ORIGINAL PAPER

Cryptic introgression between murre sister species (*Uria* spp.) in the Pacific low Arctic: frequency, cause, and implications

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Abstract As southern species undergo northward range expansions, reports of hybridization between temperate and arctic taxa are increasing, which may have important implications for the evolution, conservation, and management of arctic species. The extent of hybridization between temperate common murres (*Uria aalge*) and arctic thick-billed murres (*U. lomvia*), seabirds in the family Alcidae, has been the subject of debate. In a previous survey of variation in mitochondrial DNA (mtDNA) in common and thick-billed murres sampled from throughout the North Pacific and low Arctic, 12 of 327 common murres (∼4%) were found to possess DNA sequences characteristic of thick-billed murres. In the present study, we surveyed variation in three nuclear introns in 230 common murres and 56 thick-billed murres and report that these putative hybrids carry various combinations of intron alleles from common and thick-billed murres. Analysis using the program STRUCTURE indicated that nine of these individuals possessed high proportions of thick-billed murre intron alleles, two possessed alleles in F1 and F2 proportions, and one individual possessed predominantly common murre intron alleles. We propose that the asymmetric mtDNA introgression we observed is most likely the result of mate choice at mixed colonies based on differences in male mating behaviours. Our results highlight that hybridization between thick-billed and common murres is more prevalent than previously thought, which may have important implications for the conservation and management of arctic-dwelling thick-billed murres as common murres expand northward.

Keywords Common murre · Thick-billed murre · *Uria aalge* · *Uria lomvia* · Hybridization · Introgression

Introduction

Rates of hybridization between arctic and temperate taxa are increasing, and the potential for negative impacts on polar biodiversity appears high (Kelly et al. 2010). Hybridization between closely related species is common in nature and can have a number of outcomes. If pre- and/or postzygotic barriers to gene flow are well established, hybridization can result in wasted reproductive effort, but will not usually result in the production of offspring (Allendorf et al. 2001). When pre- and postzygotic barriers are not well established and hybrid offspring are produced, they may be less fit than, or have equal fitness to, parental species (Harrison 1993; Allendorf et al. 2001). Reduced fitness in hybrids may be caused by endogenous (i.e. hybrid breakdown) and/or exogenous (i.e. ecological or sexual) selection, but the relative influence of each mode of selection can be difficult to determine (Jiggins and Mallet 2000). When hybridization produces fit offspring, individuals may subsequently play important roles in the evolution of new species or adaptation to new environments (Anderson 1949; Arnold 1997; Coyne and Orr 2004); this

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outcome is probably more common in plants than in animals (Harrison 1993).

For hybridization to play an important role in the evolution of new species or adaptation to new environments, hybrids must be both viable and fertile, allowing gene exchange through the production of F2 and backcross individuals. Fertile hybrid offspring have been documented numerous times (e.g. Grant and Grant 1992; Seehausen 2004), leading to discussions about the importance of hybridization as a mechanism generating genetic diversity, most commonly in plants and also in a number of animal species (Grant and Grant 1992; Arnold 1997; Barton 2001).

More commonly, at least in animals, hybridization has negative consequences for the hybridizing species. Introgression can lead to the genetic swamping of rare species and loss of unique gene complexes, while wasted reproductive effort can negatively impact small, rare populations (Allendorf et al. 2001; Kelly et al. 2010). Both outcomes have important implications for the conservation and management of endangered and economically important species (Barilani et al. 2007). The potentially negative impacts of hybridization are particularly relevant to recently documented increasing rates of hybridization between temperate and arctic taxa. Many arctic species are already at risk from climate change (Burek and Gulland 2008; Post and Forchhammer 2008; Hunter et al. 2010), and hybridization with temperate taxa may represent an additional challenge to their persistence (Kelly et al. 2010). Although hybridization can result in increased biodiversity, management strategies for hybridizing arctic species may need to be modified if the goal is to preserve genetic potential, or if hybridization reduces the genetic integrity, economic importance or viability of the focal species (e.g. through wasted reproductive effort) (Allendorf et al. 2001).

