

Extra-pair paternity in waved albatrosses: genetic relationships among females, social mates and genetic sires

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(Accepted: 20 May 2010)

Summary

Interactions among close relatives are expected to be common in colonially breeding species, species with limited geographic distributions such as island endemics, or those with limited natal or breeding dispersal. The waved albatross, *Phoebastria irrorata*, a colonially nesting, endemic seabird in Galápagos, Ecuador, presents an opportunity to closely examine relationships between genetic similarity of parents and extra-pair paternity. This species' mating system is characterized by high year-to-year social mate and nest site fidelity as well as an unexpectedly high level of extra-pair paternity. The probability of hatching was lower for social pairs with high genetic similarity, suggesting an apparent cost of inbreeding. Despite this apparent cost, analyses of multilocus minisatellite band-sharing coefficients revealed that genetic similarity was somewhat negatively associated with EPF probability, inconsistent with the pattern predicted by the Genetic Similarity Hypothesis (GSH) that social pairs with extra-pair offspring would be more similar than those with within-pair offspring. We found that a model with no effect of the type of dyad the female was in (female–social mate compared to female–genetic sire) on genetic similarity was as heavily weighted as one incorporating an effect, also inconsistent with the GSH. Evidence from our analyses suggested that cuckolded males were more genetically similar to randomly drawn males than to the genetic sire of their extra-pair offspring, a finding in contrast to the main prediction of our novel EPF tolerance hypothesis that males might tolerate extra-pair offspring if the actual sire is closely related. We discuss these findings in light of information about dispersal and we present some alternative explanations for extra-pair paternity in the waved albatross.

Keywords: extra-pair paternity, DNA fingerprinting, philopatry, inbreeding avoidance, genetic similarity, waved albatross, EPF tolerance hypothesis, Akaike's Information Criterion.

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Introduction

Molecular methods to assess parentage have revolutionized our understanding of mating systems: in birds, extra-pair paternity (EPP) is now known to be widespread with only about 14% of passerine species characterized as ‘truly monogamous’ (Griffith et al., 2002). Despite how relatively common EPP is among birds, though, no omnibus explanation for EPP exists nor is it well-understood why some species have higher degrees of EPP than others. Explanations for EPP range from, for example, active female choice of extra-pair males for indirect genetic benefits such as an extra-pair male’s ‘good genes’ (see Akçay & Roughgarden, 2007, for a review), to direct material benefits such as additional provisioning by extra-pair males (e.g., Townsend et al., 2010).

A subset of genetic explanations for EPP focus on hypotheses that relate the incidence of extra-pair fertilizations (EPFs) to the degree of genetic similarity between social mates and to the benefits that dissimilarity between extra-pair mates might confer on extra-pair offspring (e.g., Blomqvist et al., 2002; Hansson et al., 2004; Eimes et al., 2005; Kleven et al., 2005; Schmoll et al., 2005; Augustin et al., 2007). These genetic similarity hypotheses posit extra-pair behaviour as a mechanism to avoid the costs of inbreeding: females pursue extra-pair copulations (EPCs) with relatively dissimilar males to avoid negative fitness effects such as lower offspring survival or reduced hatching success resulting from mating with a close relative (Brooker et al., 1990). Extra-pair matings can conceivably enhance offspring fitness directly by increasing offspring heterozygosity and lessening the effects of homozygosity of some deleterious alleles (Brown, 1997), or by improving disease resistance related to variability of the major histocompatibility complex (Brown, 1999; Penn & Potts, 1999). Regardless of the mechanism, these genetic similarity hypotheses propose a positive relationship between genetic similarity and EPF occurrence.

In the absence of a positive relationship between genetic similarity of social mates and EPF occurrence, our novel extra-pair tolerance hypothesis (ETH) is an alternative explanation for the persistence of extra-pair paternity. Faced with uncertain paternity, males of taxa with long lifespans and essential male care might (a) abandon reproductive attempts as Mauck et al. (1999) suggest, or (b) tolerate EPFs if the costs of cuckoldry are sufficiently offset by the indirect benefits of raising an extra-pair chick when the actual sire

is closely related to the caretaking male. Under the ETH, genetic similarity measures between cuckolded males and the genetic sires of their extra-pair offspring (EPO) are greater than similarity measures between these cuckolded males compared with randomly drawn breeding males. Although, to our knowledge, no studies exist that explore this tolerance hypothesis among birds, similar kin selection hypotheses have been advanced to elucidate the tolerance of parasitic eggs (e.g., McRae & Burke, 1996), the adoption of neighbouring chicks (e.g., Bukacinski et al., 2000), and potential inclusive fitness benefits among males in lekking species (e.g., McDonald & Potts, 1997; Loiselle et al., 2007).

With the exception of a few pairs, the world's population of the waved albatross (*Phoebastria irrorata*) breeds on Española, the southeasternmost island in the Galápagos Archipelago, Ecuador. Despite this extreme philopatry and expected inbreeding because of the population's relative isolation, our earlier assessment of the degree of genetic substructuring on Española indicated little genetic differentiation among three colonies (maximum distance between colonies approx. 10 km; Huyvaert & Parker, 2006), which suggests the presence of gene flow within the population. Reports of movements of banded birds from year to year also show a degree of dispersal among breeders (K.P. Huyvaert, unpubl. data). At the same time, waved albatrosses are extremely social: they breed in large, fairly dense colonies and spend long periods of their limited time on land interacting with members of the same and opposite sex (pers. obs.). Interactions range from apparent greeting behaviour to territorial defence and extra-pair copulations resulting in extra-pair fertilizations (Huyvaert, 2004; Huyvaert et al., 2006). While genetic monogamy is expected for species with biparental care and high adult survival (Mauck et al., 1999) like the waved albatross, we have found that extra-pair parentage accounts for the paternity of 14–25% of chicks examined (Huyvaert et al., 2000, 2006).

