

Small-scale dispersal and survival in a long-lived seabird, the wandering albatross

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Summary

1. Dispersal is a fundamental but still poorly known process in population dynamics and several hypotheses have been proposed to explain its patterns. We studied natal and breeding dispersal and survival in a long-lived seabird, the wandering albatross (*Diomedea exulans* L.), and examined several hypotheses concerning dispersal patterns in birds.

2. We applied multi-state capture–recapture models to a 36-year data set (1969–2004) collected at three albatross colonies on Île de Possession, Crozet Islands. Because the species has biennial reproduction, we introduced unobservable states in the model to account for the absence of individuals in those years.

3. Adults were highly faithful to their nesting colony but colony fidelity, as well as survival rate, differed slightly among colonies (fidelity ranged from 0.957 to 0.977). Breeding fidelity was highest in the colony where survival was lowest and individuals were not more likely to change colony following a failed breeding attempt than after a successful one. The colony that attracted most dispersers had the lowest density of nesting birds.

4. Philopatry (the probability that young return to breed at a birth site) was generally high but variable among colonies (ranging from 0.70 to 0.92), and survival of young differed little. Philopatry was highest in the largest colony, where the availability of potential mates was presumably greatest. However, among dispersing individuals, the colony that had the lowest density of nesting individuals, not the largest colony, attracted the most recruits.

5. Although size of the colony influenced the decision to stay or to leave in young, density was most influential in the selection of a new colony among both adult and young dispersers. Our results support the hypothesis that philopatry is the strategy favoured by most recruits and that conspecific attraction can explain variation in the level of philopatry among colonies but not settlement patterns among dispersing individuals.

Key-words: colony size, conspecific attraction, fidelity to colony, philopatry

Introduction

Dispersal is a fundamental but complex process to study in population dynamics (Clobert *et al.* 2001). Numerous theoretical models have been developed to describe how proximate factors such as sex, body condition, resources or conspecific cues and ultimate factors such as kin competition, inbreeding or dispersal costs contribute to dispersal decisions by animals (Johnson & Gaines 1990; Gandon & Michalakis 2001; Rousset & Gandon 2002; Amarasekare 2004). Despite these theoretical advances, the interpretation of dispersal patterns in natural systems remains challenging. In long-lived

seabirds, the widespread view has been that fidelity to the natal site (philopatry) is high and that breeding site fidelity among adults is very high. However, this generalization may not hold for all seabirds, and several groups do not follow this pattern (Weimerskirch 2002; Coulson & Coulson 2008). Much work has been done to elucidate mechanisms underlying dispersal patterns in long-lived seabirds, notably from a habitat selection perspective (Danchin & Cam 2002; Cam *et al.* 2004).

The life history of albatrosses represents an extreme case among seabirds. In most species, foraging takes place in pelagic waters, resulting in a disconnection between local nesting habitat quality and food availability. Albatrosses have evolved a set of life-history traits such as great longevity, late

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maturity, low reproductive rate and large body size that allow them to buffer the unpredictability of food availability at sea (Weimerskirch *et al.* 1993; Weimerskirch & Lys 2000). Although philopatry may be a central component in the evolution of this buffering strategy (Milot 2009), this hypothesis cannot account for *in situ* variation observed in dispersal patterns. Recent studies on the wandering albatross report various levels of natal dispersal at different spatial scales (Inchausti & Weimerskirch 2002; Bried *et al.* 2006; Milot, Weimerskirch & Bernatchez 2008), with rare dispersal movements among islands and archipelagos, and possibly more frequent movements among colonies within islands.

Natal dispersal may be related to the mating process (Bried & Jouventin 2002; Milot *et al.* 2008). Since breeding partners are faithful, mate choice is critical, and wandering albatrosses are among the choosiest of seabirds (Bried & Jouventin 2002). The spatial distribution of potential mates can influence habitat selection by animals (Danchin & Wagner 1997). Wandering albatrosses engaging in courtship aggregate at colonies and future recruits may be more likely to settle where the number of potential mates is greatest. Larger colonies are thus expected to attract more birds than smaller ones under conspecific attraction and dispersal rates should be asymmetric when colonies differ in size (Cam *et al.* 2004). It is unclear, however, whether colony size itself, measured as number of breeding pairs, can provide an indication of the number of unmated potential partners available. Alternatively, birds may first return to their natal colony to begin their search for a mate before moving to other sites. In this case, the settlement decision may simply depend upon where a mate has been found. These two hypotheses are not mutually exclusive and a bird that did not find a mate in its natal colony could also be more attracted to larger colonies.

Adult breeding dispersal is rare in the wandering albatross (Inchausti & Weimerskirch 2002). Mate fidelity is the rule and divorce rates are low even though pairs do not remain together during interbreeding periods. Bried, Pontier & Jouventin (2003) suggested that breeding site fidelity in procellariiforms allows mates to reunite at the beginning of each new reproductive season and to start reproduction earlier. However, nest site fidelity is low (29%) because nests disappear between seasons, and fidelity to the colony or to a restricted area surrounding the previous year's nest is sufficient for pair reunion. Under the mate reunion facilitation hypothesis, it can thus be predicted that breeding dispersal rates should be extremely low. Nonetheless, death of a partner is a factor that could promote breeding dispersal. Because albatrosses from different colonies forage in different areas at sea (Weimerskirch *et al.* 1993), they could be exposed to different mortality factors leading to colony-specific variations in survival rate, and hence breeding dispersal. Decisions to stay or to leave can also be based on previous self-reproductive performance or on the success experienced by conspecifics (Danchin & Wagner 1997).

