornithologists' Union.
- Harding, A., Van Pelt, T.I., Liffeld, J.T. & Mehlum, F.** 2004. Sex differences in Little Auk, *Alle alle*, parental care: transition from biparental to paternal-only care. *Ibis* **146**: 642–651.
- Harris, M.P. & Birkhead, T.R.** 1985. Breeding ecology of the Atlantic Alcidae. In Nettleship, D.N. & Birkhead, T.R. (eds) *The Atlantic Alcidae: The Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas*: 155–204. London: Academic Press.

- Harris, M.P. & Wanless, S. 2003. Postfledging occupancy of breeding sites by female Common Murres (*Uria aalge*). *Auk* **120**: 75–81.
- Hehgy, Z. & Sasvari, L. 1998. Parental condition and breeding effort in waders. *J. Anim. Ecol.* **67**: 41–53.
- Hipfner, J.M. & Chapdelaine, G. 2002. Razorbill (*Alca torda*). In Poole, A. & Gill, F. (eds) *The Birds of North America*, no. 635. Philadelphia, PA: Academy of Natural Sciences and Washington, DC: American Ornithologists' Union.
- Houston, A.I., Thompson, W.A. & Gaston, A.J. 1996. The use of a time and energy budget model of a parent bird to investigate limits to fledging mass in the Thick-billed Murre. *Funct. Ecol.* **10**: 432–439.
- Howe, M.A. 1982. Social organization in a nesting population of Eastern Willets (*Catoptrophorus semipalmatus*). *Auk* **99**: 88–102.
- Innsley, S.J., Paredes, R. & Jones, I. 2003. Sex differences in Razorbill (*Alca torda*) parent-offspring vocal recognition. *J. Exp. Biol.* **206**: 25–31.
- Jackson, W.M. 1991. Why do winners keep winning? *Behav. Ecol. Sociobiol.* **28**: 271–276.
- Jakubas, D. & Wojczulanis, K. 2007. Predicting the sex of Dovekies by discriminant analysis. *Waterbirds* **30**: 92–96.
- Jehl, J.R. Jr & Murray, B.G. Jr 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. In Johnston, R.F. (ed.) *Curr. Ornithol.* **3**: 92–96. New York: Plenum Press.
- Johnsgard, P.A. 1981. *The Plovers, Sandpipers and Snipes of the World*. Lincoln, NE: University of Nebraska Press.
- Jones, I.L. 1993. Sexual differences in the bill shape and external measurements of Crested Auklets (*Aethia cristatella*). *Wilson Bull.* **105**: 525–529.
- Jones, I.L. & Hunter, F.M. 1999. Experimental evidence for mutual inter- and intrasexual selection favouring a Crested Auklet ornament. *Anim. Behav.* **57**: 521–528.
- Jones, I.L. & Montgomerie, R. 1991. Mating and remating in Least Auklets (*Aethia pusilla*) relative to ornamental traits. *Behav. Ecol.* **2**: 249–257.
- Kober, K. & Gaston, A.J. 2003. Social interactions among breeding Brünnich's Guillemots *Uria lomvia* suggest constraints in relation to offspring vulnerability. *Ibis* **145**: 413–418.
- Lenington, S. 1984. The evolution of polyandry in shorebirds. In Burger, J. & Olla, B.L. (eds) *Shorebirds: Breeding Behaviour and Populations*: 149–167. New York: Plenum Press.
- Ligon, J.D. 1999. *The Evolution of Avian Breeding Systems*. Oxford: Oxford University Press.
- Lind, H. 1961. *Studies on the behaviour of the Black-Tailed Godwit (Limosa limosa (L.))*. PhD Thesis, University of Copenhagen.
- Margalida, A. & Bertran, J. 2005. Territorial defence and agonistic behaviour of breeding Bearded Vultures *Gypaetus barbatus* toward conspecifics and heterospecifics. *Ethol. Ecol. Evol.* **1**: 51–63.