Using multilocus minisatellite DNA fingerprinting data, we examined the genetic relationships among females, their social mates, and the genetic sires of their offspring to explore whether and to what extent extra-pair paternity in waved albatrosses is associated with genetic similarity. We first examine the assumption that there is a cost of inbreeding which is mediated through lower hatching success for genetically similar social mates. We also use our minisatellite band-sharing data to assess predictions from the genetic similarity and EPF tolerance hypotheses (GSH and ETH, respectively) as

possible explanations for extra-pair paternity in waved albatrosses. Under the GSH, genetically similar pairs of social mates are more likely to have EPFs than social pairs that are genetically dissimilar to avoid the cost of inbreeding. We also expect that, if the GSH applies to waved albatrosses, females caring for EPO will be more genetically similar to their social mates than to the extra-pair sires of their chicks. Under the novel ETH, genetic similarity values between cuckolded males and the genetic sires of the chicks they raise will be higher than those values for cuckolded males and breeding males drawn at random as the apparent cost to a cuckolded male of raising an EPO is tolerated because the genetic sire of the cuckolded male is more closely related (i.e., genetically similar).

Methods

Study population and field methods

We studied waved albatross extra-pair behaviour and its genetic consequences during the annual breeding seasons of 2000, 2001 and 2002. The study took place on an approx. 3500 m² study area at Punta Cevallos on the southeastern end of Española at the tip of a larger, dense colony situated in open, fairly flat, coastal habitat. Adult albatrosses ($N = 349$) were captured by hand, banded, and a small blood sample (100 μ l) was taken via brachial venipuncture. Blood samples were placed in lysis buffer (Longmire et al., 1988) and stored at ambient temperature. Copulations were documented at the study site during 36–40 days of observation at the beginning of each of the three breeding seasons. Every nesting attempt was followed until hatching of the single-egg clutch, and hatchlings were sampled 2–6 days post-hatching for parentage exclusion analyses that are reported in detail elsewhere (Huyvaert et al., 2006). In 18 cases we sampled blood or tissue from unhatched chicks when the egg had been opened by Hood mockingbirds *Nesomimus macdonaldi* or had been abandoned for more than 10 days.

Calculating genetic similarity

Genetic similarity between breeding individuals was examined using data from a total of 154 families sampled during the three breeding seasons. Multilocus minisatellite DNA fingerprinting (Jeffreys et al., 1985a,b) was used to

determine parentage in exclusion gels; we then used the same protocol to assign the genetic father from among the mother's known copulation partners and nearest neighbours on separate assignment gels (Rabenold et al., 1991). We used multilocus minisatellite data for this study given our prior experience using these markers in the same system (Huyvaert et al., 2000), the high level of genetic variability we could capture in a single efficient process, the unavailability of a sufficient number of microsatellites at the time of analysis, and the markers' high repeatability across gels and among scorers. Because our laboratory methods are detailed extensively elsewhere (Huyvaert et al., 2006), we describe them only briefly here. For all fingerprints, we digested 4 μg whole genomic DNA with an excess of the restriction endonuclease *HaeIII*. Digested fragments were separated on agarose gels using electrophoresis. Fragments were then transferred to nylon membranes via Southern blotting and were hybridized to Jeffreys' probe 33.15 (Jeffreys et al., 1985a).

In order to examine the cost of inbreeding and to examine predictions of both research hypotheses explored here, we used fingerprint band-sharing as a measure of genetic similarity. All band-sharing coefficients were calculated using the formula:

$$2N_{AB}/(2N_{AB} + N_A + N_B),$$

where N_{AB} is the number of bands shared by the members of the dyad of interest, N_A indicates the number of bands unique to individual A, and N_B the number of bands unique to B (Wetton et al., 1987; Lynch, 1990).

For our analyses, we subsetted the total number of families examined ($N = 154$) to exclude those families with incomplete genetic data or apparent adoption ($N = 4$) and to account for duplications of social pairs ($N = 32$). Because year-to-year mate fidelity is high (K.P. Huyvaert, unpubl. data), 30 pairs were represented more than once in the total sample. To avoid overrepresentation of these pairs in our analyses, we randomly sampled the set of 150 families (full sample excluding incomplete genetic data or possible adoptions) with proportionate allocation for EPFs and eggs that did not hatch (i.e., approx. 17% of the population of chicks were EPFs so approx. 17% of the cases selected randomly from among the duplicated families were EPFs). This sample of 118 mother–social father pairs was used to examine the first part of the genetic similarity hypothesis. To evaluate the cost of inbreeding assumption, we omitted all remaining cases of EPF ($N = 25$) from the subset of 118 families because the cost of interest applies only to social mates

with within-pair offspring (WPO; i.e., in the face of a cost of inbreeding, females might pursue EPCs with genetically less similar males). The sample size for the cost of inbreeding assumption analysis was 94 social mother–social father dyads.