We modelled dispersal rates and recruitment among three colonies of wandering albatrosses at Île de la Possession, Crozet Islands, and tested several hypotheses about natal

and breeding dispersal. Estimation of dispersal in long-lived animals is difficult because it requires taking into account the detection probability of individuals. The spatial recruitment model of Lebreton *et al.* (2003) is a multistate model that allows simultaneous estimation of natal dispersal, breeding dispersal and age-dependent recruitment, while controlling for detection probability. However, breeding in the wandering albatross is biennial as birds always skip breeding the year immediately following a successful nesting attempt. They are absent from the colony because care of young lasts nearly a full year and individuals must balance their energy allocation to reproduction and body maintenance (including moult) over a 2-year period. To properly model biennial reproduction, we modified the Lebreton *et al.* (2003) model to include unobservable states (Converse *et al.* 2009; Hunter & Caswell 2009). This approach also allowed us to estimate the proportion of adults that reproduce following a sabbatical year, which depends on their breeding success in the previous reproductive episode.

Using this novel approach, we examined the following hypotheses. First, we evaluated if colony fidelity, breeding dispersal and natal dispersal were asymmetric among colonies, and if differences in survival rate among colonies or colony size could explain dispersal movements. We predicted that adult dispersal should be highest in colonies with the lowest survival rate due to pair-bond breakage resulting from mortality, and that breeding and natal movements should be most frequent from the smallest to the largest colonies. Secondly, we evaluated if the probability of dispersing was dependent upon previous reproductive success. We predicted that adults should be more likely to disperse after a failed breeding attempt than after a successful one.

Materials and methods

STUDY SPECIES AND AREA

The wandering albatross nests on sub-Antarctic islands throughout the Southern Ocean. The earliest age of first reproduction is 5 years, and 9–10 years is an average age at first reproduction (Weimerskirch, Brothers & Jouventin 1997; Gauthier, Milot & Weimerskirch in press). Birds return to the breeding grounds in December and females lay a single egg in January. Chicks are reared by both parents and most young fledge in November when parents have progressively reduced chick attendance. There is no post-fledging care. Therefore, individuals that successfully rear a chick do not attempt to breed 2 years in a row but individuals that lose their egg or chick early in season may breed in the following year (Tickell 1968).

The study was conducted at Île de la Possession in the Crozet Islands, Southern Indian Ocean. On the island, wandering albatrosses nest in three distinct colonies along the coast: *Pointe Basse*, at the north-west end of the island, *Baie du Marin* at the eastern end, and *North-east Coast*, which included several loose aggregations along the north eastern coast. The latter aggregations of birds were grouped together because the number of birds in each aggregation was small. The colonies *Baie du Marin* and *North-east Coast* were separated by < 1 km but *Pointe Basse* was 8 km from the nearest colony. During the study period, the number of nests each year ranged from 125 to 250 at *Pointe Basse*, 45 to 80 at *Baie du Marin* and 70 to

200 at the *North-east Coast* colony. Annual breeding success was similar among colonies ($72.0 \pm 5.6\%$, $75.0 \pm 8.6\%$ and $75.2 \pm 6.9\%$ of nests produced a chick, respectively).

DATA COLLECTION

Adult and young albatrosses were marked with metal leg rings at the nest (see Weimerskirch *et al.* 1997 for details). Observations of marked individuals at the nest occurred every year by systematically walking each colony several times after egg laying, noting all ringed birds resighted and the status of the nest (with egg, with chick or failed). The programme started in 1966 but for this study we used data from 1969 to 2004 (36 years). Breeding attempts were classified as either successful (a young fledged), unsuccessful or unknown. During the last 20 years of the programme, individuals with unknown success were rare (< 5%) but not in earlier years (up to 50% in some years). Because we had to make a decision about the cases of unknown success for modelling purposes, these were pooled with the unsuccessful attempts, which mean that the latter category was heterogeneous because it included some successful attempts. Sex was not included in the analyses because it was unknown for many individuals.

THE MODEL

Our multistate model is an extension of the spatial recruitment model of Lebreton *et al.* (2003). Because of the size of our long-term data set and the large number of parameters in the model, we proceeded in two steps for the analysis. First, we used only adults to model adult breeding dispersal. Secondly, we included young to model natal dispersal and recruitment.

Adult model

We summarized the life cycle of adult wandering albatrosses in four stages following Hunter & Caswell (2009): (i) successful breeders (SB): individuals that fledged a young in the current year; (ii) failed breeders (FB): individuals that attempted to breed but failed to fledge a young; (iii) previous successful breeders (PSB): non-observable individuals that were successful at their last breeding attempt; and (iv) previous failed breeders (PFB): non-observable individuals that failed at their last breeding attempt (Fig. 1). These four stages were replicated at each of the three colonies and thus the adult model had 12 states according to breeding status and breeding location. A multistate model includes parameters S , the probability of apparent survival, p , the probability of capture (resightings in our case) and ψ , the probability of transition among states. Although movements among colonies on Île de la Possession were accounted for, permanent emigration to more distant colonies, though rare (Milot 2009), were confounded with losses to mortality. We structured the transition matrix ψ as a series of submatrices for transitions among colonies due to dispersal movements nested within each breeding stage (see Gauthier *et al.* in press for details). Because individuals do not breed in the year following a successful breeding attempt, the transition from SB to PSB was fixed to 1. Probabilities of capture of unobservable stages (PSB and PFB) were fixed to 0.