- Montgomerie, R.D. & Weatherhead, P.J. 1988. Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* **63**: 167–187.
- Moody, A.T. & Hobson, K.A. 2007. Alcid winter diet in the northwest Atlantic determined by stable isotope analysis. *Mar. Ornithol.* **35**: 39–46.
- Moreno, J., Bustamante, J. & Viñuela, J. 1995. Nest maintenance and stone theft in the Chinstrap Penguin (*Pygoscelis antarctica*). 1. Sex roles and effects on fitness. *Polar Biol.* **15**: 533–540.
- Nelson, J.B. 1978. *The Gannet*. Vermillion, ND: Buteo Books.
- Nelson, D.A. 1981. Sexual differences in the measurements of the Cassin's Auklet. *J. Field Orn.* **52**: 233–234.
- Nethersole-Thompson, D. 1986. *Waders: Their Breeding, Haunts and Watchers*. Calton: Poyser.
- Niizuma, Y., Takahashi, A., Kuroki, M. & Watanuki, Y. 1999. Sexing by external measurements of adult Rhinoceros Auklets breeding on Teuri Island. *Jpn. J. Ornithol.* **48**: 145–150.
- Oleendorf, S.K. & Robinson, S. 2000. Effectiveness of nest defence in the Acadian Flycatcher *Empidonax wirens*. *Ibis* **142**: 365–371.
- Oring, L.W. 1986. Avian polyandry. *Curr. Ornithol.* **3**: 309–351.
- Paredes, R., Jones, I.L. & Boness, D.J. 2005. Reduced parental care, compensatory behaviour and reproductive costs experienced by female and male Thick-billed Murres (*Uria lomvia*) equipped with data loggers. *Anim. Behav.* **69**: 197–208.
- Paredes, R., Jones, I.L. & Boness, D.J. 2006. Parental roles of male and female Thick-billed Murres at Gannet Islands, Labrador. *Behaviour* **143**: 451–481.
- Paredes, R., Jones, I.L., Boness, D.J., Tremblay, Y. & Renner, M. 2008. Sex-specific differences in diving behaviour of two sympatric Alcid species: Thick-billed Murres and Razorbills. *Can. J. Zool.* **86**: 610–622.
- Patterson, T.L., Petrinovich, L. & James, D.K. 1980. Reproductive value and appropriateness of response to predators by White-crowned Sparrows. *Behav. Ecol. Sociobiol.* **7**: 227–231.
- Pierce, E.P. 1997. Sex roles in the monogamous Purple Sandpiper *Calidris maritima* in Svalbard. *Ibis* **139**: 159–169.
- Rahn, H., Paganelli, C.V. & Ar, A. 1975. Relation of avian egg weight to body weight. *Auk* **92**: 750–762.
- Regelmann, K. & Curio, E. 1983. Determinants of brood defence in the Great Tit *Parus major* L. *Behav. Ecol. Sociobiol.* **13**: 131–145.
- Reynolds, J.D. & Székely, Y. 1997. The evolution of parental care in shorebirds: life-histories, ecology and sexual selection. *Behav. Ecol.* **8**: 126–134.
- Robertson, G.J. & Elliot, R.D. 2002. Population size and trends of seabirds breeding in the Gannet Islands, Labrador. *Can. Wildl. Serv. Tech. Rep. Series*, no. 393. Atlantic Region.
- Scott, J.M. 1990. Offshore distributional patterns, feeding habitats, and adult-chick interactions of the Common Murre in Oregon. *Stud. Avian Biol.* **14**: 103–108.
- Serrano-Meneses, M.A. & Székely, T. 2006. Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. *Oikos* **113**: 385–394.
- Sordahl, T.A. 1990. Sexual differences in antipredator behaviour of breeding American Avocets and Black-necked Stilts. *Condor* **92**: 530–532.