We were able to assign paternity in 18 of the total 26 instances of EPO that we recorded during the three seasons (Huyvaert et al., 2006). We were not able to assign paternity in 8 cases of EPF because none of the known copulation partners or nearest neighbours provided a match; it could be that we did not observe the copulation responsible for paternity in this subset of cases. To examine the second prediction of the GSH, we calculated band-sharing values for the genetic fathers and mothers of the 18 EPO for which we had assigned paternity. We also scored dyads including cuckolded social males and the genetic sire of the EPO chick ($N = 18$) and dyads of cuckolded social males and a randomly drawn breeding male ($N = 18$) to examine the EPF tolerance hypothesis.

Model development and data analysis

Logistic regression was used to assess the associations between the binary response variable, hatch (response was ‘yes’ or ‘no’) and parental genetic similarity (SOCBS) to examine the cost of inbreeding assumption. We constructed an a priori set of 9 models (including an intercept-only model) incorporating the band-sharing values of social pairs (SOCBS) and additive, single, or interactive effects of several covariates that might explain additional variation in hatching success. We included two temporal covariates in the analysis given the potential links between timing of breeding and breeding success. The year the egg was laid (YEAR) was included as a categorical variable to capture inter-annual variation. Because laying date can vary by parental experience or age, and eggs laid later in the season may be less likely to succeed (Sæther, 1990), we included the Julian date the egg was laid (LAYDATE) as a continuous variable in our model set.

Similarly, we used logistic regression to assess the associations between the binary response variable, extra-pair fertilization (response of ‘EPF’ was coded as 1 and response ‘WPO’ was coded as 0), and genetic similarity (SOCBS) to examine relationships between EPF probability and genetic similarity between mates in social pairs to analyse the first prediction of the genetic similarity hypothesis. In this model set, whether or not the egg hatched

(HATCH) was included as a categorical covariate in some models as were the temporal covariates, YEAR and LAYDATE. Logistic regression models in both model sets were analysed using ProcLOGISTIC in SAS 9.2 software (SAS Institute, 2008).

For the second prediction of the GSH, that females caring for EPO will be more genetically similar to their social mates than to the extra-pair sires of their chicks, we used a paired design and an information-theoretic approach (see below) to compare a set of two models. The null model or model of no effect was identified as

$$Y = \beta_0,$$

where Y is band-sharing and β_0 the intercept (overall mean band-sharing). The alternative model was then set as

$$Y = \beta_0 + \beta_1 X,$$

where X indicates the dyad type (social female with cuckolded male or social female with genetic sire of her EPO) and β_1 the slope of the effect of dyad type. Our approach involved computing the residual sum of squares (RSS) for each model and computing the AICc following the equation:

$$\text{AICc} = N \times \ln(\text{RSS}/N) + 2K + (2K(K + 1)/N - K - 1),$$

where N is the sample size and K the number of parameters ($K = 1$ for the null model and $K = 2$ for the alternative model; Burnham & Anderson, 2002; Anderson, 2008). Model selection and multi-model inference, detailed below, proceeded for this model set as for the logistic regression model sets.

A similar paired design and model set was used to assess the ETH that genetic similarity measures for cuckolded male–genetic sire dyads are greater than similarity measures between each of these cuckolded males and a randomly drawn breeding male. In this case, β_0 is the intercept in the model of no effect while β_1 is the slope of the effect of dyad type, X , where dyad type was now either cuckolded social male with genetic sire of the EPO or cuckolded male with a randomly drawn breeding male. After calculating the RSS and the AICc for each of these two models, we proceeded with model selection and multi-model inference, as described below.

Model selection and multi-model inference

An information-theoretic approach (Burnham & Anderson, 2002; Anderson, 2008; Garamszegi et al., 2009) was used for model selection and inference. We used Akaike's Information Criterion corrected for small sample size (AICc) to rank the models in each set (Burnham & Anderson, 2002). The model with the lowest AICc value was assumed to be the best model in the set given the data. We also calculated AICc differences (Δ_i ; difference between each model, i , and the top-ranking model) and Akaike weights (w_i ; estimates of the probability that i is the best model given the data and the model set). To account for model selection uncertainty, we model averaged across all models in a given set (Burnham & Anderson, 2002). Using model averaged values, we present unconditional parameter estimates ($\hat{\beta}$), associated standard errors, and 95% confidence intervals (Burnham & Anderson, 2002) for the effects of genetic similarity (SOCBS) in the two logistic regression analyses. We provided estimates of the effects of other important covariates in the logistic regression analyses when competing models with non-trivial Akaike weights included these covariates. We present model averaged estimates of β_1 and evidence ratios (model weight of the first ranked model relative to that of the i th model) for the two analyses with the paired design. Lastly, for the logistic regression models, we also report maximum re-scaled R^2 values (SAS Institute, 2008) as a description of the proportion of variance explained by the models.

Results

Cost of genetic similarity

In our logistic regression model set, genetic similarity of social mates was included in all of the top models and these models accounted for all of the cumulative Akaike weight in the model set (cumulative Akaike weight = 1.0; Table 1). Genetic similarity of parents was negatively related to hatching success: the model-averaged estimate of the effect of genetic similarity suggests that eggs of parents with high genetic similarity were less likely to hatch than those from parents with lower genetic similarity ($\hat{\beta} = -13.79$, unconditional SE = 4.42, 95% CI = $-4.95, -22.63$; Figure 1). Models including an effect of genetic similarity explained between 34 and 43% of the variation in the data (Table 1).

Table 1. Candidate model set and ranking of models examining the relative importance of social pair genetic similarity (measured as minisatellite band-sharing; SOCBS) on the probability of hatching in the waved albatross.

