Rape and the Prevalence of Hybrids in Broadly Sympatric Species: a Case Study using Albatrosses

Conspecific rape often increases male reproductive success. However, the haste and aggression of forced copulations suggests that males may sometimes rape heterospecific females, thus making rape a likely, but undocumented, source of hybrids between broadly sympatric species. We present evidence that heterospecific rape may be the source of hybrids between Black-footed and Laysan Albatrosses (*Phoebastria nigripes*, and *P. immutabilis*, respectively). Extensive field studies have shown that paired (but not unpaired) males of both of these albatross species use rape as a supplemental reproductive strategy. Between species differences in size, timing of laying, and aggressiveness suggest that Black-footed Albatrosses should be more successful than Laysan Albatrosses in heteropspecific rape attempts, and male Black-footed Albatrosses have been observed attempting to force copulations on female Laysan Albatrosses. Nuclear markers showed that the six hybrids we studied were F1s and mitochondrial markers showed that male Black-footed Albatrosses sired all six hybrids. The siring asymmetry found in our hybrids may have long persisted because an IM analysis suggests that long-term gene exchange between these species has been from Black-footed Albatrosses into Laysan Albatrosses. If hybrids are sired in heterospecific rapes, they presumably would be raised and sexually imprinted on Laysan Albatrosses, and two unmated hybrids in a previous study courted only Laysan Albatrosses.

1   **Rape and the Prevalence of Hybrids in Broadly Sympatric Species: a Case Study Using**

2   **Albatrosses**

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23 **Abstract**

24   Conspecific rape often increases male reproductive success. However, the haste and

25 aggression of forced copulations suggests that males may sometimes rape heterospecific females,

26 thus making rape a likely, but undocumented, source of hybrids between broadly sympatric

27 species. We present evidence that heterospecific rape may be the source of hybrids between

28 Black-footed and Laysan Albatrosses (*Phoebastria nigripes*, and *P. immutabilis*, respectively).

29 Extensive field studies have shown that paired (but not unpaired) males of both of these albatross

30 species use rape as a supplemental reproductive strategy. Between-species differences in size,

31 timing of laying, and aggressiveness suggest that Black-footed Albatrosses should be more

32 successful than Laysan Albatrosses in heteropecific rape attempts, and male Black-footed

33 Albatrosses have been observed attempting to force copulations on female Laysan Albatrosses.

34 Nuclear markers showed that the six hybrids we studied were F1s and mitochondrial markers

35 showed that male Black-footed Albatrosses sired all six hybrids. Long-term gene exchange

36 between these species has been from Black-footed Albatrosses into Laysan Albatrosses,

37 suggesting that the siring asymmetry found in our hybrids has long persisted. If hybrids are sired

38 in heterospecific rapes, they presumably would be raised and sexually imprinted on Laysan

39 Albatrosses, and two unmated hybrids in a previous study courted only Laysan Albatrosses.

40 **Introduction**

41   Unidirectional hybridization is common in nature. A recent review showed that 50 of 80

42 cases involving at least five hybrids, were predominantly unidirectional (Wirtz 1999). From a

43 long list of alternatives, a shortage of mates for females was the only general explanation

44 supported for unidirectional hybridization. In this paper we seek the beginnings of an answer to

45 the question of why hybrids vary so much in frequency between broadly sympatric species. For

46 example, hybrids between broadly sympatric species of waterfowl and grouse are far more

47 common than they are in other groups of birds (Grant and Grant 1992). Because hybridization

48 usually arises as an epiphenomenon of mating strategies within species (Price 2008), we think

49 hybrids may be disproportionately common in groups of birds characterized by forced

50 copulations, as others have suggested (Kabus 2002, McKee and Pyle 2002, Randler 2008). Forced

51 copulations are used as a supplemental reproductive tactic by males in many species of waterfowl

52 (Brennan et al. 2009, McKinney and Evarts 1998), but a comparative test by Randler (2008)

53   found more support for brood amalgamation than for forced copulations as alternative sources of

54   hybrid waterfowl.

55   Here we suggest that predicting siring asymmetries offers a promising way to evaluate the

56   importance of heterospecific rape as a source of hybrids between broadly sympatric species. In

57   general, rape supplements male reproductive success when directed toward conspecifics (Shields

58   & Shields 1983; Thornhill 1980; Thornhill & Palmer 2001; Thornhill & Sauer 1991; Thornhill &

59   Thornhill 1983) but the urgent and aggressive nature of rape may result in males sometimes

60   forcing copulations on heterospecific females. While they may be uncommon, hybrids generated

61   by heterospecific rape should be found wherever the parental species breed sympatrically, rather

62   than being confined to zones where the ranges of parapatric species pairs meet and where hybrids

63   are often abundant.

64   We illustrate our predictions using hybrids between Laysan and Black-footed Albatrosses

65   (*Phoebastria immutabilis* and *P. nigripes,* respectively) because we had genetic samples for both

66   parental species and for hybrids that could be used to test for a siring bias in F1 hybrids and to

67   evaluate long-term gene exchange between the parental species. Paired males of both of these

68   albatrosses are known to force copulations on conspecific females. If hybrids are sired through

69   heterospecific rape, differences between these albatrosses in behavior and the timing of egg

70   laying (detailed below) suggest that Black-footed Albatrosses should sire most F1 hybrids. It is

71   important that only F1 hybrids are used to evaluate siring biases predicted for heterospecific rape

72   because siring asymmetries will be lost if backcross hybrids are generated through random

73   mating with either parental species. Siring bias in F1 hybrids is easily assessed using

74   mitochondrial DNA (mtDNA) to identify the maternal species.