Young and adult model

When young were included in the model, we added one additional state for each of the three colonies, pre-breeding, PB, and m age classes among pre-breeders (Fig. 1). We can define two ages, c , the mini-

mum age at which recruitment can occur, and m , the age at which recruitment probability can be considered constant for all subsequent ages. We fixed c at 5 and m at 10 based on Gauthier *et al.* (in press). However, this resulted into a model with 15 states and 10 age classes, which had too many parameters to run on our computers due to lack of memory. Because of this limitation, we pooled colonies within the stages PSB and PFB in the young-adult model (Fig. 1). Although we lost some generality, the reduced number of states (11) allowed the model to run. Gauthier *et al.* (in press) explored the consequences of this simplification of the model on parameter estimates and found that while adult survival was still accurately estimated, some transitions from unobservable to observable states were not in adults. Thus, we report estimates of natal dispersal and young survival from this simplified model but breeding dispersal estimates were taken from the full adult model (Fig. 1).

We can estimate apparent survival of young from time of ringing to the earliest age at which individuals start to recruit (5 years) but not their annual survival because pre-breeders are non-observable. The 5-year survival rate of pre-breeders was estimated as a single parameter by fixing to unity survival for all time intervals between age 0 and 5 except the first interval. Once individuals reached the minimum age to recruit, we assumed that their survival was identical to that of adults whether they had recruited or not, because pre-breeders between age 5 and m were also unobservable.

DATA ANALYSIS

We performed goodness-of-fit tests for multistate models (Pradel, Wintrebert & Gimenez 2003) on the observable stages (SB and FB) of the combined young/adult data set using the software U-CARE 2.2.1 (Choquet *et al.* 2009). We calculated a variance inflation factor (\hat{c}) by dividing the sum of the chi-squared statistic of the relevant contingency tables by their degrees of freedom ($\hat{c} = 1.46$; see Gauthier *et al.* in press for details).

Our first analysis concentrated on the adults only, and combined individuals that were marked as adults or young but had recruited into the population. In the latter case, the initial marking as chicks was ignored and the first time that the individual was recorded breeding became the first encounter. This data set included 4090 individuals spanning 36 occasions of capture. In our most general model, capture probabilities varied among colonies, by breeding success (successful vs. failed breeders) and over time; survival varied among colonies, breeding success, breeding status (presence vs. absence at the colony) and according to a temporal trend; finally, transition probabilities differed among all states (i.e. colonies and breeding stages). For survival, we modelled a temporal trend because Weimerskirch *et al.* (1997) found evidence that survival increased in the 1970s and 1980s. We also used a quadratic term to account for the possibility that this trend may have levelled off in recent years. All effects on capture, survival and transition probabilities were interactive except the temporal trend on survival which was additive because there was no reason to believe that this trend could differ among colonies or by breeding status.

Fully parameterized models with unobservable states have identifiability problems (Lebreton *et al.* 2003; Hunter & Caswell 2009) and constraints must be applied to estimate parameters properly. We constrained parameters sequentially, starting with capture, then with survival and finishing with transition probabilities, the parameter of most interest. For capture and survival, we constrained parameters to be equal among groups (i.e. among colonies, breeding success or breeding status) or without temporal effects.