Hybridization is relatively common between closely related species of birds, and at least 200 avian hybrid zones are known to exist (Grant and Grant 1992; Coyne and Orr 2004). Recently diverged species are more prone to hybridization, and the majority of Northern Hemisphere avian hybrid zones appear to be the result of post-Pleistocene range expansions (Price 2008). Common (*Uria aalge*) and thick-billed (*U. lomvia*) murres are closely related members of the auk family (Charadriiformes: Alcidae) with Holarctic distributions (Fig. 1). Though numerous at present, both species are vulnerable to oil spills and may be challenged with food shortages as a result of global warming (Piatt et al. 1990; Gaston et al. 2002, 2003, 2005). Thick-billed murres also have economic importance as the objects of an annual hunt (Wiese et al. 2004). Common murres primarily inhabit low-Arctic and boreal waters, whereas thick-billed murres tend to inhabit arctic environments (Fig. 1). Although nesting microhabitats tend to differ, both will breed in dense colonies on cliffs, and
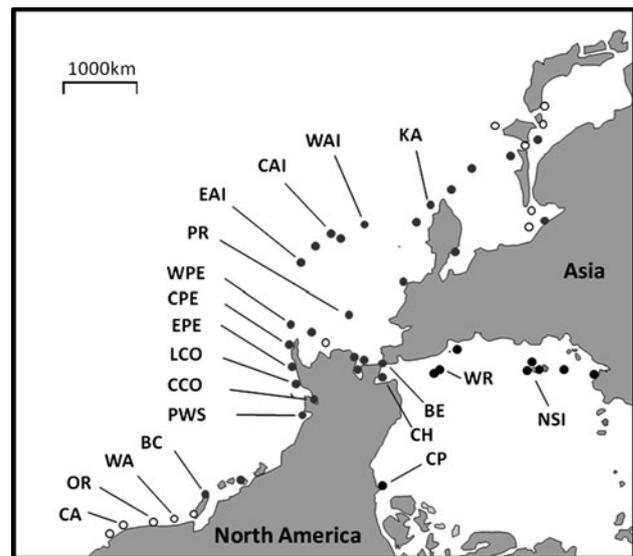

Fig. 1 Approximate breeding distribution of common and thick-billed murres in the North Pacific. *Open circles* represent major common murre colonies, *black circles* represent major thick-billed murre colonies, and *grey circles* represent mixed-species colonies. Sample sizes and colony abbreviations are listed in Table 1

mixed-species colonies exist where their ranges overlap: thick-billed murres are a true cliff-nesting species (Gaston and Hipfner 2000), while common murres will nest on cliffs, but also on more gently sloping areas (Ainley et al. 2002). The similarity of their reproductive ecology and the density at which they breed would appear to predispose them to hybridization within mixed colonies (Wirtz 1999).

Hybridization between auk species is generally considered rare; however, there is an account of possible hybridization between a common murre and a razorbill (*Alca torda*) (Wilhelm et al. 2001), and possible hybrids between common and thick-billed murres have been described from morphology (e.g. Tschanz and Wehrlin 1968; Cairns and DeYoung 1981). The validity of the reports of hybridization between murre species has been questioned (Sluys 1983). On the basis of molecular evidence, Friesen et al. (1993) identified a backcross between a female common murre/thick-billed murre hybrid and a male common murre at a Norwegian colony. This was the only hybrid individual identified during population genetic surveys that included samples from 248 common murres (Morris-Pocock et al. 2008) and 228 thick-billed murres (Birt et al. 2007) from throughout the North Atlantic. Additionally, one of 303 thick-billed murres sampled for a kinship study at the thick-billed murre colony at Coat's Island, Canada, had plumage and morphometrics intermediate between common and thick-billed murres (G. Ibarguchi, unpubl. data). Given these results, hybridization between common and thick-billed murres generally is not thought to have much significance for evolution or conservation of murres, at least in the North Atlantic.

As part of two larger studies of population differentiation in murres (Birt et al. 2007; Morris-Pocock et al. 2008), blood and solid tissue samples were collected from 327 common and 196 thick-billed murres from throughout the North Pacific and Arctic oceans. During collection, birds were classified to species on the basis of external phenotype: most notably, thick-billed murres possess black dorsal plumage and a white line along the gape, whereas common murres have brown dorsal plumage and lack the white line. The present study investigates the nuclear genotypes of 12 birds sampled as common murres but identified from Patirana (1998) as possessing mitochondrial DNA (mtDNA) sequences similar to thick-billed murres. We confirm the presence of heterotypic mtDNA in twelve birds sampled as common murres and assess their hybrid status by comparing variation at three nuclear introns in the hybrid individuals to variation in 230 North Pacific common murres and 56 North Pacific and arctic thick-billed murres. We also report heterotypic mtDNA in two birds sampled as thick-billed murres; however, the hybrid status of these individuals was not further investigated.