75   It is important to emphasize that forced and unforced extra pair copulations must be

76   distinguished before the role of heterospecific rape in the generation of hybrids can be assessed.

77   Rape will not be a source of hybrids in species groups where females control extra pair paternity

78   (Dunn and Cockburn 1999, Spottiswoode and Møller 2004, Stuchbury and Neudorf 1998).

79   However, when forced copulations are the result of extreme male aggression, sometimes carried

80   out by groups of males, rape can be a source of hybrids if males mistakenly attack heterospecific

81   females. Of course, male waterfowl have penises that can be used to forcibly inseminate resisting

82   females (Brennan et al. 2009), but even in species without penises, male rapes may be so

83   aggressive that females must acquiesce to avoid being seriously injured or killed (Brekke et al.

84   2013, Fisher 1971, Mckinney and Evarts 1998). Clear evidence of female coercion is required

85   before heterospecific rape appropriately can be considered a possible source of hybrids.

86   **Study System**

87   Laysan and Black-footed Albatrosses are closely related sister species (Nunn et al. 1996)

88   that breed sympatrically in the Northwestern Hawaiian Islands. Like other albatrosses, they are

89   long-lived, delay breeding until they are five to seven years old, form life-long pair bonds, lay

90   single eggs, and may breed for 20-50 years (Fisher 1969; Fisher 1971; Fisher 1972; Fisher 1975;

91   Fisher 1976; Rice & Kenyon 1962).

92   Our samples came from Midway Atoll where over 480,000 pairs of these albatrosses nest

93   and where the beach-nesting Black-footed Albatross comprises about five percent of all pairs (E.

94   Flint, personal communication). Although interbreeding between Black-footed and Laysan

95   Albatrosses is rare, putative hybrids have been noted for decades (Fisher 1948; Fisher 1971;

96   McKee & Pyle 2002) and up to 20 presumptive hybrids were observed at Midway Atoll between

97   1997 and 2000 (McKee & Pyle 2002).

98   Mature Black-footed Albatrosses are primarily dark brown, whereas Laysan Albatrosses

99   are largely white on the body and dark grey to black on the wings and back. Presumed hybrids are

100   intermediate between the parental species in plumage and soft part coloration, ranging in plumage

101   from very pale grey to fairly dark, with pale under wings (Fisher 1972; McKee & Pyle 2002). The

102   lightest presumptive hybrids can resemble the darkest Laysan Albatrosses in plumage color, but

103   the darkest putative hybrids are not as dark as Black-footed Albatrosses. Because both Laysan

104   Albatrosses and hybrids are variable in coloration, identifying or excluding progeny that might

105   result from backcrosses is not possible based on plumage characteristics alone (McKee & Pyle

106   2002) and requires genetic assessment.

107   Conspecific rapes are observed in both Laysan and Black-footed Albatrosses (Fisher 1971;

108   Fisher 1972), and Black-footed Albatross males sometimes direct rape attempts at Laysan females,

109   suggesting that hybrids could result from heterospecific rapes. In Laysan Albatrosses conspecific

110   rape is very aggressive, often carried out by groups of males, and sometimes results in serious

111   injury of the female (Fisher 1971). Multiple males regularly join these rape attempts, mounting

112   other males until the pile topples over. Given that albatrosses lack the explosive penis that

113   facilitates forced copulation by male waterfowl (Brennan et al. 2005), it seems likely that females

114 may sometimes evert their cloaca to receive sperm just to prevent further harassment and injury

115 by attacking males; however, we should note that Fisher (1971) found no evidence of sperm

116 transfer in albatrosses he examined closely following attacks by males. Fisher (1971) further

117 reports that he never observed an attempt by the female's mate to defend her from harassing

118 males, as does occur in waterfowl (McKinney & Evarts 1998). Although Fisher (1972) reports

119 failing to observe interspecific rape attempts, McKee & Pyle (2002) observed male Black-footed

120 Albatrosses attempting to rape female Laysan Albatrosses and believed these events to be the

121 source of hybrids. Neither Fisher (1972) nor McKee & Pyle (2002) observed mixed pairs.

122   Importantly, differences in the timing of breeding, body size, and aggressiveness all

123 suggest that F1 hybrids are sired when the larger and more aggressive male Black-footed

124 Albatrosses force copulations on female Laysan Albatrosses. Particularly important is that Black-

125 footed Albatrosses arrive at the breeding colonies and lay earlier than do Laysan Albatrosses

126 (Fisher 1969; Rice & Kenyon 1962). Because, females take the first incubation shift in these

127 albatrosses (Fisher 1971, Rice and Kenyon 1962), Laysan females are fertile and vulnerable to

128 insemination through heterospecific rape by Black-footed Albatross males that are mated to

129 females that are already incubating.

130   We evaluated the F1 status of hybrids using fixed and near-fixed differences in their

131 nuclear genome, and we assessed siring bias using mtDNA from the hybrids. We also used an

132 isolation-migration (IM) model to test the hypothesis of asymmetric gene flow between these

133 species following their divergence approximately 1.03 million years ago (Nunn et al. 1996).

