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Heritability of short-scale natal dispersal in a large-scale foraging bird, the wandering albatross

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Abstract

Natal dispersal is a key life history trait for the evolution and adaptation of wild populations. Although its evolution has repeatedly been related to the social and environmental context faced by individuals, parent–offspring regressions have also highlighted a possible heritable component. In this study, we explore heritability of natal dispersal, at the scale of the sub-Antarctic Possession Island, for a large-scale foraging seabird, the Wandering albatross *Diomedea exulans*, exploiting a pedigree spanning over four decades and a maximum of four generations. The comparison of three different methods shows that heritability on the liability scale can vary drastically depending on the type of model (heritability from 6% to 86%), with a notable underestimation by restricted maximum likelihood animal models (6%) compared to Bayesian animal models (36%). In all cases, however, our results point to significant additive genetic variance in the individual propensity to disperse, after controlling for substantial effects of sex and natal colony. These results reveal promising evolutionary potential for short-scale natal dispersal, which could play a critical role for the long-term persistence of this species on the long run.

Introduction

The movement of individuals between different locations is a major component of gene flow, and thereby a central life history trait for the evolution and adaptation of populations and species. For this reason, considerable interest has been brought to understanding the ultimate and proximate causes of and explaining the variation in traits involved in these movements, i.e. dispersal (Bohonak, 1999; Ronce *et al.*, 2001; Bowler & Benton, 2005). Some key biotic and abiotic factors, such as inbreeding avoidance, competition for food or mates and especially kin competition, condition dependence and environmental heterogeneity, have repeatedly been related to the evolution of dispersal (see e.g. Clobert *et al.*, 2001). However, a prerequisite for these forces of selection to influence the evolution of dispersal in the wild is the presence of additive genetic variance in the factors characterising the movement. Studies on plants and insects have provided evidence for additive genetic variance in dispersal traits (Olivieri & Gouyon, 1997; Roff & Fairbairn, 2001), but results on vertebrates are still scarce and ambiguous (see e.g. Massot & Clobert, 2000; Hansson *et al.*, 2003).

In particular, for the study of natal dispersal, i.e. the movement of individuals between their natal area and their location of first breeding, heritability estimates are still very limited, even for the well-studied avian species (Table 1). In a review discussing parent–offspring comparisons in dispersal behaviours (including both natal and breeding dispersal), Doligez & Part (2008) report five out of 12 studies with statistical evidence for a resemblance in dispersal propensity (natal or breeding) between parents and their offspring. However, these studies often suffer from low statistical power because of restricted sample sizes. Since 2000, four of five avian species with estimates of heritability for natal dispersal showed similarity between parents and offspring in either their propensity to disperse before their first breeding attempt or their natal dispersal distances

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Table 1 A literature review of recent heritability estimates of avian natal dispersal, published since 2000, using parent–offspring regressions or pedigree-based animal models. Doligez & Part (2008) provide an extensive review of parent–offspring resemblance in dispersal behaviour explored in birds and mammals.

Species	Data span	Trait	h^2 (SE)	Method	References
Great reed warbler *Acrocephalus arundinaceus*	1983–2001	Philopatry vs. inter-population dispersal	PS: 0.50 (0.19) FS: 0.60 (0.29) MS: 0.62 (0.33)	Parent–offspring regressions, *n* = 48	Hansson *et al.* (2003)
Red-cockaded Woodpecker *Picoides borealis*	1986–2001	Natal dispersal distance	FS: 0.30 (0.15)–0.88 (0.25) MD: 0.17 (0.10)–0.19 (0.10)	Parent–offspring regressions, *n* = 43–330	Pasinelli *et al.* (2004)
Great tit *Parus major*	1960–1998	Natal dispersal distance	Male: 0.247 (0.063) Female: 0.253 (0.058)	Restricted maximum likelihood animal model, *n* = 1607 males and 1758 females	McCleery *et al.* (2004)
	1994–2002	Natal dispersal distance	FS: −0.12 (0.22) MD: 0.05 (0.20)	Parent–offspring regressions, *n* = 92, 86	Matthysen *et al.* (2005)
Blue tit *Cyanistes caeruleus*	1994–2002	Natal dispersal distance	FS: 0.05 (0.28) MD: −0.06 (0.58)	Parent–offspring regressions, *n* = 46, 31	Matthysen *et al.* (2005)
Collared flycatcher *Ficedula albicollis*	1980–2005	Philopatry vs. inter-plot dispersal	PO: 0.469 (0.098) FO: 0.458 (0.069) MO: 0.330 (0.074)	Parent–offspring regressions, threshold model, *n* = 404, 946, 985	Doligez *et al.* (2009)
	1980–2005	Philopatry vs. inter-plot dispersal	0.39, Credible Interval: [0.31; 0.47]	Bayesian animal model, *n* = 4848	Doligez *et al.* (2011)

For parent–offspring regressions, estimates were based on comparisons of values between mid-parent and offspring (PO), father and offspring (FO), mother and offspring (MO), father and son (FS) or mother and daughter (MD). The use of a threshold model in the last two studies on collared flycatchers implies that heritability of the binary trait (philopatry-dispersal) has been transformed to heritability of liability to disperse (Falconer & Mackay, 1996).