Model	R^2	$\log(L)$	K	AICc	Δ_i	w_i
SOCBS + YEAR	0.43	-22.19	4	52.82	0.00	0.53
SOCBS + YEAR + LAYDATE	0.43	-22.11	5	54.89	2.07	0.19
SOCBS	0.32	-25.44	2	55.01	2.19	0.18
SOCBS + LAYDATE	0.34	-24.94	3	56.15	3.33	0.10
YEAR	0.20	-28.93	3	64.12	11.30	0.00
YEAR + LAYDATE	0.21	-28.55	4	65.54	12.72	0.00
YEAR + LAYDATE + YEAR \times LAYDATE	0.25	-27.54	6	68.05	15.23	0.00
INTERCEPT-ONLY	0.00	-33.93	1	69.90	17.08	0.00

The model set also includes models incorporating biologically relevant covariates singly or in combination to account for variation among years (YEAR) and Julian date the egg was laid (LAYDATE). R^2 values are maximum rescaled R^2 values. The maximized log-likelihood ($\log(L)$), the number of parameters (K) in each model, and the small sample size-corrected AICc values (AICc) are shown. Models are ranked by their AICc differences (Δ_i) relative to the best model in the set and Akaike weights (w_i) quantify the probability that a particular model is the best model in the set given the data and the model set.

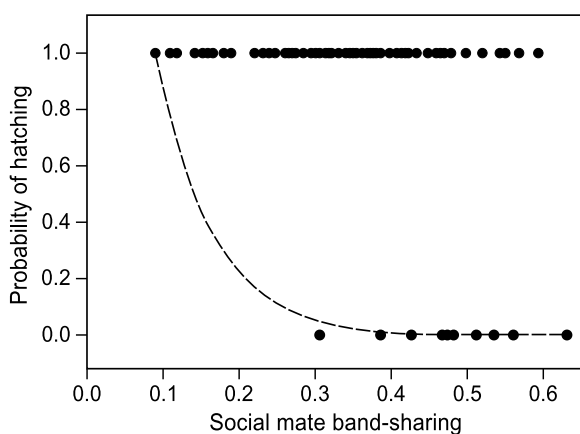


Figure 1. Relationship between hatching probability and social pair genetic similarity for waved albatrosses. Points indicate multilocus minisatellite band-sharing values for dyads of females and their social mates for families with within-pair offspring and the dashed line is the logistic regression line from models examining the cost of genetic similarity assumption. The slope and intercept parameters of the line were model-averaged across all models that included genetic similarity (see also Table 1). Genetic similarity of pairs of social mates is negatively related to hatching probability indicating a cost of inbreeding in this species.

Genetic similarity hypothesis

We first examined the relationship between genetic similarity of pairs and EPF probability using logistic regression. Genetic similarity of social pairs was included in 3 of the 4 top-ranked models with a cumulative Akaike weight of 0.86. We found that genetic similarity of social pairs was somewhat negatively associated with EPF probability ($\hat{\beta} = -4.97$, unconditional SE = 5.27, 95% CI = $-15.30, 5.36$; Figure 2). While this finding is inconsistent with the prediction of the GSH that mates with EPOs would have higher genetic similarities than social parents with within-pair offspring, the 95% CI included zero, suggesting, at most, a weak effect. Models including genetic similarity of social mates explained between 8 and 15% of the variation in the data (Table 2).

Two other covariates were represented in the top two models, the Julian date the egg was laid and whether or not the egg hatched. EPF probability was influenced by the Julian date the egg was laid ($\hat{\beta} = -0.06$, unconditional

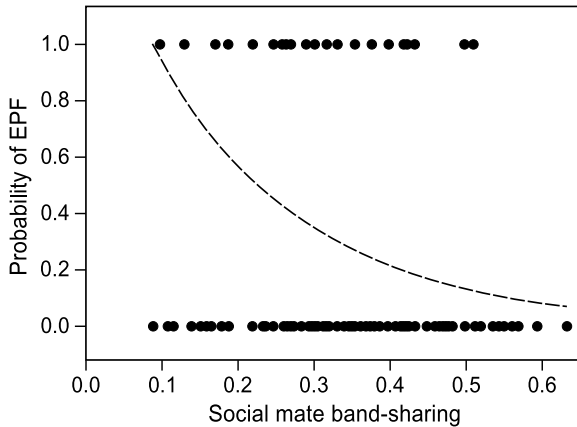


Figure 2. Relationship between probability of an extra-pair fertilization (EPF) and social pair genetic similarity for waved albatrosses. Points indicate multilocus minisatellite band-sharing values for dyads of females and their social mates for families with within-pair offspring (probability of EPF = 0) and for families with an extra-pair offspring (probability of EPF = 1). The dashed line is the logistic regression line from models exploring the Genetic Similarity Hypothesis prediction that pairs with extra-pair offspring would have higher genetic similarities than social parents with within-pair offspring. The slope and intercept parameters of the line were model-averaged across all models including genetic similarity in them (see also Table 2).

Table 2. Candidate model set and ranking of models examining the relative importance of social pair genetic similarity (measured as minisatellite band-sharing; SOCBS) on the probability of extra-pair paternity in the waved albatross.