Materials and methods

Sampling and DNA extraction

Tissue samples were obtained from 327 common murres and 196 thick-billed murres from sites of both allopatry and sympatry throughout the North Pacific (Table 1, Fig. 1). The majority of samples consisted of blood from adults or chicks caught at nests and are archived in the Department of Biology at Queen's University. DNA was extracted using a standard protease-K phenol/chloroform technique (Sambrook and Russell 2001; Birt et al. 2007; Morris-Pocock et al. 2008).

Laboratory protocols

Sequence was obtained previously for 761 base pairs (bp) of the mitochondrial control region for 327 common murres from the Pacific Ocean (Morris-Pocock et al. 2008) and for 743 bp of the control region for 196 thick-billed murres from the Pacific and Arctic oceans (Birt et al. 2007). In Morris-Pocock et al. (2008), 351 Pacific Ocean common murres were surveyed at three introns in the genes for α-enolase (ENOL), crystallin (CRYS), and lactate dehydrogenase (LDH) using a combination of single-strand conformation polymorphisms (SSCPs) and direct sequencing (Morris-Pocock et al. 2008). For the present study, sequence variation was surveyed at the same introns in ENOL, CRYS, and LDH in 56 thick-billed murres from the Pacific and Arctic oceans using the same primers, PCR

conditions, and sequencing facilities described in Morris-Pocock et al. (2008).

Sequence analysis

Mitochondrial DNA sequences were aligned manually using BIOEDIT (version 7.0.5.3, Hall 1999) treating indels as transversions and a multibase insertion in one individual as a single mutational event. A minimum evolution gene tree was constructed using MEGA (version 4.0, Tamura et al. 2007) and Kimura's two-parameter model of substitution (Kimura 1980) with a gamma distributed rate parameter of 0.45 (based on estimates for control region sequences that include Domains I, II, and III in other avian species; Baker and Marshall 1997). Support for branches was determined using an interior branch test (Tamura et al. 2007).

Thick-billed murre intron sequences were aligned manually using BIOEDIT. In homozygous individuals or if only one polymorphic site existed in a heterozygote, allele sequences were inferred directly. To determine the allele sequences for heterozygous thick-billed murres when a homozygous individual for each allele was not present among the samples, the program PHASE (version 2.1, Stephens et al. 2001; Stephens and Donnelly 2003) was used. Appropriate run length was determined by examining the consistency of the haplotype frequency estimates across ten runs. For each intron data set, all 56 individuals were run with a burn-in of 1,000 iterations, 2,000 iterations after burn-in, and the default thinning interval of one. Phase determination was conservatively accepted at probabilities of 0.85 and higher because Harrigan et al. (2008) found that haplotypes inferred by PHASE with a probability greater than 0.60 are likely to reflect haplotypes found during cloning. Eleven individuals (7 for ENOL, 2 for CRYS, and 2 for LDH) for which the program could not determine the allele phase with this level of certainty were removed from subsequent analyses. Removing individuals for which phase determination probabilities fell between 0.85 and 0.95 did not alter the results. Thick-billed murre sequences were then aligned with common murre sequences from Morris-Pocock et al. (2008) in BIOEDIT, and TCS (version. 1.21, Clement et al. 2000) was utilized both to determine which alleles were shared between the species and to generate intron allele networks.