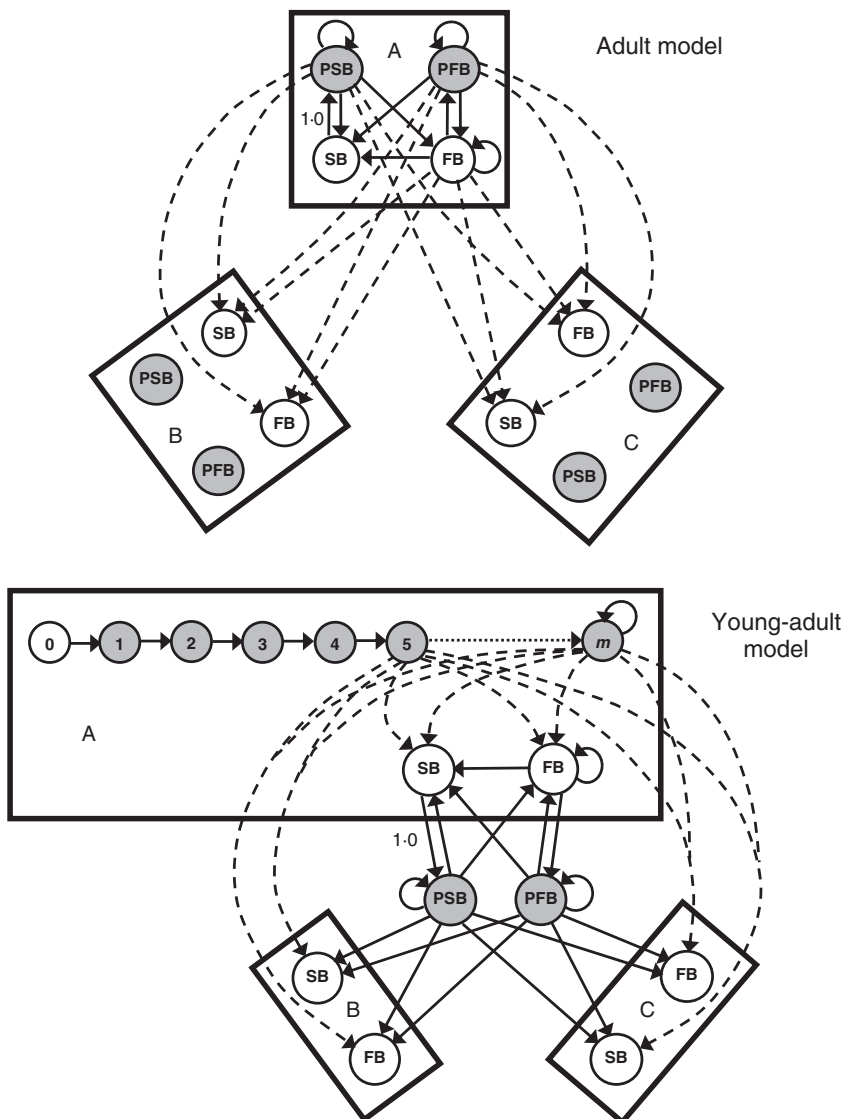


Fig. 1. Life cycle model structure of wandering albatrosses. Boxes represent the three colonies (denoted A, B and C), white circles are observable states and grey circles are unobservable states. Adult model: only state transitions within colony A (solid lines) and from colony A to other colonies (breeding dispersal; dashed line) are shown for sake of clarity but the same transitions apply to colonies B and C. SB, successful breeders; FB, failed breeders; PSB, previous successful breeders; PFB, previous failed breeders. Young-adult model: only recruitment and natal dispersal (stippled lines) for chicks born at colony A and adult state transitions of colony A (solid lines) are shown but the same transitions apply to adults and chicks born in colonies B and C. Numbers refer to age classes among pre-breeders and recruitment can occur at any age between age 5 and m (age at which recruitment probability becomes constant).

For transitions, we constrained parameters to be equal among states to test specific hypotheses. To determine if adult fidelity and breeding dispersal were asymmetrical among colonies, we fitted models where (i) fidelity was equal across colonies and (ii) dispersal was equal across colonies, considering separately the colony of departure and arrival, within each breeding stage. We could not test whether the probability of dispersing was dependent upon previous reproductive success by simple constraints in the transition matrix because states were a mixture of movements among colonies and breeding stages. To address this question, we summed ψ values corresponding to fidelity to a specific colony across breeding stages at arrival on each line of the matrix (e.g. for stage FB and colony A, we summed the ψ_{FB-SB}^{AA} , ψ_{FB-FB}^{AA} and ψ_{FB-PFB}^{AA} , where superscripts refer to the departure and arrival colonies and subscript refer to the departure and arrival breeding stages). We then averaged fidelity rates across the three colonies (i.e. across lines of the matrix) within each departure breeding stage, FB, PSB and PFB. This approach provided an overall estimate of average fidelity according to previous breeding success. The SEs of the derived parameters were calculated using the delta method (Seber 1982). We used the same approach to examine the overall probabilities of moving across breeding stages. In this case, we summed ψ values across arrival colonies (e.g. the ψ^{AA} , ψ^{AB} and ψ^{AC}

for the first line) and we averaged among the departure colonies [e.g. the $\psi^{A\bullet}$, $\psi^{B\bullet}$ and $\psi^{C\bullet}$, where $\bullet = (A + B + C)$], all within each breeding stage.

Our second analysis included individuals ringed as adults and all individuals ringed as chicks in the nest. Because of the large number of parameters to estimate in the time-varying model, we reduced the data set from 36 to 30 years (1975–2004), again due to computer limitations. This data set included 8346 individuals. We started the modelling process by using the second best model in the previous analysis (see Results). Because individuals were never recaptured in the pre-breeder stage after initial marking, capture probability of this stage was fixed to zero. In our most general model for this data set, survival of young varied among colonies and according to the same temporal trend as in adults; transitions within the PB stage, which represents natal dispersal, varied according to colony; finally, transitions from the stage PB to breeding stages SB or FB, which represents recruitment, were age-specific. As with adults, we modelled the survival of young first and then the transition probabilities. Survival estimates for the last five time intervals were ignored because no young ringed in the last five cohorts could have started to recruit by the end of the study. As in adults, we determined if natal dispersal was asymmetric among colonies by constraining

transition probabilities to be equal among either the departure of arrival colony.

All data analyses were conducted with the software M-SURGE 1.8 (Choquet *et al.* 2004). Because multistate models are prone to local minima during the likelihood maximization routine, we ran the same models three to six times with different starting values to ensure that each model converged to the lowest deviance. We selected models based on their QAIC value (i.e. AIC modified by a variance inflation factor) and their QAIC weights (Burnham & Anderson 1998). We did not use QAICc because sample size was large. Although a large number of reduced models were adjusted with each data set (especially for transition probabilities in the adult data set, where all possible combinations were tested), only the best fitting models or those relevant to the specific hypotheses tested are presented.