Model	R^2	$\log(L)$	K	AICc	Δ_i	w_i
SOCBS + LAYDATE	0.15	-54.80	3	115.80	0.00	0.51
SOCBS + LAYDATE + HATCH	0.15	-54.77	4	117.89	2.09	0.18
SOCBS	0.08	-57.63	2	119.36	3.56	0.09
LAYDATE	0.08	-57.68	2	119.45	3.65	0.08
HATCH + LAYDATE	0.09	-57.60	3	121.40	5.60	0.03
SOCBS + HATCH	0.09	-57.61	3	121.43	5.63	0.03
SOCBS + YEAR	0.10	-56.88	4	122.10	6.30	0.02
YEAR + LAYDATE	0.10	-57.06	4	122.46	6.66	0.02
HATCH + LAYDATE + HATCH \times LAYDATE	0.09	-57.48	4	123.31	7.51	0.01
INTERCEPT-ONLY	0.00	-60.94	1	123.91	8.11	0.01
SOCBS + YEAR + HATCH	0.10	-56.86	5	124.25	8.45	0.01
HATCH	0.00	-60.78	2	125.66	9.86	0.00
YEAR	0.02	-63.05	3	126.30	10.50	0.00
HATCH + YEAR	0.03	-59.92	4	128.19	12.39	0.00

The model set also includes models incorporating biologically relevant covariates singly or in combination to account for variation among years (YEAR), Julian date the egg was laid (LAYDATE), and whether or not the offspring came from a hatched egg (HATCH). R^2 values are maximum rescaled R^2 values. The maximized log-likelihood ($\log(L)$), the number of parameters (K) in each model, and the small sample size-corrected AICc values (AICc) are shown. Models are ranked by their AICc differences (Δ_i) relative to the best model in the set and Akaike weights (w_i) quantify the probability that a particular model is the best model in the set given the data and the model set.

SE = 0.03, 95% CI = -0.01, -0.12; Figure 3) indicating that eggs laid earlier in the season were more likely to be EPFs ($\text{mean}_{\text{laydate epf}} = 122$, SE = 2, 95% CI = 118, 126; $\text{mean}_{\text{laydate wpo}} = 129$, SE = 1, 95% CI = 127, 131). Models including the laydate covariate carried a cumulative weight of 0.83. Whether or not the egg hatched was included in the second-ranked model in this set and had a cumulative Akaike weight of 0.26 (Table 2).

With respect to the second prediction of the GSH, that female-social mate dyads have higher genetic similarity than female-genetic sire dyads for the subset of families with EPFs and known paternity, the model of no effect was only slightly less likely than the model incorporating an effect of band-sharing dyad type: the evidence ratio of the two models indicated that model H_A was 1.14 times as likely as H_0 (Table 3). The 95% CI's of the model av-

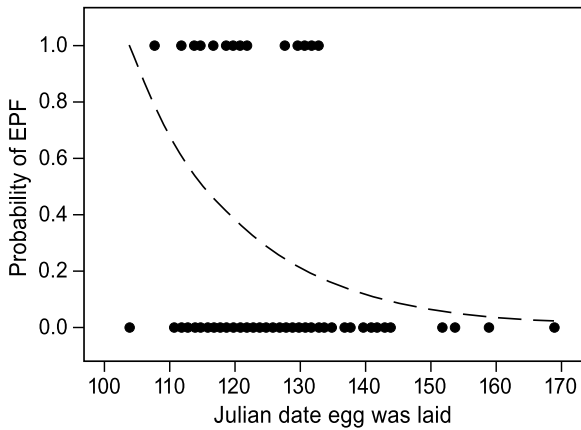


Figure 3. Relationship between probability of an extra-pair fertilization (EPF) and Julian date the egg was laid for waved albatrosses. Points indicate Julian laying date for eggs that were determined to be within-pair (probability of EPF = 0) and for eggs determined to be extra-pair (probability of EPF = 1). The dashed line is the logistic regression line from models including LAYDATE as a factors influencing EPF probability. The slope and intercept parameters of the line were model-averaged across all models including LAYDATE (see also Table 2).

Table 3. Model set and model rankings for two hypotheses relating band-sharing values to dyad type for waved albatross families with extra-pair offspring (EPO).

Model	RSS	K	L	AICc	Δ_i	w_i	ER
$H_0 (Y = \beta_0)^a$	0.34	1	0.87	-69.30	0.27	0.47	
$H_A (Y = \beta_0 + \beta_1 X)^b$	0.29	2	1.0	-69.57	0.00	0.53	1.14

A comparison of these models was used to assess the prediction of the GSH that females with EPO will be more genetically similar to their social mates than to the extra-pair sires of their EPO. Dyad types were females with their cuckolded social mate or females with the genetic sire of her EPO ($N = 18$ dyads of each type). The residual sum of squares (RSS), the number of parameters (K) in each model, the model likelihoods (L), and the small sample size-corrected AICc values (AICc) are shown. Models are ranked by their AICc differences (Δ_i) relative to the best model in the set and Akaike weights (w_i) quantify the probability that a particular model is the best model in the set given the data and the model set. The evidence ratio (ER) is a ratio of the weights of the two models of interest. In this model set, the model with an effect, H_A , is approx. 1.1 times more likely than the null model, H_0 .

^aModel of no effect; Y is band-sharing; β_0 is the overall mean of band-sharing (intercept).

^bModel with an effect; X is band-sharing dyad type (female-cuckolded social mate vs. female-genetic sire of EPO); β_1 is the slope of the effect of dyad type.