Hybrid status

The extent of introgression at nuclear loci was inferred using the program STRUCTURE (version 2.2, Pritchard et al. 2000). Analyses were conducted for the entire sample set including the 12 common murres with thick-billed murre mtDNA. Analyses with STRUCTURE were run with

Table 1 Colony abbreviations, census sizes, species ratios, and numbers of individuals typed at mtDNA

Sample site	Code	Census size (number of adult birds)		Ratio	Number of individuals typed		
		Common murre	Thick-billed murre		Common murre	Thick-billed murre	Heterotypics[f]
Kamchatka, Russia	KA	4,000 (1980)[a]	8,000	1:2	24	54	0
Chukchi Sea (including Capes Thompson and Lisburn), Alaska	CH	70,000 (1977)[a]	130,000	1:2	0	42	5
Cape Parry, Northwest Territories	CP	200 (1979)[b]	800	1:4	0	33	0
New Siberia Islands, Russia	NSI	no data	no data		0	6	0
Wrangle Island, Russia	WR	275 (2000)[d]	50,000	1:180	0	8	0
Fairway Rock, Bering Strait	BE	5,000 (1976)[a]	15,000	1:3	0	5	0
St. George, St. Paul and Pribilof Islands, Alaska	PR	216,156 (1989)[a]	1,174,665	1:5	33	24	0
Attu and Buldir Islands, Western Aleutian Islands	WAI	1,100 (1976)[a]	12,300	1:12	13	19	0
Kagamil and Bogoslov Islands, Central Aleutian Islands	CAI	7,000 (1982)[a]	27,000	1:4	6	13	0
Aiktak Island	EAI	12,600 (1980)[a]	2,400	5:1	27	13	1
Midun Island, Western Alaska Peninsula	WPE	766 (1994)[a]	511	2:1	7	0	0
Big Koniuji and Poperechenoi Islands, Central Alaska Peninsula	CPE	449 (1997)[a]	1,299	1:3	10	3	1
Chowiet Island, Eastern Alaska Peninsula	EPE	2,20,000 (1979)[a, g]			18	0	1
Amatuli and Barren Islands, Lower Cook Inlet	LCO	88,500 (1979)[a]	11,500	8:1	26	3	4
Chisik, Duck and Gull Islands, Central Cook Inlet	CCO	22,500 (1970)[a]	no data		43	0	0
Middleton Island, Prince William Sound	PWS	10,000 (1986)[a]	100	10:1	20	0	0
Triangle Island, British Colombia	BC	6,000 (2007)[c]	N/A	–	22	0	0
Cape Flattery, Washington	WA	2,000 (1999)[e]	N/A	–	11	0	0
Newport, Oregon	OR	15,440 (2002)[e]	N/A	–	21	0	0
Farallon Islands, California	CA	63,500 (2002)[e]	N/A	–	12	0	0

Date of census indicated beside common murre census size. N/A indicates absence of the species at that colony

[a] USFWS 2009

[b] Johnson and Ward 1985

[c] Hipfner and Greenwood 2008

[d] Kondratyev et al. 2000

[e] Carter et al. 2002

[f] Common murres with thick-billed murre mitochondrial DNA

[g] EPE census did not differentiate between murre species

an admixture model, a burn-in of 15,000 cycles (determined from initial runs to be sufficient for parameter stabilization), an additional 150,000 cycles after the burn-in, and the correlated allele frequency setting with $\lambda = 1$. One set of runs included species as prior information; the other set of runs did not. Results did not vary between the two sets of runs. No attempts were made to infer population genetic structure within species (Morris-Pocock et al. 2008). Instead, the program was run 20 times at $K = 2$ for each data set to determine which individuals in the sample possessed nuclear alleles from both species. STRUCTURE analyses were also run with non-correlated allele frequencies

and an admixture model, as well as using a reduced data set that excluded individuals (except hybrids) from mixed-species colonies. The conclusions from these analyses did not differ from initial runs.

Results

Mitochondrial control region

Mitochondrial haplotype characteristics were detailed previously (Birt et al. 2007; Morris-Pocock et al. 2008).

Fig. 2 Minimum evolution tree for mitochondrial control region haplotypes from common murres (*open circles*) and thick-billed murres (*black circles*). The *number* on the branch is interior branch test support for the species split. Branch length (Kimura two-parameter-corrected sequence divergence) is indicted at the *top* of the figure

With the exception of ten haplotypes found in 12 birds sampled as common murres and two found in two birds sampled as thick-billed murres, common and thick-billed murre haplotypes were reciprocally monophyletic on a minimum evolution gene tree with 0.99 support from an interior branch test for the species split (Fig. 2). Of the ten common murre haplotypes that grouped with thick-billed murre haplotypes, all occurred at colonies where both species breed (Table S1).