134 **Materials and Methods**

135 *Sampling*

136   Blood was sampled from 29 breeding Black-footed Albatrosses, 28 Laysan Albatrosses,

137 and six presumed hybrids (morphologically intermediate between the two species in plumage

138 coloration) at Midway Atoll National Wildlife Refuge (28°13' N, 177°22' W). Genomic DNA

139 was extracted from blood samples either by a standard phenol:chloroform procedure (Sambrook

140 et al. 1989) or using the Wizard SV Genomic DNA Purification System (Promega). All work was

141 conducted in accordance with University of Washington Institutional Animal Care and Use

142 Committee (protocol 2846-13).

143 *Molecular methods*

144   To assess gene flow between the parental species, we collected DNA sequence data for

145 eight anonymous nuclear loci, one coding nuclear locus (a fragment of a Major

146 Histocompatibility Complex (MHC) gene (Walsh & Edwards 2005), and the mtDNA *cytochrome-*

147 *b* (*cyt-b*) locus . Anonymous loci were derived from a fosmid library for Black-footed Albatross

148 (Table 1). "FWD" and "REV" designations indicate loci that were taken from opposite ends of a

149 fosmid insert, and therefore are separated by ~ 35 kb in the genome. Optimized PCR reactions

150 for anonymous loci contained 0.4 μM primer, 0.2 mM of an equimolar solution of dNTPs, 0.2 U

151 of Taq DNA polymerase (Roche, Indiana, USA), and approximately 20 ng of template DNA in 10

152 μl reaction volumes. Thermal cycler reaction profiles consisted of initial denaturation at 94°C for

153 1 minute 30 seconds, followed by 30 cycles of 94°C for 30 seconds, 50-68°C for 30

154 seconds, 72°C for 45 to 60 seconds, and a final extension step of three minutes at 72°C.

155   We assigned quality scores to base calls in sequence trace files using Phred (Ewing &

156 Green 1998; Ewing et al. 1998) and aligned homologous sequences using Phrap (Green 1994).

157 Polymorphic sites were identified using the program PolyPhred (Nickerson et al. 1997).

158 Assemblies were visualized in Consed (Gordon et al. 1998) and single nucleotide polymorphisms

159 (SNPs) and genotypes at each locus were confirmed by eye. Nuclear haplotypes were resolved

160 using PHASE v.2.1.1 (Stephens & Donnelly 2003; Stephens et al. 2001). All sequences have been

161 deposited in GenBank (accession numbers KF475302-KF475698).

162   Putative hybrids were sexed using primers 2550F and 2718R (Fridolfsson & Ellegren

163 1999); sex was scored by eye, with two bands indicating female and a single-band indicating

164 male. Sexing the hybrids enabled us to assess whether hybrid females (the heterogametic sex in

165 birds) were inviable, which could be expected under Haldane's rule (Haldane 1922).

166 *Hybrid identification*

167   We computed two hybrid indices, both varying from 0 (pure Laysan Albatrosses) to 1

168 (pure Black-footed Albatrosses). The first is most intuitive and includes only loci with fixed or

169 near-fixed sequence differences between Black-footed and Laysan Albatrosses (Table 1). Using

170 these same loci, we also computed the probability that the six phenotypically intermediate

171 specimens were first generation (F1) hybrids or backcrosses (Table 2). For the second hybrid

172   index we used maximum likelihood in the introgress package implemented in R (Gompert &

173   Buerkle 2009), and included all of the nuclear loci.

174   Siring asymmetries for the hybrids were assessed using a binomial test on mtDNA data.

175   *Migration estimation*

176   To assess the rate and direction of gene flow between Black-footed and Laysan

177   Albatrosses, we used the IM model implemented in IMa2 (Hey & Nielsen 2004; Hey 2010). We

178   applied the HKY mutation model of nucleotide substitution and nuclear mutation rate scalars

179   were free to vary in the model. The nuclear and mitochondrial genes were assigned an inheritance

180   scalar of 1.0 and 0.25, respectively. To avoid violating the assumptions of no recombination and

181   neutrality of markers, we tested for within-locus recombination using the four-gamete test

182   (Hudson & Kaplan 1985) for each locus and within each species; we tested neutrality of markers

183   using Tajima's D implemented in R package PEGAS (Paradis 2010) (Table 1).

184   We ran 12 replicate IMa2 analyses, each using different starting seeds and 40-50

185   concurrent chains, for 10-50 million steps after an initial burn-in phase of 50,000-100,000

186   generations. To rescale estimates of population size and migration parameters into demographic

187   units, we used the geometric mean of previous mtDNA rate estimates for albatrosses of 3×10^{-5}

188   substitutions per locus per year for our fragment of *cyt-b*; (Nunn & Stanley 1998), and a

189   generation time of 25 years (Cousins & Cooper 2000). The results of these independent runs were

190   combined into a single L-mode analysis to evaluate the probabilities for all possible nested

191   models. For explanation of nested models, see the standard IMa2 documentation (Hey 2010). We

192   conducted model selection following Carstens et al. 2009.

193   **Results**

194   *Hybrid indices and probability of hybrid genotypes*

195   All six putative hybrids were heterozygous at five diagnostic nuclear SNPs (Table 1).

196   Using just these diagnostic loci the hybrid index for a true F1 hybrid is expected to be 0.51

197   because Laysan Albatrosses share in low frequency (10%) a single diagnostic SNP (dSNP2 in

198   Tables 1 & 2) that is fixed in Black-footed Albatrosses (Fig. 1).

199   In Table 2 we use the observed population allele frequencies to calculate the probability of

200   producing the genotype found in all six hybrids, under the assumption that they were either F1

201   hybrids or first generation backcrosses. The probability of producing the observed hybrid

202   genotype was 0.90 for a parental cross. The probability that the hybrid genotype resulted from a

203   backcross to either of the parental species varies by the sex of the hybrid and the sex and species

204   of the backcross parent (Table 2). Because all hybrids carried Laysan mtDNA haplotypes, the

205   probability of a backcross to a female Black-footed Albatross is 0. For the three other backcross

206   combinations, the probability of observing the hybrid genotype is either 0.028 or 0.034 (Table 2).