(Table 1). Additionally to these direct estimates of heritability, studies with lower sample sizes have found that siblings dispersed similar distances and/or in similar directions (Sharp *et al.*, 2008), although in several cases it was suggested that the similarity resulted from siblings sharing environmental conditions (Forero *et al.*, 2002; Dale, 2010). Finally, natal dispersal has been shown to correlate with heritable personality traits such as exploratory behaviour (Dingemanse *et al.*, 2003), thereby suggesting that natal dispersal is not only a condition-dependent trait, but it is also explained in part by genetic effects.

The scarcity of heritability estimates for natal dispersal is very likely the result of methodological issues, especially the problem raised and underlined by van Noordwijk (1984) regarding nonrandom spatial distribution of possible dispersing sites when comparing dispersal distances between parents and offspring. A bypass to this obstacle is to collect natal dispersal data between populations at a scale larger than the species' average dispersal distance (Hansson *et al.*, 2003), rather than focusing on one population, and/or to analyse the propensity to disperse between different plots or sub-populations (as a binary 0/1 trait), rather than dispersal distance (Doligez & Part, 2008; Doligez *et al.*, 2009). Another challenge yet to take up is to gather sufficient dispersal distances or statuses on related individuals during long-term studies, in order to conduct powerful quantitative genetic analyses. Table 1 illustrates that in short- and medium-lived passerines, monitoring during one or two decades rarely provides more than 50 parent–offspring pairs with known natal dispersal status or distance. For this reason, combining comparisons between different types of relatives in the same model as allowed by pedigree-based 'animal model' techniques (Kruuk, 2004) may represent a very helpful improvement in exploiting all the available data. Finally, dispersal data add an additional complexity to the analysis because they usually display non-Gaussian distributions, especially in the binary coding of dispersers and nondispersers. In this case, Bayesian approaches might prove more powerful than classic frequentist (maximum likelihood) approaches, because they can properly model non-normal responses and can provide a measure of confidence for heritability estimates (O'Hara *et al.*, 2008). Bayesian animal models have been developed already some time ago to model heritability of economically important traits in animal breeding science (e.g. Sorensen & Gianola, 2002), yet their application to characters measured on wild animals or plants is very recent and limited to a restricted number of case studies (Papaïx *et al.*, 2010; Serbezov *et al.*, 2010; Steinsland & Jensen, 2010), with one application to the study of (natal) dispersal (Doligez *et al.*, 2011).

Seabirds are an interesting case for the study of natal dispersal because they are well known for their wide-ranging capacities and dispersive behaviour at sea, yet most species are highly philopatric, returning close to their land-based natal site to breed. Albatrosses represent an extreme case in this regard, among seabirds. They breed on remote oceanic islands and have slow demographic life histories, with late sexual maturity, low fecundity (one egg clutch, some species breed every second year only) and high longevity (Weimerskirch, 1992). Although they can cover several thousands of kilometres during foraging trips and range over oceanic basins, they show very low natal dispersal from their colony of birth, and even higher fidelity to their breeding colony after they have started breeding. However, short-scale natal dispersal between colonies of the same island does occur regularly (Bried *et al.*, 2007), as well as occasionally long-distance dispersal between islands as far as 900 km apart (Inchausti & Weimerskirch, 2002). The long-term monitoring of wandering albatrosses (*Diomedea exulans*) initiated in 1966 on the sub-Antarctic Possession Island in the Crozet Archipelago (Weimerskirch *et al.*, 1997) offers a unique opportunity to gather pedigree data along with phenotypic data on natal dispersal between colonies of one island, in order to estimate heritability of natal dispersal propensity at a short scale. Here, we investigated whether part of the variation in natal philopatry observed in this species can be attributed to a heritable component by examining the heritability of philopatry versus natal dispersal between the breeding colonies of the entire island, where most of the dispersive movements occur.