Results

ADULT SURVIVAL AND DISPERSAL

The model with the lowest QAIC retained full time, colony and breeding success effects on capture probabilities. These probabilities were quite variable during the first 15 years of the study, but less so over the following 20 years, the period during which most of the data came from. Capture probabilities were almost twice as high in successful than in failed breeders. From 1985 to 2004, mean annual capture rate for successful and failed breeders, respectively, were 0.971 (range: 0.704–1.0) and 0.518 (0.340–0.707) at *Pointe Basse*, 0.945 (0.745–1.0) and 0.556 (0.303–1.0) at *Baie du Marin*, and 0.896 (0.697–1.0) and 0.638 (0.333–1.0) at the *North-east coast*.

Among models with constraints on survival, the one with the lowest QAIC included a quadratic temporal trend, as well as colony and breeding success effects on adult survival (Table 1). Adult survival increased during the first half of the study period but eventually levelled off (Fig. 2). Survival was higher in successful than in failed breeders, and slightly higher at *Baie du Marin* than at the two other colonies. Over-

all, mean apparent survival ranged from 0.937 (SE = 0.004) to 0.948 (SE = 0.006) for successful breeders and from 0.907 (SE = 0.007) to 0.924 (SE = 0.010) for failed breeders depending on the colony.

We found strong evidence that both colony fidelity and breeding dispersal were asymmetric among the three colonies. In the top-ranked model, the probability of dispersal was equal among colonies for individuals after a failed breeding (stage PFB) but not for individuals in other stages (PSB or FB); however, the fit of the model with full colony effect on dispersal was close (QAIC weights = 0.469 vs. 0.293; Table 2). Colony fidelity was high at all colonies (Fig. 3), being comparable at the *Pointe Basse* (0.977) and *North-east Coast* (0.973) colonies but slightly lower at *Baie du Marin* (0.957). Dispersing individuals were twice as likely to move from either *Pointe Basse* or *Baie du Marin* to the *North-east Coast* than the reverse (Fig. 3).

Although the probability of movement varied among breeding stages and colonies (Table 2), fidelity to a colony

Table 1. Results of model selection of adult survival. For all models, capture probabilities depend upon time, colony and reproductive success and movement probabilities depend upon colony and reproductive status. Models are ranked in order of increasing QAIC values with respect to the model with the lowest QAIC value (in bold) and their QAIC weights (ω_i) among the set of candidate models

No.	Effect	Deviance	n_p	Δ QAIC	ω_i
1	$t(x) + t(x^2) + \text{colony}^*$ success	60 021.02	269	0.00	0.931
2	$t(x) + \text{colony}^* \text{success}$	60 032.51	268	5.90	0.049
3	$t(x) + \text{success}$	60 041.20	266	7.87	0.018
4	$t(x^2) + \text{colony}^* \text{success}$	60 041.65	268	12.18	0.002
5	Colony*presence	60 064.09	267	25.61	< 0.001
6	Colony*success	60 064.14	267	25.64	< 0.001
7	Colony*success*presence	60 064.38	267	25.80	< 0.001

n_p , number of parameters; $t(x)$, linear temporal effect; $t(x^2)$, quadratic temporal effect; success, reproductive success; presence, presence or absence at the colony.

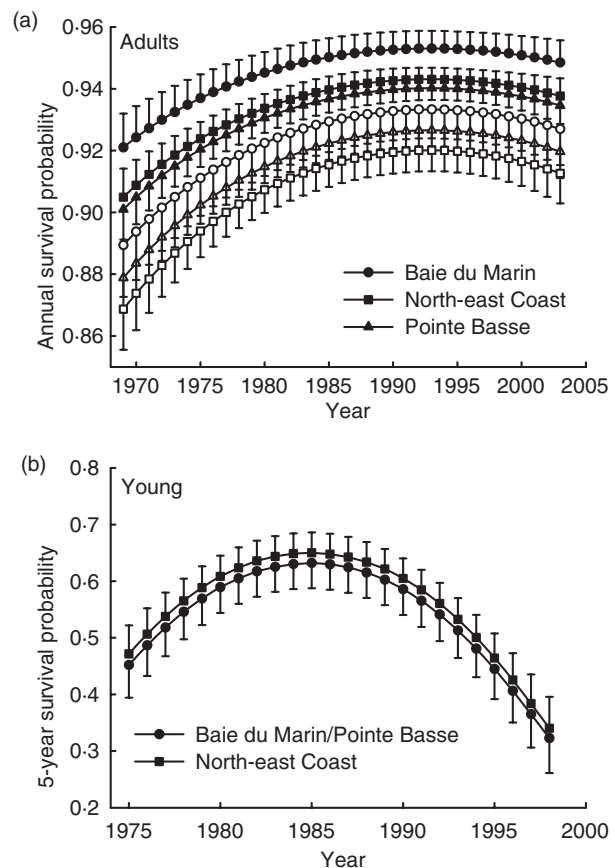


Fig. 2. Survival probability (mean with SE) of wandering albatrosses at three breeding colonies on Île de Possession, Crozet Islands. Adult annual survival (black dots, successful breeders; white dots, failed breeders) (a), and young survival from the year of marking at the nest until age at first recruitment (5 years; survival at *Pointe Basse* is indistinguishable from the one at *Baie du Marin*) (b). Survival probabilities are estimated from models with a quadratic effect (adults: Model 1 in Table 1; young, Model Y1 in Table 3). Note different scales for (a) and (b).