207   These calculations, based on the five diagnostic SNPs, show that the six hybrids are almost

208   certainly F1s and not backcross individuals.

209   We also evaluated the status of the six hybrids using a maximum likelihood estimator

210   (Gompert & Buerkle 2010), including in this analysis the four nuclear SNPs that were not

211   diagnostic (Table 1). All six hybrids received a score of 0.56, with a 95% confidence interval of

212   0.22 – 0.85.

213   *Siring bias and sex for the hybrids*

214   All six hybrids carried the Laysan Albatross mtDNA haplotype, indicating that F1 hybrids

215   result from male Black-footed Albatrosses inseminating female Laysan Albatrosses ($p = 0.031$).

216   Three of the hybrids were male and three were female, suggesting no inviability of the

217   heterogametic sex (Haldane 1922).

218   *Gene flow*

219   Tajima's D values showed no significant deviation from neutrality for any of the loci

220   examined (Table 1) and no evidence of recombination within loci was found.

221   Under the IM model, the rate of gene flow was significantly higher from Black-footed

222   Albatrosses into Laysan Albatrosses ($p=0.028$). The mean rate of gene flow ($2Nm$) was 0.09 gene

223   copies per generation from Black-footed Albatross into Laysan Albatross (95% highest

224   probability density (HPD) 0.024 - 0.23), whereas this rate was zero in the reverse direction (95%

225   HPD 0 - 0.10).

226   Asymmetrical gene flow from Laysan to Black-footed Albatross was constrained to zero

227   in the top four models, which, together, account for 55% of the variation in the weighted AIC

228   (Table 3). A commonly used standard for AIC model ranking is that models within two units of

229   the best model cannot be dismissed. The 5th ranked model does not support unidirectional gene

230   flow (Table 3) and is within two AIC units of the best model. However, this model differs from

231   the best model by one parameter (k= 3 vs. 4) and the maximized log-likelihood value of model #5

232   is similar to that of the best model. This suggests that the larger model #5 is not competitive with

233   the best model and instead is "close" only because it adds one parameter, even though the fit is

234   not improved (Burnham & Anderson 2002).

235   **Discussion**

236   Using diagnostic nuclear loci, we show that all six presumed hybrids between Laysan and

237   Black-footed Albatross were F1 hybrids. All six carried Laysan mtDNA haplotypes, indicating

238   that male Black-footed Albatrosses were their sires. This contradicts the hypothesis that a scarcity

239   of mates for females of the rare species results in hybrid pairings (Wirtz 1999) because all six

240   hybrids had Laysan Albatross mothers, instead of mothers of the much less abundant Black-

241   footed Albatross. Finally, we found limited, but significant gene flow from Black-footed

242   Albatrosses into Laysan Albatrosses, suggesting that past F1 hybrids have backcrossed to Laysan

243   Albatrosses. As we discuss below, this further supports our hypothesis that forced copulations are

244   asymmetrical.

245   *Effects of phenology and behavior on insemination biases*

246   Black-footed Albatrosses lay eggs 10 days to two weeks earlier than Laysan Albatrosses

247   (Fisher 1969; Rice & Kenyon 1962), so most female Black-footed Albatross have begun

248   incubating when Laysan females are fertile. This difference in breeding schedules undoubtedly

249   contributes strongly to the asymmetry in inseminations that generate hybrids because only paired

250   males have been reported to engage in rape attempts in these albatrosses (Fisher 1971; McKee &

251   Pyle 2002). Unmated males spend their time at breeding colonies courting females and have not

252   been observed attempting rapes (Fisher 1971). Other factors may also contribute to the observed

253   siring asymmetry. Notably, female Laysan Albatrosses are 5-10% smaller than male Black-footed

254   Albatrosses (Dunning 2007), and male Black-footed Albatrosses are much more aggressive in

255   conspecific rape attempts than are male Laysan Albatrosses (Fisher 1972). Finally, because Black-

256   footed Albatrosses constitute only 5% of the population of these two species breeding at Midway

257   Atoll, they have far more opportunity to engage in forced heterospecific copulations than do

258   Laysan Albatrosses. These differences suggest that male Black-footed Albatrosses are more likely

259   to sire hybrids through rapes, and all reported heterospecific rape attempts have involved male

260   Black-footed Albatrosses and female Laysan Albatrosses (McKee & Pyle 2002).

261   The asymmetry in gene exchange revealed by the isolation-migration model suggests a

262   long history of unidirectional gene flow from Black-footed Albatrosses into Laysan Albatrosses.

263   Although modern hybrids appear to have no success in attracting mates (Fisher 1972; McKee &

264   Pyle 2002; Rice & Kenyon 1962), two carefully observed hybrids (unsuccessfully) addressed all

265   courtship attempts at Laysan Albatrosses (Fisher 1972). Hybrids sired by male Black-footed

266   Albatrosses raping female Laysan Albatrosses would be raised by and sexually imprinted on

267   Laysan Albatrosses (Slagsvold et al. 2002; ten Cate & Vos 1999) and expected to prefer pairing

268   with Laysans.

269   *Alternative explanations for asymmetric gene flow*

270   We can think of two alternatives to our hypothesis of heterospecific rape as the cause of

271   the observed asymmetry in gene flow between Black-footed and Laysan Albatrosses. First, is the

272   possibility that F1 backcrosses into the Black-footed Albatross population have not been viable.