Materials and methods

Colonies, population monitoring and pedigree

The entire population of wandering albatrosses on Possession Island, the largest of the Crozet Islands (south western Indian Ocean), has been monitored annually since 1966. The population has presently around 380 pairs breeding annually. It had *c.* 500 breeding pairs in the 1960s, declined steeply in the 1970s to reach 260 pairs and increased progressively to the present numbers (Weimerskirch *et al.*, 1997; Delord *et al.*, 2008). As the species has a biennial breeding cycle, the entire breeding population consists presently of *c.* 600 breeding pairs. The species breeds in loose aggregations, called colonies, that are located on the northern and eastern coasts of the island (Fig. 1). Colonies are divided by geographical barriers (such as a river or ridges) unsuitable as breeding grounds, which allow a clear spatial separation of aggregations. In total, eight colonies can be distinguished, six of them located on the eastern part of the island on northern and southern slopes of rivers (e.g. the Baie du Marin location is split between a northern and southern colony, see Fig. 1).

For every year since 1966, all of the nests have been located after the egg-laying period (around January 15th). For each nest, the incubating bird present is identified using its unique metal band number, or banded if it is its first capture. Two other visits take place 10 and 20 days later to identify the bird's partner. In April, the presence of a hatched chick is recorded, and thereafter its survival is monitored every second month until it fledges, in November. The chick is banded in October. Using this procedure, after 2000 only 4–27 individuals (average 18.6) were captured annually without a band as opposed to *c.* 600 individuals captured with a band (the few unringed birds can be immigrants, chicks missed during the banding operations or adults having lost their bands). This low number of birds without bands is the result of a systematic banding programme for breeding adults and chicks on Possession Island, coupled with very high natal philopatry and recruitment rate (Inchausti & Weimerskirch, 2002). For all birds banded as chicks and that do not disperse outside the island, we can determine their short-scale dispersal from their birth colony: we considered that local natal dispersal occurred when a bird reproduced for the first time in a colony of Possession Island different from its birth colony on the same island.

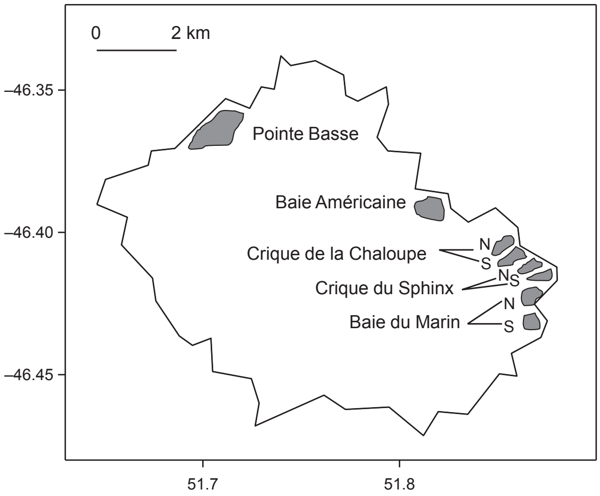

Fig. 1 Map of Possession Island, in the southern Indian Ocean, with eight colonies of wandering albatross (N: North; S: South).

Monitoring of other wandering albatross colonies outside Possession Island is very heterogeneous. In the Indian Ocean, only Marion Island (1070 km away from Possession) and the eastern part of Kerguelen (1450 km away) have annual banding and recapture programmes comparable with that on Possession Island, but all other breeding sites of the species have been monitored irregularly for banded birds. Using the same data set and a similar span as ours, Milot *et al.* (2008) reported only 28 natal dispersers from Possession (19 of which were birds breeding on Marion Island), representing approximately 0.3% of birds banded as chicks on the island. The heterogeneity of recapture efforts outside Possession Island hampered a global analysis of natal dispersal, but anyway the very limited proportion of long-range dispersal in this species would not allow any statistical powerful analysis. For this reason, and also because colony philopatry is very high, we restrict out interpretation to local natal dispersal.

The long-term monitoring of wandering albatrosses on Possession Island allowed us to use a quantitative genetic approach to investigate additive genetic effects on dispersal behaviour, based on a pedigree of 2797 individuals over four generations (see Appendix S1 for descriptive statistics on the pedigree). Although the wandering albatross is a highly socially faithful monogamous species, paternity analyses on 75 breeding pairs from Possession Island have previously revealed 10.7% of extra-pair offspring (Jouventin *et al.*, 2007), possibly induced by the male-biased adult sex ratio. This implies that the social pedigree we use here for our quantitative genetic analysis includes some errors in the paternity links, which could result in some underestimation of the additive genetic variance and heritability, although simulations have shown that rates of paternity errors around 5–20% induce little bias on heritability estimation (Wilson *et al.*, 2003; Charmantier & Réale, 2005; Morrissey *et al.*, 2007).