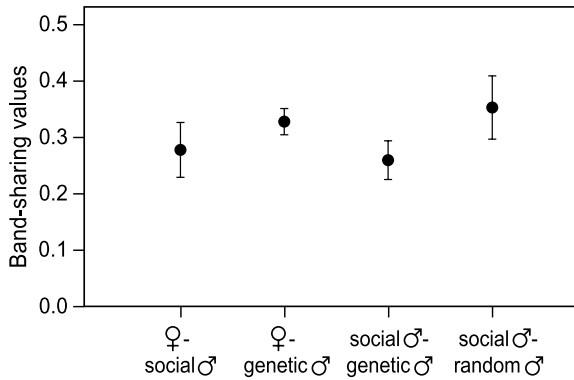


Figure 4. Mean band-sharing values (filled circles) and 95% confidence intervals (whiskers) for sets of dyads examined with respect to the Genetic Similarity Hypothesis (GSH; left-hand side) and the EPF Tolerance Hypothesis (ETH; right-hand side) in waved albatrosses. The two points on the left-hand side display the means and 95% CI's for females (♀) with their social mates (social ♂) compared to females with the genetic sire (genetic ♂) for the subset of families with EPF and known paternity ($N = 18$). Similarly, the points and error bars on the right hand-side display the means and 95% CI's for cuckolded males (social ♂) with the genetic sire (genetic ♂) of the extra-pair offspring in their nest compared to dyads of cuckolded males (social ♂) with a randomly selected breeding male (random ♂).

eraged effect size of dyad type ($\hat{\beta} = -0.03$, unconditional SE = 0.05, 95% CI = $-0.13, 0.08$) substantially overlapped zero also providing little additional evidence of an effect of dyad type. Similarly, 95% CI's around the estimates of mean band-sharing for female–social mate dyads (mean_{soc} = 0.28, 95% CI = 0.24, 0.32) overlapped appreciably with the mean for female–genetic sire dyads (mean_{gen} = 0.33, 95% CI = 0.27, 0.39; Figure 4) for the subset of families with EPFs and known paternity.

EPF tolerance hypothesis

Regarding the ETH suggesting that cuckolded males might tolerate an EPO in their nest if the actual sire is a close relative, the model of no effect was less likely than the model incorporating an effect of band-sharing dyad type suggesting that an effect of dyad type exists. The evidence ratio of the two models indicated that model H_A was 2.94 times more likely than H_0 (Table 4). However, the sign of the model averaged effect size (the slope) was positive ($\hat{\beta} = 0.07$, unconditional SE = 0.04, 95% CI = $-0.02, 0.15$), suggesting that cuckolded males are more genetically similar to randomly drawn

Table 4. Model set and model rankings for two hypotheses relating band-sharing values to dyad type for breeding waved albatross males.

Model	RSS	K	L	AICc	Δ_i	w_i	ER
$H_0 (Y = \beta_0)^a$	0.68	1	0.34	-56.63	2.15	0.25	2.94
$H_A (Y = \beta_0 + \beta_1 X)^b$	0.53	2	1.0	-58.78	0.00	0.75	

A comparison of these models was used to assess the ETH that cuckolded males tolerate raising an extra-pair offspring (EPO) because they are more genetically similar the genetic sires of their EPO than to a randomly drawn breeding male. Dyad types were cuckolded males with the genetic sire of the EPO he was raising and cuckolded males with a randomly drawn breeding male ($N = 18$ dyads of each type). The residual sum of squares (RSS), the number of parameters (K) in each model, the model likelihoods (L) and the small sample size-corrected AICc values (AICc) are shown. Models are ranked by their AICc differences (Δ_i) relative to the best model in the set and Akaike weights (w_i) quantify the probability that a particular model is the best model in the set given the data and the model set. The evidence ratio (ER), a ratio of the weights of the two models of interest, is also given. In this model set, the model with an effect, H_A , is approx. 2.9 times more likely than the null model, H_0 .

^aModel of no effect; Y is band-sharing; β_0 is the overall mean of band-sharing (intercept).

^bModel with an effect; X is band-sharing dyad type (cuckolded male–genetic sire vs. cuckolded male–random male); β_1 is the slope of the effect of dyad type.

males than to the genetic sire of their EPO. While the evidence supports an effect, that the 95% CI's around this effect narrowly overlapped zero underscores that the effect was not very strong. Accordingly, the 95% CI's around the estimates of mean band-sharing for cuckolded male–genetic sire dyads ($\text{mean}_{\text{gen}} = 0.26$, 95% CI = 0.20, 0.32) overlapped narrowly with the mean for cuckolded male–random breeding male dyads ($\text{mean}_{\text{ran}} = 0.35$, 95% CI = 0.29, 0.42; Figure 4) for the subset of families with EPFs and known paternity.

Discussion

An apparent cost of inbreeding

Genetic similarity of social parents was negatively related to the probability that an egg would hatch in the waved albatross; that is, parents of eggs that hatched were less genetically similar than parents of eggs that did not hatch. Hatching success was an important cost of inbreeding in several other species of bird and a snail (Crnokrak & Roff, 1999) while other measures of

fitness such as offspring survival, reproductive success, and characteristics of sperm quality, were lower for inbred compared to outbred individuals of several mammal species (Crnokrak & Roff, 1999). Survival to fledging of a very small subset of waved albatross chicks hatched in 2002 did not appear linked to social parent band-sharing (unpubl. data), but a deeper analysis including chicks from other years (2002 was a mild El Niño year) and information about recruitment may reveal a pattern in keeping with the cost at hatching explored here. Nevertheless, our findings suggest that a cost of genetic similarity, at least in terms of hatching, exists in this species and warrants exploration of the relationships among social behaviour, paternity and genetic similarity among individuals.

Genetic similarity and extra-pair paternity

Models including genetic similarity of social pairs and the Julian date the egg was laid garnered most of the Akaike weight in our model set examining relationships between EPF probability and genetic similarity. While the sign of the model-averaged effect of genetic similarity was negative, opposite that predicted by the GSH, the effect was not very strong.