273   Definitively addressing this alternative would require breeding experiments, but Fisher's (1972)

274   observation that two closely observed hybrids courted only Laysan Albatrosses tends to refute

275   this alternative; although he closely observed just two hybrids, the number of Laysan Albatrosses

276   they attempted to court was large.

277   Second, if hybrids were intermediate in their breeding schedule relative to the parental

278   species, then hybrids may have had greater opportunity to mate with Laysan Albatrosses, which

279   return later to the breeding colonies than Black-footed Albatrosses. However, this explanation

280   untenably assumes that hybrids form life-long pair-bonds and breed the first year that they return

281   to their breeding islands. Instead, pre-breeding Laysan Albatrosses typically spend one or two

282   years choosing mates (Fisher 1972), making the two-week difference in laying dates unlikely to

283   bias the pattern of backcross matings toward Laysan Albatrosses.

284   It seems most likely to us that the gene flow revealed by the IM analysis reflects gene

285   exchange that took place as the species were diverging in coloration. This is supported by the fact

286   that courting birds focus their attention on the breasts of their dance partners, where the two

287   species differ most in color (Fisher 1972), and by the failure of field workers to find any hybrids

288   that were paired (Fisher 1972; McKee & Pyle 2002).

289   *Tests with other groups*

290   The contrast between species in which conspecific extra-pair copulations (EPC) are

291   forced, as opposed to species in which females accept or solicit such copulations, is critical to our

292   thesis that hybrids between broadly sympatric species will be more common in groups where

293   forced copulations are frequent. Although EPC are common in many passerines, they are mostly

294   unforced and apparently controlled by females to increase the genetic quality of offspring (Dunn

295   & Cockburn 1998; Dunn & Cockburn 1999; Spottiswoode & Møller 2004; Stutchbury & Neudorf

296   1998). Unfortunately, whether EPC are forced or accepted is rarely described in the literature

297   (although there are good descriptions of rape in albatrosses, waterfowl, bee-eaters, swallows and

298   the New Zealand Hihi (*Notiomystis cincta*) (Brekke et al. 2013; Emlen & Wrege 1986; Kabus

299   2002; Martin 1980). Obviously heterospecific rape should not be entertained as a source of

300   hybrids except in groups for which conspecific EPC are clearly forced.

301   Naturally occurring hybrids are abundant in waterfowl (Grant & Grant 1992; Randler

302   1998; Randler 2008) and male ducks are known to direct rape attempts at females of other species

303   (Muñez-Fuentes et al. 2007; Randler 2002; Seymour 1990). However, we could find no genetic

304   assessments of insemination biases in the generation of hybrids between naturally sympatric

305   waterfowl. An obvious test would be to compare insemination bias when one parental species is

306   characterized by forced copulations and the other is not. For example, hybrids between Northern

307   Shovelers (*Anas clypeata)* and both Mallards (*Anas platyrynchos)* and Northern Pintails (*Anas*

308   *acuta*) are reported from North America and Eurasia (McCarthy 2006). Because Northern

309   Shoveler males are territorial, and seldom attempt conspecific rapes, the heterospecific rape

310   hypothesis predicts F1 hybrids will have Mallard or Northern Pintail sires (McKinney & Evarts

311   1998). Siring bias can also be predicted for the abundant hybrids between Common Pochards and

312   Tufted Ducks (*Aythya ferrina* x *Aythya fuligula,* respectively) (Randler 2008). Because

313   conspecific rape is unreported in Common Pochards but frequent in Tufted Ducks (McKinney &

314   Evarts 1998), F1 hybrids should be sired by Tufted Ducks if they were produced through

315   heterospecific rape.

316   Heterospecific rape probably accounts for the frequent hybrids reported between Barn

317   Swallows (*Hirundo rustica*) and House Martins (*Delichon urbica*) in Europe and between Barn

318   Swallows and Cliff Swallows (*Petrochelidon pyrrhonota*) in North America. Barn Swallows are

319 characterized by many EPCs, but females choose whether or not to accept these EPCs, which are

320 almost never forced (Møller 1994). In contrast, aggressive conspecific rape is frequently observed

321 in both Cliff Swallows and House Martins at communal mud-gathering sites (Brown & Brown

322 1996; Møller 1994). That male Cliff Swallows and House Martins are characterized by

323 conspecific rape, presumably, renders female Barn Swallows vulnerable to heterospecific rape

324 when they gather mud at sites frequented by males of these two species. Correspondingly, when

325 identified as nestlings, hybrids between Barn Swallows and House Martins were always found in

326 Barn Swallow nests, had Barn Swallow siblings, and had two Barn Swallow parents (Kabus

327 2002); similarly, nestling hybrids between Barn Swallows and Cliff Swallows or Cave Swallows

328 (*P. fulva*) were found, in all cases but one, in Barn Swallow nests, attended by two Barn Swallow

329 parents (Martin 1980). Given that male Barn Swallows do not force copulations on females, but

330 that males of the three other parental species do force copulations on conspecific females, it

331 seems plausible that most of these were F1s, sired through heterospecific rapes.

332 *Broader implications*

333 Two comparative studies have addressed the role of EPC in the generation of avian

334 hybrids. In a survey of open nesting birds Randler (2006) found EPC to be uncorrelated with the

335 production of hybrids; however, this study failed to distinguish forced and unforced extra pair

336 copulations and failed to consider whether hybrids were rare or common. In another study

337 Randler (2005) assessed the roles of forced EPC and brood amalgamation on the production of

338 hybrid waterfowl, and found a significant effect only of brood amalgamation when both factors

339 were included in the model. However, both causal variables were treated as binary characters,

340 which masks their relative importance in species pairs where both factors occur but one generates

341 far more hybrids than the other. Over 800 Common Pochard x Tufted Duck hybrids were reported

342 from Europe (Randler 2008), yet these were treated as equivalent to a single report of a natural

343 hybrid between other species pairs. If most of these 800 hybrids were caused by either factor, then

344 the importance of that factor will be greatly underestimated by failing to account for hybrid

345 frequency.