Colony- and sex-specific dispersion

We restricted the data set to cohorts of at least 30 individuals ringed at birth and recaptured as breeders (see Fig. S1 for all sample sizes), hence birds born between 1970 and 1999. The last year of breeding included in this analysis was 2007. When restricting the data set to birds with known sexes, and born between 1970 and 1999, natal dispersal status (disperser/non-disperser) was known for 1890 individuals, including 421 father–offspring pairs (with 60 dispersing fathers) and 413 mother–offspring pairs (112 dispersing mothers). Overall, the data set included 21.8% of natal dispersing individuals, yet males dispersed much less than females: 14.0% of males were dispersers versus 30.0% of females. Preliminary logistic regression models exploring individual and environmental fixed effects influencing natal dispersal behaviour showed significant natal colony and sex effects, and insignificant cohort effects. The high significance of natal colony in these preliminary analyses, as well as in all models described below, is in accordance with the recent demonstration that the rate of natal dispersal varies from 0.70 to 0.92 according to the colony of origin on Possession Island (Gauthier *et al.*, 2010).

Classical frequentist estimation of additive genetic variance and heritability for liability to disperse

Dispersal behaviour can be viewed as a threshold character, whereby the trait has an underlying (unobserved) continuous distribution, called liability, with a threshold determining the discontinuous phenotype (Falconer & Mackay, 1996): in our case, individuals above the threshold would disperse, and those below would not disperse. The phenotypic distribution on the liability scale can be assumed normal, and resulting from genetic and environmental differences between individuals, as any quantitative trait. Several approaches can then be used to estimate the heritability of the character on its underlying liability scale h_c^2.

First, we used a simple approach based on similar reasoning as classic parent–offspring regressions, whereby incidences in the parental generation and in their progeny are used to estimate the mean liability of the parents displaying the character (dispersing parents) and their offspring (Lynch & Walsh, 1998). One way to evaluate the validity of such a threshold model is to compare estimates obtained using different types of relatedness; hence, we based our estimations on father/offspring, mother/offspring, father/son and mother/daughter incidences. We used Edwards' equation detailed by Lynch & Walsh (1998, Equation 25.2 page 733) where the exact phenotypic correlation between relatives on the underlying normal scale is approximated, in order to obtain a simple equation whereby the heritability is directly estimated from the incidences. Unfortunately, this method does not allow a good assessment of the uncertainty of the estimation, because no confidence interval or standard error is associated with the estimation of heritability on the underlying scale.

Second, we modelled the natal dispersal behaviour using a generalised linear mixed model (GLMM) with a logit link function relating the binary data to the underlying normal scale and a restricted maximum likelihood (REML) procedure (Knott *et al.*, 1995; Lynch & Walsh, 1998) run with ASReml 2.0 (Gilmour *et al.*, 2006). This GLMM 'Animal Model' partitioned the variance into an additive genetic and an environmental variance component (Kruuk, 2004). For the analysis of binary data, ASReml uses an approximate likelihood technique called penalised quasi-likelihood (PQL, Breslow & Clayton, 1993), which has caused a call for caution in the use of these models (see our Discussion). It is ill-advised to use the quasi-likelihood computed by PQL as a means of statistical inference (Bolker *et al.*, 2009). However, there is presently no formally rigorous test to evaluate whether the additive genetic variance and heritability estimates obtained using a generalised linear mixed animal model are significant. We chose to run similar models using a normal scale and compared the REML models with/without an additive genetic variance using the standard Akaike's information criterion (A Gilmour, pers. com., Burnham & Anderson, 2002). As justified above, individual sex (male/female) and natal colony were included as fixed effects. For each individual i, we denote the dispersal event y_i, which takes values 1 if it has dispersed and 0 otherwise. This binary random variable was assumed to be related to a continuous underlying latent variable l_i such that $y_i = 1$ if $l_i \geq 0$ and 0 otherwise. The random variable l_i is usually referred to as the liability for individual *i* and was assumed to be normally distributed with mean η_i and some variance (see below for a decomposition of this variance). The natal dispersal probability $\Pr(y_i = 1)$ was related to the mean liability on the scale of a link function g via $g(\Pr(y_i = 1)) = \eta_i$. In turn, the mean liability was modelled as:

$$\eta_i = \mu + \text{sex} + \text{natal colony} + a_i + e_i,$$

where μ is the population mean, a_i is the individual's additive genetic value, and e_i is the random residual value. Hence, the total phenotypic variance in the liability to disperse (V_P) was portioned into a variance attributed to additive genetic effects (V_A) and a residual variance (V_R): $V_P = V_A + V_R$. In various species of plants and animals, the propensity to disperse is under strong maternal influence (e.g. Venable & Burquez, 1989; Mousseau & Dingle, 1991; Massot & Clobert, 1995). Hence, a maternal identity was also fitted as an extra random effect but it explained an insignificant portion of the variance and was removed. Heritability of short-scale natal dispersal behaviour (h_c^2) was calculated using $V_R = \pi^2/3$ if g was the logit link function and $V_R = 1$ if it was the probit (Nakagawa & Schielzeth, 2010). Both link functions gave very similar results (see Results section).