Table 2. Results of model selection of adult breeding dispersal and colony fidelity probabilities. For all models, capture probabilities depend upon time, colony and reproductive success and survival probabilities are according to the preferred model in Table 1. Models are ranked in order of increasing QAIC values with respect to the model with the lowest QAIC value (in bold) and their QAIC weights (ω_i) among the set of candidate models

No.	Dispersal	Fidelity	Deviance	n_p	Δ QAIC	ω_i
8	Equal among colony in PFB only	Colony*breeding status	60 040.02	262	0.00	0.469
1	Colony*breeding status	Colony*breeding status	60 021.02	269	0.94	0.293
9	Equal among arriving colony in PFB only	Colony*breeding status	60 039.48	263	1.63	0.208
10	Equal among departing colony in PFB only	Colony*breeding status	60 036.41	266	5.52	0.030
11	Colony*breeding status	Equal among colony in PSB and PFB	60 099.74	252	21.04	<0.001
12	Colony*breeding status	Equal among colony in PSB only	60 053.42	268	21.21	<0.001
13	Colony*breeding status	Equal among colony in FB only	60 059.25	268	25.21	<0.001
14	Colony*breeding status	Equal among colony in PFB only	60 064.36	268	28.73	<0.001
15	Colony*breeding status	Equal among colony in FB and PSB	60 086.12	264	35.68	<0.001

n_p , number of parameters; FB, failed breeders; PSB, previous successful breeders; PFB, previous failed breeders.

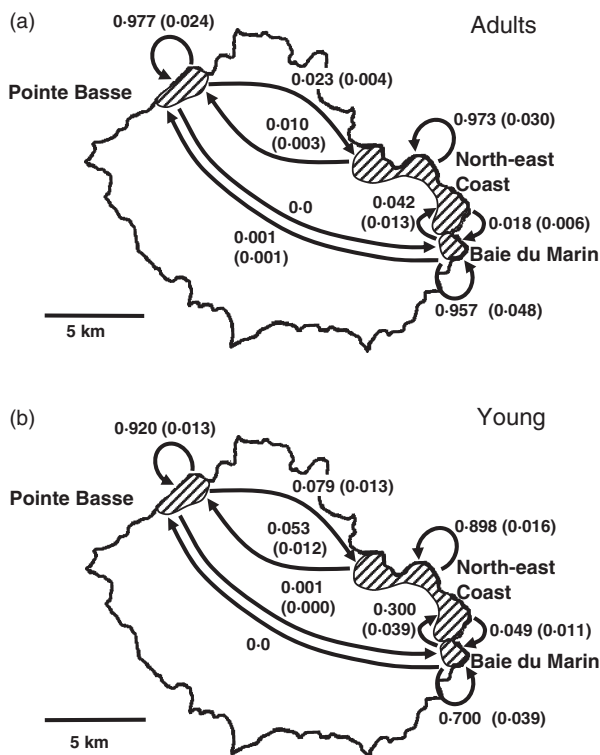


Fig. 3. Annual movement probabilities (mean with SE) of adult (a) and young (b) wandering albatrosses among three colonies of Île de Possession, Crozet Islands. Self loops returning to the same colony represent colony fidelity.

was not higher after a successful breeding (average fidelity, stage PSB: 0.956, SE = 0.025) than after a failed breeding attempt (average fidelity, stage FB: 0.974, SE = 0.032; stage PFB: 0.977, SE = 0.045). However, because breeding success was unknown for a high proportion of nests in the early years of the study and these nests were pooled with failed ones, we repeated the same analysis using only the last 20 years of the data set, when success was known for > 95% of the nests, to assess any possible bias. The results of this new analysis were identical to the previous one. Individuals

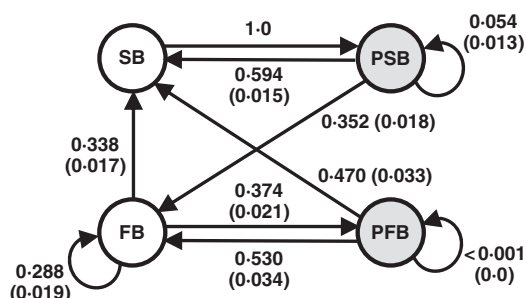


Fig. 4. Probability of moving among breeding stages for wandering albatrosses averaged across colonies (mean with SE). Probability of SB → PSB is fixed to 1.0. SB, successful breeders; FB, failed breeders; PSB, previous successful breeders; PFB, previous failed breeders. White circles are observable states and grey circles are unobservable states.

coming back from a sabbatical year after successful breeding were more likely to breed again successfully (0.594) than those coming back from a skip year after a breeding failure (0.470) or from a breeding failure in the previous year (0.338; Fig. 4). Sometimes, individuals that skipped a breeding year after a successful reproduction skipped again (0.054) but individuals never skipped breeding 2 years in a row after a failure.