Intron variation

All three introns were highly variable in both common (Morris-Pocock et al. 2008) and thick-billed murres, with between eight and 20 alleles in common murres and five and 17 alleles in thick-billed murres (Accession # FJ374455-FJ374495, JQ246917-JQ246948) (Table S1). Most differences between alleles involved transitions. Common and thick-billed murre alleles were not reciprocally monophyletic on any of the three intron allele networks (Fig. 3). Three ENOL alleles, three CRYS alleles, and one LDH allele were shared between common and thick-billed murres (Fig. 3; Supplementary Table 1). A number of intron alleles were found only in common murre individuals with heterotypic mtDNA, including ENOL alleles 9, 10, and 11, and CRYS alleles 8, 9, 11, 12, 14, and 18.
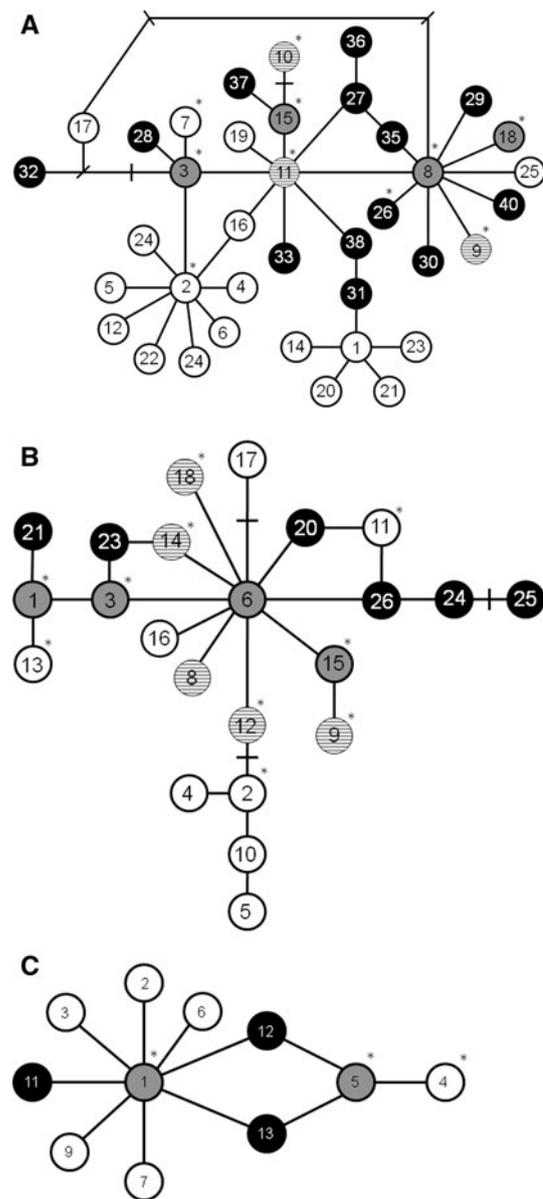

Fig. 3 Statistical parsimony networks for intron alleles for three loci: **a** α-enolase, **b** crystallin, **c** lactate dehydrogenase. *White circles* represent alleles found only in common murres, *black circles* represent alleles found only in thick-billed murres, *grey circles* represent alleles shared between species and hatched *grey circles* represent haplotypes found only in individuals that possessed heterotypic mitochondrial DNA. *Indicates allele was found in a putative hybrid

Hybrid status

Putative hybrid common murres had various combinations of intron alleles from each parental species for each locus (Table S1). Analyses with STRUCTURE indicated that nine individuals possessed high proportions of intron alleles characteristic of thick-billed murres, two possessed alleles in approximately F1 or F2 proportions, and one
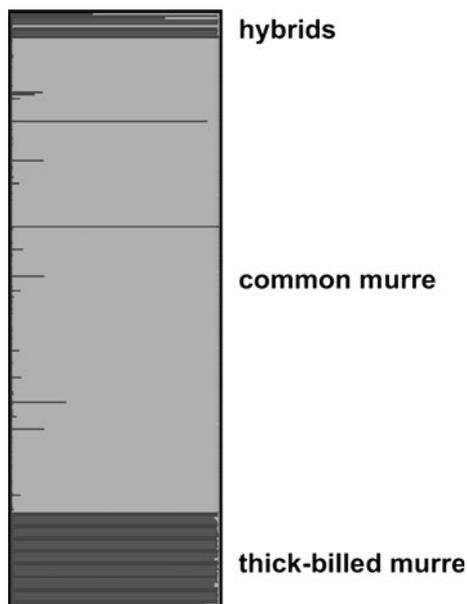
Fig. 4 Bayesian assignment probabilities for individual hybrid, common, and thick-billed murres at $K = 2$. Each *horizontal line* represents an individual, and the *shades of grey* indicate the probability that an individual's genotype assigned to a particular genetic population