Bayesian animal model

As a third method for estimating heritability of liability to disperse (h_c^2), we ran animal models with Bayesian inference (e.g. Papaïx *et al.*, 2010) incorporating the same random and fixed effects as described above for the REML animal model. We adopted a Bayesian approach using Markov chain Monte Carlo (MCMC) algorithms because it provides a flexible framework in quantitative genetics to analyse non-normal data (Damgaard, 2007; Waldmann, 2009). The Bayesian approach combines the likelihood (i.e. information derived from observed data) and the prior distribution of the unknown quantities (i.e. knowledge available before the data were observed) to produce the joint probability distribution of all models unknowns conditionally on the observed data. The joint posterior distribution of all parameters was obtained by means of MCMC sampling as implemented in the OpenBUGS software (Lunn *et al.*, 2009; code available in Appendix S2). We ran two parallel MCMC chains and retained 45 000 iterations after an initial burning of 5000 iterations with a thinning of each 10th iteration. Convergence of MCMC sampling was assessed by means of the Brooks–Gelman–Rubin diagnostics (Brooks & Gelman, 1998) and visual inspection of the chains (Fig. S2).

A Bayesian analysis requires specifying prior probability distributions for the model parameters. All priors were selected as sufficiently vague in order to induce little prior knowledge (Clark, 2005; McCarthy & Masters, 2005), which ensures that posterior distributions reflect mainly the information from the data. An uninformative (or vague) prior corresponds to a uniform distribution or normal distribution with large variance (see below for specific prior choices). When fitting animal models, the use of noninformative priors on the standard deviations of the random effects is usually used. However, noninformative priors on the additive genetic standard deviations lead to an informative prior on the heritability associated, which can influence posterior results in the case of weakly informative data (Gelman, 2006). We used the probit link function, hence $V_R = 1$ and the heritability h_c^2 was fully dependent on the additive genetic variance ($h_c^2 = V_A/(V_A + 1)$). Thereby, the higher the additive genetic variance (through a noninformative prior) was, the higher the probability for the heritability would be close to 1. To address this issue, we assigned noninformative priors on the heritability h_c^2 (U[0,1]). The one-to-one transformation relating V_A to h_c^2 ($V_A = h_c^2/(1 - h_c^2)$) thereby induces a relatively noninformative prior on V_A (see Fig. 2). Regarding the regression coefficients of the fixed effects (intercept μ, sex effect α and natal colony β), normal distributions with mean 0 and variance 10 were used. We conducted a prior

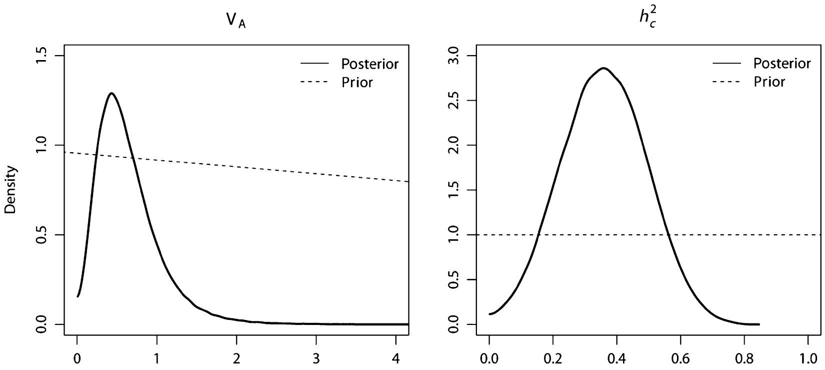

Fig. 2 Posterior density distributions (full lines) for additive genetic variance and heritability in propensity for natal dispersal estimated using a Bayesian animal model. Prior density distributions are also displayed (dotted lines). Notation: V_A is the additive genetic variance and h_c^2 is the heritability estimated on an underlying continuous liability scale.

sensitivity analysis to make sure that information in the data was sufficient to update the prior.

Bayesian animal models with/without an additive genetic variance were compared using the deviance information criterion (DIC, Spiegelhalter *et al.*, 2002). Several other methods exist to compare models in a Bayesian framework (O'Hara *et al.*, 2008); we adopted the DIC following the advice of Hadfield (2010) and as implemented in MCMCglmm.