YOUNG SURVIVAL AND DISPERSAL

For the adult component of the young-adult model (Fig. 1), we retained the constraints of Model 1 in Table 2. Although this was the second best model in that selection, it was similar in structure to Model 8 and it was more general with more parameters and a lower deviance. The lowest QAIC model for this data set included a quadratic temporal effect and a marginal colony effect on survival of young since the model without colony effect had a similar QAIC weight (0.511 vs. 0.486, respectively; Table 3). The 5-year apparent survival probability of young increased from 0.459 (SE = 0.050) in 1975 to 0.638 (SE = 0.036) in 1985 but decreased afterward to reach a low value of 0.329 (SE = 0.057) in 1998 (Fig. 2).

Table 3. Results of model selection of survival and natal dispersal probabilities of young. For all models, capture probabilities depend upon time, colony and reproductive success and adult survival and transition probabilities according to the preferred model in Table 1. Models are ranked in order of increasing QAIC values with respect to the model with the lowest QAIC value (in bold) and their QAIC weights (ω_i) among the set of candidate models

No.	Young survival	Natal dispersal	Deviance	n_p	Δ QAIC	ω_i
Y1	$t(x) + t(x^2) + \text{colony}$	Colony	79 125.43	139	0	0.511
Y2	$t(x) + t(x^2)$	Colony	79 134.32	136	0.10	0.486
Y3	Constant	Colony	79 155.85	134	10.90	0.002
Y4	Colony	Colony	79 155.50	136	14.66	< 0.001
Y5	$t(x^2) + \text{colony}$	Colony	79 150.07	138	14.93	< 0.001
Y6	$t(x) + \text{colony}$	Colony	79 154.40	138	17.90	< 0.001
Y7	Colony	Equal among arriving colony	79 306.70	132	110.58	< 0.001
Y8	Colony	Equal among departing colony	79 339.53	135	139.14	< 0.001

n_p , number of parameters; $t(x)$, linear temporal effect; $t(x^2)$, quadratic temporal effect.

Natal dispersal was colony specific because models where it was set equal among departing or arriving colonies had a much higher QAIC (Table 3). To test reduced models of natal dispersal, we had to ignore temporal variation in survival of young, otherwise models failed to converge. Natal philopatry was high for two colonies (0.920 for *Pointe Basse* and 0.898 for *North-east Coast*) but comparatively low for *Baie du Marin* (0.700; Fig. 3). Natal dispersal was generally higher among colonies that were closest to each others (*Baie du Marin* vs. *North-east Coast* and *North-east Coast* vs. *Pointe Basse*) than between more distant ones (*Pointe Basse* vs. *Baie du Marin*). The probability of dispersing from or to some colonies was asymmetrical: individuals born at *Pointe Basse* were 1.5 times more likely to move to the *North-east Coast* colony than the reverse (0.079 vs. 0.053) and those from *Baie du Marin* were six times more likely to move to the *North-east Coast* colony than the reverse (0.300 vs. 0.049).

Discussion

ADULT DISPERSAL AND SURVIVAL

Wandering albatrosses exhibited a very high fidelity to specific breeding colonies at Île de la Possession but it was not absolute because breeding dispersal was as high as 4% on one colony. The colony fidelity rates measured here (0.957–0.977) are among the highest reported in seabirds (Gaston *et al.* 1994; Lebreton *et al.* 2003; Cam, Cooch & Monnat 2005; Stenhouse & Robertson 2005). Nonetheless, considering that the average life span of an adult albatross is 16 years (based on an annual survival of 0.94) and that a bird may breed at least eight times during this period, then the probability that individuals will change colony at least once in their lifetime can be as high as 0.27 if we assume independence among events.

Because albatrosses have strong, long-term pair bonds, colony fidelity may be a by-product of mate fidelity (Bried *et al.* 2003) and the question of whether 'to stay or to leave' may be relevant only when a pair bond is broken. Indeed, among 200 individuals that changed colonies and whose partners were known, all birds also changed partners,

apparently because of mate loss in several cases. Therefore, we expected that asymmetry in fidelity among colonies could be explained by the observed differences in survival. However, contrary to our expectation, we found that the colony where fidelity was the lowest (*Baie du Marin*) was the one where adult survival was the highest. This result suggests that mate loss may not be the only factor involved in decisions to move. Other factors, such as dispersal movements following a divorce, may be sufficient to confound the relationship between survival and dispersal given the low dispersal rates.

Many studies have shown that past reproductive success influences breeding site selection in birds (Gauthier 1990; Switzer 1997; Hoover 2003). Contrary to our initial prediction, wandering albatrosses were not more likely to change colony after a failed breeding attempt than after a successful one, as found in some other colonial seabirds (Cam *et al.* 2004). This result could be due to the disconnection between local nesting habitat and food availability in albatrosses. In colonial seabirds, the reproductive success of neighbouring conspecifics may influence the dispersal decision of breeding individuals (public information hypothesis; Boulinier *et al.* 1996; Danchin & Wagner 1997). However, because the three colonies had similar breeding success, this factor could not really explain the asymmetry in dispersal among colonies. The opportunity to use public information is also more limited in the wandering albatross than in other species because, as pairs raise only one chick per breeding attempt, the amount of available information about the reproductive success may be less than in species with a larger clutch size. Moreover, nest cups are generally destroyed from one year to the next, regardless of the outcome of the breeding attempt. A cue which is perhaps more frequently used by seabirds is the presence of conspecifics. In Audouin's gulls (*Larus audouinii*), movement probabilities were higher from the smaller to the larger colonies although the larger colony also had a higher mean breeding success (Cam *et al.* 2004). In great cormorants (*Phalacrocorax carbo*), experienced breeders dispersed towards the largest colonies independently of mean breeding success at the colony (Henaux, Bregnballe & Lebreton 2007). However, the albatross colony that attracted most adult dispersers (*North-east Coast*) was not the largest

but the least dense and was in fact composed of many loose aggregations, which does not support the conspecific attraction hypothesis.