Support for analogous genetic similarity-type hypotheses exists for some groups of animals but not others. Genetic similarity of alpine marmot parents had a negative effect on offspring heterozygosity and a strong positive effect on offspring-mother genetic similarity (Cohas et al., 2007) providing mixed support for a 'genetic compatibility' hypothesis for EPP in this mammal species. In dragon lizards, approx. 8% of matings was classified as 'inbred', while matings by genetically similar pairs did not have a cost in terms of offspring survival (LeBas, 2002).

The vast majority of studies linking genetic similarity of parents with extra-pair paternity are in birds. Studies of great reed warblers (Bensch et al., 1994), of three shorebird species (Blomqvist et al., 2002) and of Mexican jays (Eimes et al., 2005) demonstrate positive relationships between EPF probability and social mate genetic similarity, in contrast to our findings in the waved albatross. Avoidance of close inbreeding also was not a sufficient explanation for EPFs in blue tits (Kempnaers et al., 1996) or coal tits (Schmoll et al., 2005).

Although they have several life history characteristics in common, social structure presents an important difference between Mexican jays and

the waved albatross: Mexican jays are cooperative breeders with 2–4 adults of each sex helping in a single group (Eimes et al., 2005), including some close relatives (Brown & Brown, 1981). Potential costs of EPFs in Mexican jays (e.g., withdrawal of parental care, fewer future mating opportunities) might be reconciled by the benefits of having closely related helpers in a cooperative system whereas the costs of EPF in a system with strictly biparental care and pelagic foraging cannot be offset in the same way. Another important difference is clutch size. Great reed warblers, Mexican jays, and several shorebird species all have clutches of multiple eggs and many can re-nest in the same season if the first clutch fails. Multi-egg clutches often result in mixed broods, containing both EPO and WPO, whereas the waved albatross has a single egg clutch and they nest, at most, once annually. Any potential cost or benefit (such as inbreeding avoidance) to an EPF will be amortized differently by species with different life histories: species with shorter reproductive lifespans might tolerate extra-pair paternity in a brood because future reproductive attempts have relatively less weight than those of long-lived species (Mauck et al., 1999).

We found a stronger relationship between the Julian date the egg was laid and the probability of extra-pair paternity: eggs laid earlier were more likely to be EPF's. While this result does not bear on the issue of genetic similarity directly, the finding is in keeping with our study of protandry in this species. Waved albatross males typically arrive 6 to 10 days earlier to the colony than their social mates do and this translates into increased opportunities for EPCs for early-arriving males (Huyvaert et al., 2006). While early arrival was not strongly associated with EPF probability in the previous study, it may be that the fitness benefit of a male's early-arrival is improved hatching success which is mediated through an interaction of a male's genetic similarity with his mate and the date the egg was laid. Eggs that are more likely to hatch are laid earlier, are more likely to be EPO, and come from social mates that are, on average, less genetically similar than other sets of mates.

We documented little evidence of an effect of dyad type on genetic similarity in our paired analysis. The ratio of the weights of the null model compared to the model including an effect of dyad type was 1.14, indicating that the effect model was 1.14 times more likely than the null model which we judge to be very weak evidence of an effect. Among other studies of birds, support varies across taxa for the prediction that genetic similarity between a female and her social mate will be higher than that between a female and

her extra-pair partner. In 4 of 5 cases in a great reed warbler population at Lake Kvismaren, Sweden, estimates of genetic similarity between social mates were higher than between females and their EPF partners (Bensch et al., 1994). Interestingly, in an extended analysis of extra-pair paternity from the Lake Kvismaren population, Hansson et al. (2004) found no difference in genetic similarity of females with their social mates compared to females and extra-pair sires. No difference was reported for similar pairings in blue tits (Kempnaers et al., 1996) or coal tits (Schmoll et al., 2005). In contrast, females' extra-pair partners of the barn swallow tended to be more closely related than if partners were chosen at random (Kleven et al., 2005), a finding in keeping with our own in waved albatrosses. While our results did not support the key predictions of the GSH, they do leave the possibility open that females benefit in some unexplored way or that cuckolded caretaking males tolerate the presence of EPO in their nest if the actual sire is a close relative.

Alternative explanations

The costs of inbreeding and, thus, the adaptive value of seeking genetically dissimilar mates have been well-documented (for reviews, see Charlesworth & Charlesworth, 1987; Keller & Waller, 2002). Under some circumstances, though, females might pursue EPCs with genetically similar males to offset genetic or other costs of extreme outbreeding (Bateson, 1983; Pusey & Wolf, 1996; Kokko & Ots, 2006). Our results suggest that females might choose mates to maximize genetic complementarity (Mays et al., 2008) instead of strictly avoiding inbreeding or maximizing outbreeding. While the patterns of female choice for mates depending on complementarity vary widely, Mays et al. (2008) make the important point that females may choose for complementarity of both social mates and extra-pair mates because genetic complementarity, if it affects offspring survival, will contribute whether the young is extra-pair or within-pair. Thus, no strong difference in genetic similarities between female–social mates compared to female–genetic mates, as we found for waved albatrosses, may not mean that female choice for complementarity is unimportant; it may play an important role in a female's choice of a long-term social partner.