Results

Overall, 22% of the birds ringed as chicks on Possession Island were captured breeding in a different colony from their birth colony (minimum and maximum dispersal distances within the island were 100 m and 12 km). These natal dispersal rates focus on a small-distance scale compared to the great flight capabilities of wandering albatrosses, yet these rates are close to that found in a previous study investigating dispersal between six islands of the Southern Ocean, with colonies as far as 6050 km (23% of natal dispersal from the birth colony, including within- and between-island groups, the longest natal dispersal distance observed was 1450 km, Inchausti & Weimerskirch, 2002). This suggests that long-distance natal dispersal remains exceptional in this species. Mean natal dispersal distance within the island was 0.67 km overall (SD = 2.21), 0.89 km (SD = 2.46) for females and 0.46 km (SD = 1.92) for males.

The occurrence of local natal dispersal in offspring from dispersing fathers or mothers was notably higher than the mean population occurrence (Table 2), suggesting a clear heritable basis for this character. This translated in heritabilities of liability to disperse locally estimated between 0.31 and 0.86 using parent–offspring occurrences (Table 2). The smaller estimate came from a father–son regression and the largest estimate from a mother–daughter regression, suggesting that maternal effects could partly confound this latter heritability estimate, although this was not confirmed by animal models because none of the models below showed significant maternal effects. Alternatively, the known extra-pair paternities in this species (Jouventin *et al.*, 2007) could partly explain the difference between father–son and mother–daughter regression estimates.

The heritability of the liability to disperse, as estimated using a generalised linear mixed animal model, was $h_c^2 = 0.06 \pm 0.05$ (SE, these estimates are the same using a logit or probit link function), and the additive genetic variance $V_A = 0.20 \pm 0.19$ ($V_A = 0.06 \pm 0.07$ using a probit link). Although standard errors of these estimates were high, AICs were lower for models with additive genetic variance compared to without (−1959.1 vs. −1951.8 for GLMMs on normal scale), supporting the presence of a heritable component in the propensity for natal dispersal, even though the absolute heritability value was small.

Finally, the results from the Bayesian animal models also showed significant heritability for the propensity to disperse, with $h_c^2 = 0.36$ (95% credible interval [0.10; 0.62]): the model incorporating an additive genetic effect was associated with the smallest DIC value (DIC: 1042 vs. 1094 when excluding the additive genetic variance). The posterior distributions are displayed in Fig. 2, and the resulting summary estimates are presented in Table 3. The comparison of posterior to prior distributions suggested that the information contained in the data led to considerable updating of the prior distributions (see Fig. 2).

Discussion

Our analyses based on the long-term monitoring of wandering albatrosses on Possession Island revealed that additive genetic effects contribute to heritable variation for short-scale propensity to disperse between birth and first breeding colonies. All three methods used to estimate heritability pointed to significant heritable effects on short-distance natal dispersal, yet the estimations varied substantially between methods (see Discussion below). The heritability of natal dispersal measured over a few hundred metres is notable considering the great flight capabilities and extreme navigation performance of these birds. Natal dispersal outside the natal island in wandering albatrosses, although rare, can be as far as 6050 km (H. Weimerskirch, unpublished data), and they can travel even longer distances during foraging trips while breeding (e.g. Lecomte *et al.*, 2010) and especially during their sabbatical year when they can circumnavigate Antarctica and pass close to all the

Table 2 Heritability of natal dispersal behaviour in the wandering albatross estimated on the underlying continuous scale (h_c^2) using Edwards' approximation method based on the behavioural occurrences in parents (M = males, F = females) and offspring.

	Occurrence of natal dispersal			
	In population (n = 960 M + 930 F)	In offspring of dispersing parents	Number of dispersing parents	h_c^2
Father–offspring	M + F: 0.218	0.383	60	0.586
Mother–offspring	M + F: 0.218	0.393	112	0.618
Father–son	M: 0.140	0.216	37	0.312
Mother–daughter	F: 0.300	0.536	56	0.860

Table 3 Parameter estimates from the Bayesian animal model of propensity for natal dispersal. Posterior means, medians, standard deviations (SD) and 95% credible intervals (CI) are provided: μ is the intercept, α is the sex effect (female), β is the colony of birth effect, V_A is the additive genetic variance and h_c^2 is the heritability estimated on an underlying continuous liability scale.