346 In some cases evaluating siring asymmetries can generate strong tests of the hypothesis

347 that heterospecific brood parasitism results in ducks forming heterospecific pair bonds (Randler

348 2005). For example, Redheads (*Aythya americana*) are facultative brood parasites of

349 Canvasbacks (*Aythya valisineria*), whereas Canvasbacks do not parasitize Redhead nests

350 (Sorenson et al. 2010). Redhead ducklings raised by Canvasback females in broods of mostly

351 Canvasback ducklings should be sexually imprinted on Canvasbacks and, therefore, be more

352 willing to pair or at least mate with Canvasbacks. Indeed, males of both species cross-fostered

353 into broods predominated by the other species (without hens) preferentially courted heterospecific

354 females (Sorenson et al. 2010). An excess of adult males in both species predicts the siring bias:

355 Female Redheads imprinted on Canvasbacks (Sorenson et al. 2010), should be able to attract

356 unmated male Canvasbacks as mates. In contrast, male Redheads imprinted on Canvasbacks

357 would be unlikely to attract Canvasback mates because Canvasback females have many unmated

358 males to choose from. Thus Canvasback males should sire F1 hybrids between these species, if

359 hybrids are generated by brood parasitism and sexual imprinting. In contrast, Barrow's

360 (*Bucephala islandica*) and Common (*B. clangula*) Goldeneyes parasitize each other, so males of

361 both species are expected to be sires of hybrids. Although rare, hybrids between both the

362 *Bucephala* and the *Aythya* species pairs are regularly reported (McCarthy 2006), and none of the

363 parentals are characterized by conspecific rape.

364   Among *Anas* ducks gene sharing through hybridization apparently has strongly affected

365 effective population sizes. For Northern Pintails and Green-winged Teal (*Anas crecca*), census

366 population sizes are too small for certain shared alleles to have persisted for more than 2 and 2.6

367 million years. But these alleles, which are shared with Mallards, are estimated to have persisted

368 for 6.2 and 7.9 million years, respectively, suggesting a long history of horizontal gene exchange

369 with Mallards, which have a much larger effective population size (Kraus et al. 2012).

370 Heterospecific rapes may be responsible for generating F1 hybrids between these ducks and,

371 unlike the situation in albatrosses, F1 hybrid females in these short-lived ducks may form pair-

372 bonds and breed. Hybrid female ducks should be sexually imprinted on the species that raised

373 them (ten Cate & Vos 1999) and the strong male bias in the breeding sex ratios of north temperate

374 ducks should facilitate pairing and breeding by hybrid females.

375 **Conclusion**

376   Although unidirectional hybridization often predominates in nature, only a shortage of

377 mates for females previously had emerged from a long list of alternative hypotheses as a general

378 explanation for asymmetric hybridization (Wirtz 1999). Here we attempt to make the general

point that, if hybrids result from heterospecific rape, differences in behavior and life history of the parental species can be used to predict the direction of crosses. Predicting the mother and father species of F1 hybrids from different parental combinations has the potential to considerably refine our understanding of the importance of heterospecific forced copulation (and brood parasitism), in the generation of hybrids (McKee & Pyle 2002; Møller 1994; Randler 2005). Although heterospecific rape is unlikely to be adaptive, it has the potential to explain differences in the prevalence of F1 hybrids between broadly sympatric species pairs according to whether or not they are characterized by conspecific forced copulations.

Several authors have suggested that heterospecific rape may be an important source of avian hybrids (McKee & Pyle 2002; Møller 1994; Randler 2005), but Randler's (2005) comparative study of waterfowl found only weak support for this hypothesis. We believe that testing for siring asymmetries will provide a stronger assessment of this hypothesis in waterfowl, a group for which wild hybrids have been reported between many pairs of broadly sympatric species (Grant & Grant 1992). Forced copulations have been reported for various insects (Arnqvist 1989; Thornhill 1980; Thornhill & Sauer 1991), fish (Valero et al. 2008), lizards (Cooper 1985; Olsson 1995; Rodda 1992) and mammals (Harris et al. 2010), but whether or not forced copulations generate hybrids in these groups has not yet been addressed.

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Primer and locus information.

Diagnostic nuclear loci (dSNP) that provided at least a 90% probability of distinguishing between the parental species are starred. Tajima's D of NA indicates no variation occurring at that locus; BF = Black-footed Albatross, LA = Laysan Albatross.