Several alternative explanations unrelated to genetic similarity may explain the extra-pair behaviour we see among waved albatrosses. Ecological factors such as colony density (Westneat & Sherman, 1997) may affect

the occurrence of EPFs: extra-pair paternity might be higher in more dense colonies if density is correlated with encounter opportunities (Birkhead & Møller, 1992). Our study colony is relatively dense compared to other portions of the main breeding island, Española. It could also be that males are unaware of the potential for cuckoldry because they are not present on the island when EPCs occur or they cannot recognize their social mate when she is engaging in a copulation with another male. Lastly, EPF's may be a result of male coercion of females by extra-pair males. Aggressive chases occasionally precede copulations that we see in the colony (pers. obs.) but we have not yet explored whether these apparently aggressive copulations result in the EPFs that we have documented.

EPF tolerance hypothesis

We documented a negative effect of dyad type on band-sharing between cuckolded males and the genetic sires of their chicks compared to cuckolded males paired with randomly chosen males, in contrast to the key prediction of the ETH that cuckolded males would be very genetically similar to the genetic sires of their EPO. Instead, cuckolded males in our study were more genetically similar to randomly chosen breeding males than to the genetic sires of their EPO. This could be the case if overall relatedness (genetic similarity) in the breeding colony is higher than the genetic similarity of females and their social mates, indicating that females choose more similar males as extra-pair partners. This explanation is consistent with our findings for the GSH: EPFs were more likely for social pairs with lower genetic similarity and the model with an effect of dyad type on genetic similarity was slightly more heavily weighted than the model of no effect (Table 3); additional families with EPOs would help clarify the strength of these relationships.

Social monogamy is the principal mating system in most seabird species (e.g., see Ligon, 1999, for a review), likely because distant foraging sites and lengthy development periods require extensive biparental care. A number of molecular studies of parentage in procellariiform species (the tubenoses including petrels, shearwaters, and albatrosses) suggest that the degree of genetic monogamy is also high. However, our data and data from grey-headed, black-browed, and wandering albatrosses show that EPFs account for 0–21% of young albatrosses (Huyvaert et al., 2006; Burg & Croxall, 2006; Jouventin et al., 2007). A number of genetic hypotheses have been proposed to account

for intra- and interspecific variation in EPFs and Jouventin et al. (2007) describe some support for an association between social pair relatedness and extra-pair paternity in wandering albatrosses, yet neither hypothesis examined here completely explains why approx. 17% of families are affected by EPP in waved albatrosses. Nonetheless, further evaluating interspecific relationships among genetic variability (e.g., Petrie et al., 1998), ecology, or behaviour and extra-pair paternity among albatrosses and those procellariiforms showing an absence of EPP, as in a meta-analytical framework, could prove fruitful in better understanding mating behaviour in long-lived seabirds.

Philopatry and extra-pair paternity

Extent of philopatry and degree of dispersal may play an important role in studies of genetic similarity and extra-pair behaviour. While the causes for dispersal are likely diverse and situation-dependent, inbreeding avoidance has had a central role in the evolution of natal dispersal (Perrin & Goudet, 2001). In the absence of substantial dispersal, though, EPFs might serve an inbreeding avoidance function. Non-migratory Mexican jays are subject to extremely low levels of dispersal; accordingly, a positive relationship exists between genetic similarity and the probability of having an EPO in the nest (Eimes et al., 2005). An alternative perspective is that extra-pair matings change the timing and degree of dispersal as in European badgers (Dugdale et al., 2007) where cubs in the same litter can have different fathers. In this case, kin competition and the potential for inbreeding might be mediated by extra-pair paternity rather than dispersal, although these authors suggest that additional study of lower density European badger populations is needed to clarify relationships between paternity and dispersal.

Long-distance emigration is an important life history trait across many seabirds, so breeding populations are more likely to include individuals from disparate geographic origins, making breeding by close relatives unlikely. In waved albatrosses, breeding dispersal has not been documented directly (Harris, 1973), but natal dispersal may be of sufficient distance to promote mixis: with a small number of markers, we have documented an absence of genetic differentiation that is consistent with the presence of gene flow among subcolonies of waved albatrosses (Huyvaert & Parker, 2006). A few anecdotal reports of adults breeding distant from the subcolony where they

were banded support this idea (K.P. Huyvaert, unpubl. data). Thus, dispersal, even at apparently low levels, might mean that the potential for inbreeding may be too low to favour EPF as an inbreeding avoidance strategy in this species. Instead, the patterns that we have described provide a small piece to the complex puzzle of relationships amongst many long-lived individuals. Clearly, additional work in a variety of taxa is called for to help clarify whether particular characteristics such as philopatry or migration habits are correlated with relationships between genetic similarity and EPF probability.

Acknowledgements

We are grateful for help from a number of field workers; in particular, we thank J.L. Bollmer, M.A. Westbrook and N.K. Whiteman for assistance collecting blood samples, and D.J. Anderson for extensive logistical support and encouragement throughout the study. We appreciate K.O. Halbert's help troubleshooting in the laboratory. N.J. Van Lanen, L.L. Bailey and especially D.R. Anderson provided helpful feedback on the statistical analysis. Previous drafts of the manuscript were improved by comments from the Parker Lab Group and two anonymous referees. Financial support came from the University of Missouri-St. Louis, the Des Lee Collaborative Vision in Zoological Studies and the International Center for Tropical Ecology at the University of Missouri-St. Louis, the Field Research for Conservation Program at the St. Louis Zoological Park, The Ohio State University, Sigma Xi and Wake Forest University. This study was conducted with permission to sample and handle birds from the Galápagos National Park Service and with logistical support from the Charles Darwin Research Station and TAME airlines. All observation, capture, and sampling procedures were approved by the Institutional Animal Care and Use Committee at the University of Missouri-St. Louis and Galápagos National Park Service, Ecuador.

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