	Mean	SD	Median	CI
μ	–3.07	0.37	–3.05	[–3.86; –2.46]
α	1.03	0.16	1.02	[0.75; 1.39]
β_2	1.58	0.28	1.56	[1.08; 2.19]
β_3	2.02	0.40	2.00	[1.28; 2.88]
β_4	2.72	0.36	2.68	[2.13; 3.57]
β_5	2.72	0.40	2.68	[2.04; 3.59]
β_6	2.26	0.31	2.23	[1.74; 2.95]
β_7	2.14	0.30	2.11	[1.64; 2.81]
β_8	1.80	0.28	1.77	[1.35; 2.44]
V_A	0.64	0.39	0.56	[0.11; 1.63]
h_c^2	0.36	0.13	0.36	[0.10; 0.62]

breeding sites of the species (Weimerskirch, unpublished data). Yet, we have shown here that if we consider only the birds that remain faithful to one island, the local-scale dispersal within one island is heritable. This result suggests that microevolution in natal dispersal behaviour is possible, especially in situations where selection will operate towards higher dispersal, e.g. in disturbed habitats (Bowler & Benton, 2005). Unfortunately, the very long lifespan of wandering albatrosses prevents us from testing how philopatry relates to lifetime fitness in order to measure selection acting on this life history choice in this species.

Since 1966, all breeding wandering albatrosses and their chicks have been banded on Possession Island. This amounts to 8707 ringed chicks, of which, up until 2006, 28 were found breeding in other islands of the Southern Ocean (Kerguelen, Cochons Island, Prince Edward and South Georgia, see Milot *et al.*, 2008). Natal dispersal movements between these islands were asymmetric, at least between Marion Island (Prince Edward Islands) and Possession Island where similar mark–recapture efforts are carried out, with more natal dispersers witnessed coming from Possession. In any case, these recent analyses of capture–mark–recapture data and genetic diversity and structure (Milot *et al.*, 2008) demonstrate ongoing gene flow between the different islands, which is not surprising considering the flight abilities of wandering albatrosses. However, this rate of dispersal remains extremely low, and the few cases available do not allow statistical analysis. Here, we have chosen to use records of natal dispersal within one island comprising eight colonies in order to estimate quantitative genetic parameters by comparing related and unrelated individuals. It is difficult to envisage how the long-distance natal dispersal would affect our estimates if data were available to investigate natal dispersal both on small and on large scales, yet if anything our short-scale restriction should only underestimate natal dispersal heritability by ignoring a few dispersing individuals, in the same way that ignoring extra-pair paternity might reduce the resemblance between fathers and offspring in their dispersal behaviour.

Our results offer support to previous analyses based mostly on parent–offspring regressions, showing within-family resemblance in dispersal liability (e.g. most recently Doligez *et al.*, 2011), and they widen the phylogenetic range of study because previous work focused on short-lived species, mainly passerines (Table 1), yet they also highlight important differences in estimates of heritability depending on the statistical approach used. As animal models control for various fixed and random effects and use information from across the pedigree, they often provide lower estimates of heritability compared to the classic parent–offspring regression (Quinn *et al.*, 2006; Postma & Charmantier, 2007), with a decline of typically 5–30% in heritability estimation (Kruuk *et al.*, 2001; MacColl & Hatchwell, 2003; McCleery *et al.*, 2004). In a recent study that compared heritability of natal dispersal using parent–offspring regression versus Bayesian animal model, a decline of 17% was observed (Doligez *et al.*, 2011; see Table 1). Here, however, the REML animal model provided an estimate of heritability for the liability to disperse (0.06 ± 0.05) 80–90% lower than estimates from parent–offspring regressions (Table 2). Notably, this REML estimate was also smaller than the 95% credible interval estimated with the Bayesian animal model (CI = [0.10; 0.62]). We view this as a worrying result that confirms the doubts over the robustness of using linear mixed models with non-Gaussian data (Bolker *et al.*, 2009). Indeed, it has been suggested that animal models based on generalised linear mixed models using the PQL technique as implemented in ASReml may provide biased estimates (Gilmour *et al.*, 2006), especially so for binary data where PQL would underestimate the variance components, as well as the absolute value of fixed effects (Breslow & Clayton, 1993). These warnings suggest that our results from the Bayesian animal model may be more robust than those with the two other methods, yet it is beyond the scope of this study to evaluate the validity of the GLMMs on binary data. This would necessitate a simulation study in order to draw conclusions on the type of bias induced by this practice, especially whether it will consistently under-estimate heritability on a liability scale. However, we feel our results underline that it is presently useful for evolutionary biologists to compare estimates from the most commonly implemented approaches, while keeping an eye on the ongoing work carried out by biostatisticians to investigate the suitability of the different approaches.