Table 2 Mitochondrial control region haplotypes and genotypes at three nuclear introns for 12 birds sampled as common murres with thick-billed murre mitochondrial haplotypes

Specimen	Collection site	MtDNA haplotype	Genotype		
			Enol	Crys	LDH
CL4695	Cape Lisburne	C35	02, 18	01, 02	01, 04
CT0395	Cape Thompson	C40	08, 26	03, 14[a]	01, 01
CT0495	Cape Thompson	C41	08, 18	01, 01	01, 04
CT0695	Cape Thompson	C42	11[a], 15	15, 18[a]	01, 04
CT1295	Cape Thompson	C41	11[a], 15	03, 03	01, 04
CT4095	Cape Thompson	C46	15, 15	03, 15	01, 01
96-02	St. Paul Island	C35	02, 02	01, 13	01, 01
95-67	Chowiet	C55	08, 15	06, 06	01, 01
95-27	Amatuli Island	C12	03, 10[a]	06, 08[a]	04, 05
95-28	Amatuli Island	C13	08, 07	11, 12[a]	01, 01
95-34	Amatuli Island	C18	08, 11[a]	06, 09[a]	01, 01
96-70	Barren Island	C25	09[a], 15	08[a], 11	04, 04

[a] Found only in individuals with heterotypic mtDNA

individual possessed predominantly common murre intron alleles. Results from STRUCTURE also revealed that two common murres with conspecific mtDNA possessed a high proportion of thick-billed murre nuclear DNA (Fig. 4).

Discussion

Hybridization or retained ancestral polymorphism?

The occurrence of thick-billed murre mitochondrial genotypes in 12 birds with the morphology of common murres indicates either retention of ancestral mtDNA polymorphisms or interspecific hybridization. The control region haplotypes of these murres differed from other common murre haplotypes by between 43 and 47 substitutions in 762 bp ($\sim 6\%$). Especially in the absence of intermediate haplotypes, retention of such divergent haplotypes is unlikely. Avise et al. (1984) argued that populations will be reciprocally monophyletic on a mitochondrial gene tree if time since divergence (in generations) is greater than four times the female effective population size ($4N_e$), after which the presence of conspecific mtDNA in an individual would more likely be the result of interspecific hybridization than shared ancestral polymorphism. Assuming similar-sized populations for common and thick-billed murres in the North Pacific (Piatt unpubl data.), a generation time of 10 years (Southern et al. 1965), and a long-term female effective population size of 7,400 (Friesen et al. 1996), the estimate of $4N_e$ for murres in the North Pacific is 29,600. These species diverged around 420,000 generations ago (Moum et al. 1994) so interspecific hybridization is the most parsimonious explanation for the presence of heterospecific mtDNA in birds with the morphology of common murres.

Nature of murre hybridization

Common murres with heterotypic mtDNA accounted for $\sim 4\%$ of the 339 common murres sampled from the North Pacific and all were sampled from sites of sympatry with thick-billed murres. None of the introgressed mitochondrial haplotypes were common and they also occurred only in areas of sympatry. Introgression of mtDNA may be limited to zones of sympatry because of the philopatric nature of these birds: both species exhibit extreme natal philopatry, regularly returning to the ledge on which they hatched to nest (Harris et al. 1996; Steiner and Gaston 2005).