- Stempniewicz, L. 1995. Predator-prey interactions between Glaucous Gull *Larus hyperboreus* and Little Auk *Alle alle* at Spitsbergen. *Acta Ornithol.* **29**: 155–170.
- Stenhouse, I.J., Gilchrist, H.G. & Montevecchi, W.A. 2005. An experimental study examining the anti-predator behaviour of Sabine's Gulls, *Xema sabini*, during breeding. *J. Ethol.* **23**: 103–108.

- Stewart, D.T.** 1993. Sexual dimorphism in Thick-billed Murres, *Uria lomvia*. *Can. J. Zool.* **71**: 346–351.
- Székely, T.** 1996. Brood reduction in Kentish Plover *Charadrius alexandrinus*: an experimental test of parental quality and remating opportunities. *Ibis* **138**: 749–755.
- Székely, T. & Lessens, C.M.** 1993. Mate change by Kentish Plovers *Charadrius alexandrinus*. *Ornis Scand.* **24**: 317–322.
- Székely, T., Reynolds, J.D. & Figuerola, J.** 2000. Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. *Evolution* **54**: 1404–1413.
- Székely, T., Thomas, G.H. & Cuthill, I.C.** 2006. Sexual conflict, ecology, and breeding systems in shorebirds. *Bioscience* **56**: 801–808.
- Székely, T., Lislevand, T. & Figuerola, J.** 2007. Sexual size, dimorphism in birds. In Fairbairn, D.J., Blanckenhorn, W.U. & Székely, T. (eds) *Sex, Size, and Gender Roles*. 27–38. Oxford: Oxford University Press.
- Thaxter, C.B., Daunt, F., Hamer, K.H., Watanuki, Y., Harris, M.P., Grémillet, D., Peters, G. & Wanless, S.** 2009. Sex-specific food provisioning in a monomorphic seabird, the Common Guillemot *Uria aalge*: nest defence, foraging efficiency or parental effort? *J. Avian Biol.* **40**: 75–84.
- Tuck, L.M.** 1960. The murres: their distribution, populations and biology. *Can. Wildl. Serv. Monogr.* no. 1, Ottawa: Canada.
- Wagner, R.H.** 1992. The pursuit of extra-pair copulations by monogamous female Razorbills: how do females benefit? *Behav. Ecol. Sociobiol.* **29**: 455–464.
- Wagner, R.H.** 1999. Sexual size dimorphism and assortative mating in Razorbills (*Alca torda*). *Auk* **116**: 542–544.
- Wanless, S. & Harris, M.P.** 1986. Time spent at the colony by male and female Guillemots *Uria aalge* and Razorbills *Alca torda*. *Bird Study* **33**: 168–176.
- Welcker, J., Harald, S., Harding, A. & Gabrielsen, G.** 2009. Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy. *Ibis* **151**: 502–513.
- Wilhelm, S.I.** 2004. *Behavioural and physiological responses of breeding Common Murres (Uria aalge): exploring inter-annual variability among individuals*. PhD Thesis, Memorial University of Newfoundland.
- Williams, T.D.** 2005. Mechanisms underlying the costs of egg production. *Bioscience* **55**: 39–48.
- Winkler, D.W.** 1992. Causes and consequences of variation in parental defence behavior by Tree Swallows. *Condor* **94**: 502–520.
- Yasué, M. & Dearden, P.** 2007. Parental sex roles of Malaysian Plovers during territory acquisition, incubation and chick-rearing. *J. Ethol.* **26**: 99–112.
- Ydenberg, R.C.** 1989. Growth-mortality trade-offs and juvenile life history in the Alcidae. *Ecology* **70**: 1494–1506.
- Yorio, P. & Quintana, F.** 1997. Predation by Kelp Gulls *Larus dominicanus* at a mixed-species colony of Royal Terns *Sterna maxima* and Cayenne Terns *Sterna eurygnatha* in Patagonia. *Ibis* **139**: 536–541.

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