On the other hand, REML and Bayesian animal models provided similar evaluations for the explored factors affecting the decision to disperse before breeding, including the major effect of individual sex, with twice as many females dispersing as males, and their birth colony. The latter confirms recent multi-state mark–recapture models showing that on Possession Island, philopatry varies from 70% to 92%, depending on the colonies (Gauthier *et al.*, 2010), with lower natal dispersal in larger colonies, and least dense colonies attracting dispersers. Sex-specific liability to disperse is also in line with the mark–recapture analysis and confirms that natal dispersal is partly a condition-dependent trait. Maternal effects did not statistically influence the natal dispersal propensity, as opposed to the only other study, to our knowledge, that investigated maternal effects by partitioning the variance in dispersal behaviour (natal dispersal distance in the great tit *Parus major*, McCleery *et al.*, 2004) into components attributed to additive genetic and environmental effects. The heritable component shows that condition-dependent and environmental traits do not explain all the individual variance displayed in the propensity to disperse. The origin of the heritable variation revealed here is however not necessarily purely additive genetic, and in this type of study it is especially important to consider the possibility of family-specific correlations owing to ecological or cultural inheritance. We have attempted to control for potential influences of maternal care and several environmental factors, yet other common environment effects such as local habitat quality could be involved if they are shared closely by relatives. As females lay one egg every 2 years, sibs are likely to share less local environmental effects than in passerine avian model species with large clutches. Also, it is difficult to envisage how wandering albatross offspring could assess the natal dispersal status of their parents, unless natal dispersal is strongly correlated with other behaviours they can witness. Hence, we believe our estimation of heritability of local natal dispersal is most likely not inflated by nongenetic inheritance. In any case, if one is interested in the potential for evolution of a character, one should estimate the heritable variation displayed by this trait, on which natural selection will operate, regardless of the mode of transmission. Note that removing nongenetic effects from heritability estimation is most optimally carried out by cross-fostering experiments in the field, a prospect difficult to consider in such long-lived species as albatrosses.

In this study, we have attempted to estimate additive genetic variance and heritability of the liability for local natal dispersal, attributing the status of disperser or nondisperser to each wandering albatross born and breeding on Possession Island. After controlling for the fixed effects discussed above, a large portion of the variance between birds in their liability to disperse was not explained by additive genetic effects and remained unexplained in our models. We know from past research that the decision to disperse or not is highly dependent on a suite of environmental factors. Hence, as has been previously suggested (Ronce *et al.*, 2001), an interesting avenue would be to consider dispersal as a plastic response to a set of biotic and abiotic conditions rather than a fixed dispersal status, although obviously such a reaction norm approach cannot be undertaken on the single event of natal dispersal but rather on breeding dispersal. Although breeding dispersal remains very low in wandering albatrosses (rate of breeding fidelity to a nesting colony ranges from 0.957 to 0.977 on Possession Island, Gauthier *et al.*, 2010), another interesting follow-up to this study would be relating natal and breeding dispersal, both on a phenotypic level and also genetically. Obviously, these enterprises would be very challenging as they would require an even greater amount of data on the natal and breeding conditions for related and unrelated individuals than has been gathered until now in long-term bird studies (Table 1). However, the study of how plastic dispersal strategies depend on environmental conditions remains a necessary step for evolutionary biologists interested in the evolution of dispersal (Kokko & Lopez-Sepulcre, 2006). In part, it will contribute to understanding how such high levels of additive genetic variance for a major behavioural character is maintained, and how fast dispersal can evolve. Natal and breeding dispersal are complex life history traits, which interact closely with population demography (Ronce *et al.*, 2001) and population genetic structure and display strong genetic covariance with other major life history characters (Roff & Fairbairn, 2001). Hence, this will add further complexity when estimating the forces of selection acting on dispersal, and predicting its evolution.

The wandering albatross status in the IUCN Red List of Threatened Species (http://www.iucnredlist.org) is presently vulnerable with a global population decline. In the past, this decline has largely been attributed to incidental catch in fisheries (Weimerskirch *et al.*, 1997). Recent studies have shown that wandering albatrosses as well as other albatrosses are also strongly influenced by environmental variation, and thus susceptible to future climate change (Rolland *et al.*, 2009). In the context of environmental change, some islands presently occupied by breeding sites of these central place foragers are likely to become less optimal breeding sites in the near future. Similarly, several present breeding sites were not available for breeding during the last glaciations, suggesting that natal dispersal has, and will in the future, play(ed) a critical role for the long-term persistence of these species. Natal dispersal in this long-lived bird is of major importance for the dynamics and conservation of their global populations. Hence, if areas in the bird distribution are affected negatively by environmental changes, an evolution towards higher natal dispersal or higher plasticity in dispersal can constitute a keystone for the population persistence. In any case, the slow pace of life of this species as illustrated by its generation time of 18.9 years (Weimerskirch, unpublished estimate) suggests that such a microevolutionary process would require several decades before any significant change in dispersal behaviour.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Summary statistics for the wandering albatross pedigree used.

Appendix S2 R script and OpenBUGS code for the Bayesian animal model.

Figure S1 Annual sample sizes of records of natal dispersal for wandering albatrosses on Possession Island.

Figure S2 Mixing of the MCMC algorithm used to fit the Bayesian animal model to the wandering albatross data.

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