The majority of individuals with heterotypic mtDNA also had a high assignment probability to the thick-billed murre genetic population, generally in backcross proportions (Table 2). The presence of thick-billed murre nuclear DNA and mtDNA in birds sampled as common murres suggests that intranuclear and nuclear–mitochondrial interactions are not lethal between these species. Introgression of DNA is not restricted to the mitochondrial genome, and the presence of potential backcross individuals indicates, as was found in the North Atlantic, that F1

Table 3 Possible backcrosses between thick-billed and common murres, and mtDNA and predominant nuclear DNA of backcross offspring

Cross no.	Parental species		Hybrid sex	Backcross species	mtDNA	Predominant nuclear DNA
	♀	♂				
1	CM	TBM	♀	TBM	CM	TBM
2	CM	TBM	♀	CM	CM	CM
3	CM	TBM	♂	TBM	TBM	TBM
4	CM	TBM	♂	CM	CM	CM
5	TBM	CM	♀	TBM	TBM	TBM
6	TBM	CM	♀	CM	TBM	CM
7	TBM	CM	♂	TBM	TBM	TBM
8	TBM	CM	♂	CM	CM	CM

♀ female, ♂ male, *CM* common murre, *TBM* thick-billed murre

offspring of heterospecific pairings are both viable and fertile (Friesen et al. 1993).

No animals with the morphological constitution of F1 hybrids were found during this study (see Cairns and DeYoung 1981); however, a single individual had an equal probability of assignment to either common or thick-billed murres. The absence of morphological differences between individuals possessing heterotypic mtDNA and common murres with homotypic mtDNA may be due to phenotypic dominance (Butlin and Neems 1994). The majority of the common murres with heterotypic DNA were likely backcross hybrids. Eight backcrosses are possible (Table 3); all would result in transfer of nuclear DNA between species. Cross 1 would result in introgression of common murre mtDNA into thick-billed murres, and cross 6 would result in introgression of thick-billed murre mtDNA into common murres. The presence of only two common murre mitochondrial genotypes among 218 thick-billed murres from throughout the North Pacific suggests either that crosses 1 through 4 rarely occur or that offspring of these crosses have low viability or fertility.

Asymmetric gene flow

In nearly equivalent samples, we detected a significantly higher proportion of introgressed mtDNA in common murres ($\sim4\%$) than in thick-billed murres ($\sim1\%$), indicating generally asymmetric mitochondrial gene flow between these species (chi-squared contingency test: $\chi^2_{df=1} = 480$, $P < 0.001$). Unidirectional or restricted gene flow during hybridization is common (Wirtz 1999) and can be caused by a number of factors that are not mutually exclusive, including biased sex ratios at colonies, Haldane's rule for one or both possible crosses, unequal numbers at colonies, and mate choice.

Biased sex ratios

Female-biased sex ratios may increase the likelihood that unpaired females will choose to mate with heterospecific males, while male-biased sex ratios may increase the likelihood that unpaired males will court heterospecific females (Wirtz 1999). Though many nesting colonies of birds have male-biased sex ratios (Wirtz 1999), studies of both common and thick-billed murres report equal ratios (Hudson 1985; Gaston and Jones 1998), suggesting that biased sex ratios are not responsible for the asymmetric hybridization we observed.

Unequal numbers at colonies

In a review of unidirectional hybridization, Wirtz (1999) presented the sexual selection hypothesis predicting that the female in a hybridizing pair, and thus the source of mtDNA, will most often be the rarer of the parental species. The rationale is that the longer that females of the rare species in mixed mating populations search for conspecific mates, the less discriminating they become, which leads to mating between females of the rare species and males of the common species (Wirtz 1999). Avise and Saunders (1984) found support for this hypothesis in *Lepomis* sunfish; however, Randler (2002) found that males of a rare species are as likely to be involved in heterospecific pairs as females. Most recently, Servedio and Lande (2006) highlighted that examples of male and mutual mate choice are becoming more numerous. If thick-billed murres are generally the uncommon species in mixed colonies, Wirtz's hypothesis would explain the asymmetric hybridization we observed. Given that thick-billed murres are the more numerous species in mixed colonies in the Chukchi Sea and Bering Sea where half of the hybrids were sampled, but are less numerous in the Eastern Aleutian Islands, Gulf of Alaska, and the Alaska Peninsula (Table 1), and the same proportion of hybrids were found in this region (Byrd et al. 1993), our results fall between the conclusions of Wirtz (1999) and Randler (2002): something other than the cost of searching appears to be directing mate choice.

Haldane's rule

According to Haldane's rule (Haldane 1922), hybrid fertility will be more severely reduced in the heterogametic sex, that is, in female birds (e.g. Tegelström and Gelter 1990). The present results indicate that female offspring of crosses between male common and female thick-billed murres in the North Pacific are viable, as well as fertile, consistent with the conclusions of Friesen et al. (1993) in their examination of an Atlantic backcross individual. The directional mtDNA introgression we observed could be the

result of poorer success of female offspring from crosses involving female common murres and male thick-billed murres (Table 3).