Locus	dSNP	Freq. of dSNP in LA	Forward Primer (5'-3')	Reverse Primer (5'-3')	Length (bp)	%GC	% Identical Sites	D BF	D LA
cyt-b	−	--	TTTGCCCTATCTATCCT	GATCCTGTTTCGTGGAGGAAGGT	609	48	97.7	-1.51	NA
MHC*	1	1.0	CCGGCAGCAGTACGTGCACTTCGNACAGCGA	GATGGGCTGCTGCAGGCTGGTGTGCT	571	63.5	99.1	-0.22	-1.28
1FWD*	2	0.90	GTGCCACCCATGTAACACCT	TGTGCTTTGGATGAACAGTTG	429	55	99.5	NA	-0.26
1REV*	3,4,5	1.0	ACTGTGTCACCCCATGCTC	CTGAGTCATTTCCATTCCTGG	407	58.7	99.0	-0.87	NA
4FWD*	6	1.0	TGGGCCAGGTTGTTAGGTAG	TATTGGTGGAATGGGCTTGT	464	34.3	99.4	-1.16	NA
4REV*	7	1.0	GGCTGGGGGTTTGGAATTA	CTTTCTACAGAGAAATAAACAAAGACC	443	36.9	99.5	-0.24	NA
6FWD	−	--	AGGGGTCTCTCAAACAGCAA	CTGGCCCTTTAGATAATAGCC	418	35.8	99.8	1.53	NA
6REV	−	--	GAACTCGTAGTGAAGTATAACATCGTG	ATGCTGAGGGTGCCATCTTA	458	39.5	98.9	0.47	-1.76
10FWD	−	--	GGCAAAGGCTAAAGGCAAAG	TCAGAATTATTATAGCTTCAGGTGAG	548	43.4	99.6	NA	0.06
10REV	−	--	GGTGGTAGAACAGAAAGTCT	TTACCACCTTCCACCACACA	495	36.2	99.6	0.87	NA

Probabilities of F1 and backcross hybrids carrying the observed hybrid genotype.

All six hybrids carried genotype (LA)(A/G)(A/C)(CAG/TGC)(C/T)(A/C); frequencies of the diagonistic SNPs are given in Table 1. The fixed mitochondrial differences render some parental combinations impossible. The shared polymorphism at dSNP 2 makes it possible that the observed hybrid genotype derives from backcrossing, albeit at very low probabilities (<0.05). Abbreviations: LA, Laysan Albatross; BF, Black-footed Albatross; f, female; m, male.

F1 genotype		
F1 combinations	**mtDNA**	**Probability**
LA f x BF m	LA (1.0)	0.90
LA m x BF f	BF (1.0)	0.00[1]

Backcross genotype		
Backcross combinations	**mtDNA**	**Probability**
F1 f x BF m	LA (1.0)	0.028
F1 f x LA m	LA (1.0)	0.034
F1 m x LA f	LA (1.0)	0.034
F1 m x BF f	BF (1.0)	0.00[1]

[1]Probability is 0 due to the absence of BF mitochondrial haplotype in the observed hybrid genotype.

AIC ranking of models using IMa2 based on ~ 300,000 sampled genealogies.

Model subscripts of population size (q) and migration (m) parameters identify populations used in the analysis; 0, 1, and 2 represent the estimated population sizes for Black-footed Albatrosses, Laysan Albatrosses, and the ancestral population, respectively. In each model brackets denote fixed parameters; other parameters were estimated.

Model	Log(P)	k	AIC	Delta (AIC)	w	q0	q1	q2	M0>1	M1>0
Pop. size BF = LA; Mig. from LA to BF = 0	2.48	3	1.04	0.00	0.16	0.2388	[0.2388]	0.0085	[0]	0.2236
Mig. from LA to BF = 0	3.39	4	1.22	0.18	0.15	0.2244	0.07	0.00087	[0]	2.5594
Anc. pop. size = BF; Mig. from LA to BF = 0	2.16	3	1.68	0.64	0.12	0.3008	0.1094	[0.3008]	[0]	1.8228
Anc pop. size = LA; Mig. from LA to BF = 0	2.16	3	1.69	0.65	0.12	0.3043	0.1101	[0.1101]	[0]	1.7566
Mig. from BF to LA = mig. from LA to BF	2.99	4	2.03	0.99	0.10	0.2465	0.1291	0.0026	0.1998	[0.1998]
Pop. size LA = BF	2.48	4	3.04	2.00	0.06	0.2388	[0.2388]	0.0085	0	0.2236
Mig. from LA to BF = 0; Pop. size LA & BF = anc	0.30	2	3.40	2.36	0.05	0.1761	[0.1761]	[0.1761]	[0]	1.4231
Anc pop. Size = BF	2.16	4	3.68	2.64	0.04	0.3008	0.1094	[0.3008]	0	1.8228
LA pop. size = anc	2.16	4	3.69	2.65	0.04	0.3043	0.1101	[0.1101]	0	1.7566
BF pop. size = LA; Mig. from LA to BF = BF to LA	0.93	3	4.15	3.11	0.03	0.2388	[0.2388]	0.0085	0.1034	[0.1034]
Full model	2.60	5	4.80	3.76	0.02	0.3394	0.1015	0.0171	0	1.6769
BF pop. size = LA & anc	0.30	3	5.40	4.36	0.02	0.1761	[0.1761]	[0.1761]	0	1.4231
BF pop. size = LA; Both mig. = 0	-0.83	2	5.66	4.62	0.02	0.2595	[0.2595]	0.5181	[0]	[0]
Both mig. = 0	-0.19	3	6.38	5.34	0.0	0.250	0.2732	0.5181	[0]	[0]