Mate choice

Differences in mate choice and mating behaviour between thick-billed and common murres may explain asymmetric hybridization. Thick-billed murres exhibit less ritualized mating behaviour and are generally less vigorous than common murres during mating and social interactions (Gaston and Jones 1998). If these ritualized behaviours are the product of sexual selection, it seems unlikely that female common murres would choose to mate with male thick-billed murres: male thick-billed murres may act like very low-quality common murres. Female thick-billed murres may, however, choose to mate with male common murres even when conspecific males are common (Table 1): the exaggerated mating behaviour of male common murres may make them more attractive than conspecific males to female thick-billed murres (Wirtz 1999; Price 2008). Additionally, male common murres tend to be larger than male thick-billed murres, which may give them a competitive advantage during social interactions (Spring 1971). Similar patterns have been observed in North America where the breeding ranges of Mallard (*Anas platyrhynchos*) and Black Ducks (*Anas rubripes*) overlap. Male Mallards exhibit higher levels of sexual aggression during courtship than male Black Ducks and are preferentially selected as mates (D'Eon et al. 1994).

Cryptic introgression

The results of this study represent an additional example of cryptic mitochondrial and nuclear introgression: morphologically the sampled birds appeared to be common murres, but their mitochondrial genomes grouped distinctly with thick-billed murre mitochondrial sequence and they possessed, to varying degrees, thick-billed murre intron alleles. Cryptic introgression of heterospecific mitochondrial and nuclear DNA has been documented in mammals (Good et al. 2003; Deffontane et al. 2005; Melo-Ferreira et al. 2005), amphibians (Plötner et al. 2008), and birds (Rohwer et al. 2001; Weckstein et al. 2001; Irwin et al. 2009), but more frequently for mitochondrial than nuclear DNA due to differences in effective population size (Ballard and Whitlock 2004; Bryson et al. 2010). The potential for mitochondria to be under selection is being increasingly recognized in the literature (Ballard and Whitlock 2004), and in extreme cases complete mitochondrial replacement has been documented (Irwin et al. 2009). We did not find evidence of this in murres; however, the possibility that thick-billed murre mitochondrial DNA, and possibly nuclear DNA, is superior at high latitudes is intriguing and warrants further investigation.

Implications

Hybridization of common and thick-billed murres is more common in the North Pacific than in the North Atlantic, likely because breeding colonies of these two species overlap to a greater degree in the Pacific. Hybridization often has negative consequences in vertebrates. Consequently, conservation and management of thick-billed murres in the North Pacific should seek to gain a better understanding of the impact of hybridization on genetic diversity within thick-billed murres, on the reproductive success of hybrids, and on the costs incurred by individuals that hybridize (i.e. wasted reproductive effort): increased hybridization between murres in the North pacific as a result of range shifts of common murres northwards could impact thick-billed murres.

On the other hand, hybridization could potentially play an important role in generating the genetic variability that enables adaptation of species to variable environments (Anderson 1949). Our results indicate that female thick-billed murres will mate with male common murres, even when thick-billed murres are the more numerous species. This potential preference for male common murres should be further explored. Understanding the causes and consequences of hybridization in North Pacific murres is important for gaining a better understanding of speciation and species integrity. As climate change alters the subarctic and arctic environments in which common and thick-billed murres breed, the potential for hybridization may increase. The possibility that hybridization has played a role in the evolutionary history of these two species is intriguing and warrants further study. A genomic approach may be particularly useful.

Summary

Hybridization between thick-billed and common murres is more common than previously thought and has played a role in their evolutionary history in the North Pacific. We found evidence of both contemporary and historical hybridization events, suggesting that hybridization occurs intermittently in zones of contact between these closely related members of the auk family. We also found that hybridization is either more common between female thick-billed murres and male common murres, potentially because of mate choice, or more likely to result in viable and fertile offspring than the opposite cross. Prior to this study, the frequency of hybridization between common and thick-billed murres was assumed to be negligible, and no documentation of cryptic introgression had been made in

any auk. Our results indicate that hybridization between these species should be considered as it relates both to their evolutionary history and to their conservation and management.

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