Model										
BF pop. size = LA & anc; Mig. From LA to BF = BF to LA	-1.21	2	6.42	5.38	0.01	0.2907	[0.2907]	[0.2907]	0.1121	[0.1121]
LA pop. size = anc; Mig. from LA to BF = BF to LA	-0.69	3	7.38	6.34	0.01	0.2053	0.1214	[0.1214]	0.6553	[0.6553]
BF pop. size = anc; Both mig. = 0	-1.78	2	7.55	6.51	0.01	0.4489	0.3151	[0.4489]	[0]	[0]
BF pop. size = LA; Mig. from BF to LA = 0	-0.83	3	7.66	6.62	0.01	0.2595	[0.2595]	0.5181	0	[0]
BF pop. size = anc; Mig. from LA to BF = BF to LA	-0.85	3	7.71	6.67	0.01	0.2568	0.1392	[0.2568]	0.2261	[0.2261]
LA pop. size = anc; Mig. from BF to LA =0	-0.86	3	7.73	6.69	0.01	0.4036	0.1815	[0.1815]	0.1434	[0]
BF pop. size = LA & anc; Mig. from BF to LA = 0	-2.06	2	8.13	7.09	0.00	0.2717	[0.2717]	[0.2717]	0.4307	[0]
Mig. from BF to LA = 0	-0.19	4	8.38	7.34	0.00	0.2509	0.2732	0.5181	0	[0]
BF pop. size = anc; Mig. from BF to LA = 0	-1.60	3	9.21	8.17	0.00	0.2659	0.0985	[0.2659]	1.0792	[0]
LA pop. size = anc; Both mig. = 0	-3.53	2	11.05	10.01	0.00	0.2509	0.2846	[0.2846]	[0]	[0]
BF pop. size = LA & anc.; Both mig. = 0	-4.97	1	11.94	10.90	0.00	0.2644	[0.2644]	[0.2644]	[0]	[0]

Figure 1

Hybrid scores based on the five diagnostic SNPS (Table 1).

Pure Black-footed Albatrosses are scored as 0 and pure Laysan Albatrosses are scored as 1. The six putative hybrids all scored as 0.51, rather than 0.50, because Laysan Albatrosses share a rare allele with Black-footed Albatrosses at one of the diagnostic loci.
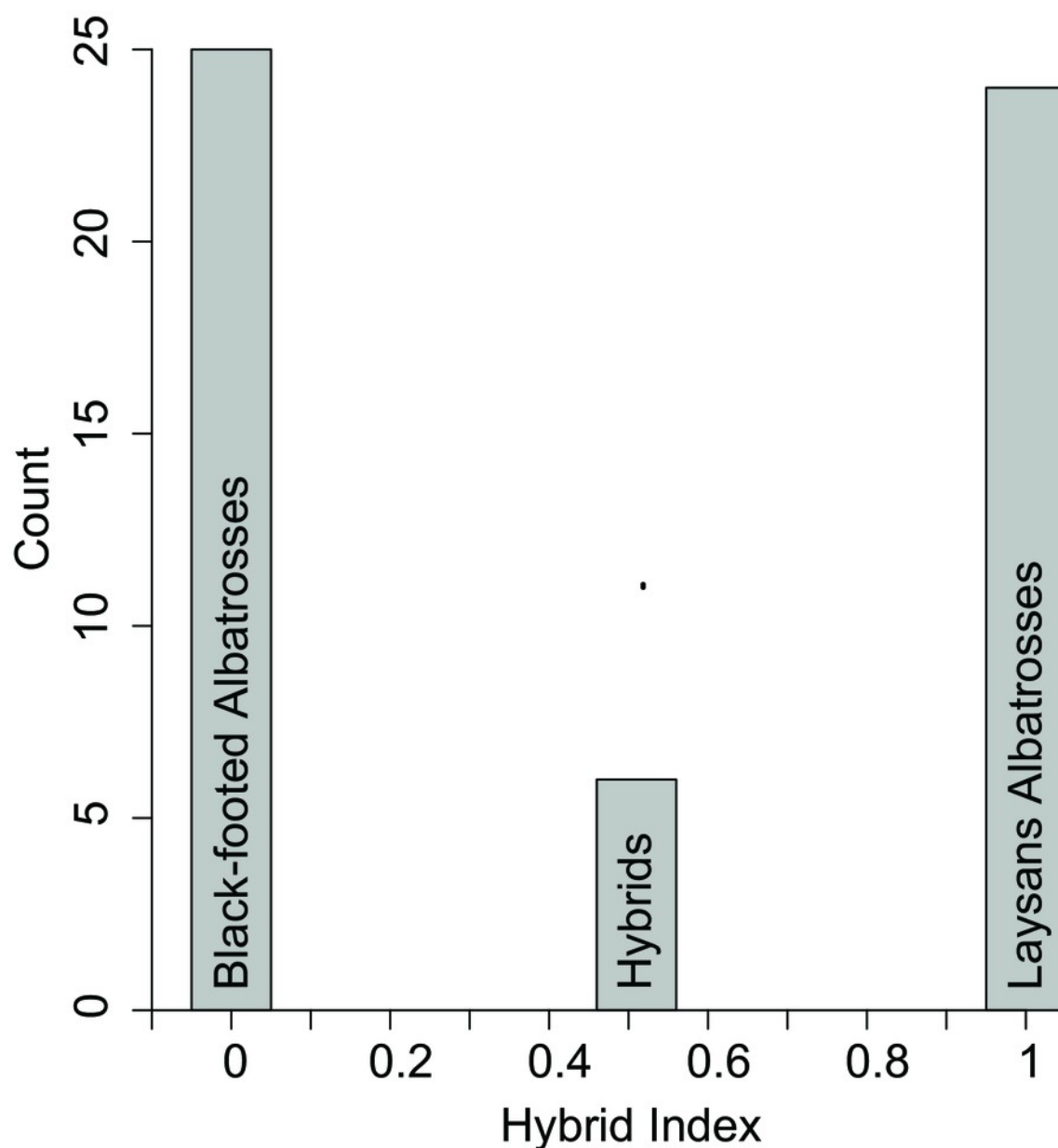
Figure 2

A recently documented hybrid that is mated to a Laysan Albatross and has raised chicks.

H. Ronco of the USFWS provided the photo.