Adults returning after a breeding skip had more chances to breed successfully if their last breeding attempt was successful than if it was a failure, and the opposite was true if their previous attempt was a failure. The same result was found by Converse *et al.* (2009) in the grey-headed albatross (*Thalassarche chrysostoma*). Such pattern is expected if some individuals performed consistently better than others in terms of breeding success although other factors, such as breeding experience, may lead to the same result.

The temporal trends in apparent survival that we detected are consistent with previous analyses of this population using simple capture–recapture methods and are related to changes in by-catch mortality from long-line fishing (Weimerskirch & Jouventin 1987; Weimerskirch *et al.* 1997). The survival of successful breeders was 2–3% higher than that of failed breeder, a non-trivial difference for a species with a high survival rate such as the albatross. However, it is unclear if this is an effect of high-quality individuals experiencing both high breeding success and survival or because of the lengthy breeding cycle, which lasts up to a year (Weimerskirch & Jouventin 1987). Indeed, if an individual dies during the breeding season, this will lead to a breeding failure because a single parent is unable to raise a chick (Tickell 1968).

NATAL DISPERSAL AND SURVIVAL

Young wandering albatrosses were generally highly philopatric to their natal colony as found in other seabirds (Sagar, Stahl & Molloy 1998; Lebreton *et al.* 2003; Steiner & Gaston 2005; Van Bekkum *et al.* 2006). Nevertheless, the level of philopatry varied considerably among colonies (from 0.70 to 0.92). Because survival of young was controlled in the analysis and differed little among colonies, it cannot explain variation in philopatry, which indicates that some colonies were more attractive than others. The level of philopatry to a colony was correlated with colony size, as philopatry was highest for the largest colony (*Pointe Basse*), and lowest for the smallest one (*Baie du Marin*), suggesting that colony size may be a factor involved in decisions to stay or to leave. Settlement pattern of philopatric young thus supported the conspecific attraction hypothesis. Because the biggest colonies also have the largest pool of recruits, these colonies may offer greater prospects of finding a mate to young birds than smaller colonies. However, *Pointe Basse* was located at a farther distance than the other colonies, and thus isolation may also have favoured a higher philopatry at this colony. Finally, because *Baie du Marin* is located near the only human settlement on Île de la Possession, birds nesting there may be more exposed to disturbance due to human activity. The latter may influence the decision of young settlers as breeding wandering albatrosses are sensitive to disturbance (Wheeler, deVilliers & Majiedt 2009).

Among individuals that dispersed from their natal site, movements were asymmetrical among colonies but, contrary

to the pattern found for philopatry, the largest colony did not attract most dispersers as the probability of movement was highest towards the *North-east Coast*, the intermediate size colony. Interestingly, this colony was also the one that attracted most adult dispersers. Due to its large area, the *North-east Coast* colony had the lowest density of nests (two to three times lower than the other colonies; Weimerskirch & Jouventin 1987), which suggests that density-dependent effects may limit to some extent the settlement of immigrants in the densest colonies. In kittiwakes (*Rissa tridactyla*), Coulson & Coulson (2008) found that, as the colony grew in size, it failed to attract proportionally as many recruits as it did when it was smaller. In great cormorants, first-time breeders recruited more to smaller colonies where they could expect better breeding success than in their natal colony (Henaux *et al.* 2007). Therefore, overall, we found only partial support for the hypothesis that the size of the colony played a role in the settlement pattern of recruits. Apparently, size of the colony influenced the decision to stay or to leave (i.e. philopatry) but among those that left the natal colony, density was more influential on the selection of a colony than size per se.

The increase in survival of young during the first half of the study was similar to the adults but, in contrast to them, young survival apparently declined since the late 1980s. The difference may arise because adults and pre-breeders forage in different areas, with the latter using subtropical waters where long-line fishing effort is the highest (Weimerskirch, Åkesson & Pinaud 2006). Even though not all cohorts of pre-breeders had fully recruited by the end of the study, this should not affect the estimation of their survival rate because we modelled recruitment and survival processes separately (R. Pradel, pers. comm.).

METHODOLOGICAL CONSIDERATIONS

The use of recent developments in multi-state models, including unobservable states to account for breeding skips, is an improvement over previous methods to study breeding and natal dispersal (Lebreton *et al.* 2003; Cam *et al.* 2005). We found that rates of movement of adult albatrosses among colonies were higher than previously reported (Weimerskirch & Jouventin 1987; Bried *et al.* 2006). Although we cannot exclude the possibility that movements increased over time, it is likely that the approach that we use allowed for a more accurate and robust estimation of movement rates. Nonetheless, these models still present some limitations due to necessary constraints, such as equality of survival among individuals that have recruited vs. those that have not (Reed *et al.* 2003; Cam *et al.* 2005) or of equality of survival between observable and unobservable states, which must be used to solve parameter identifiability problems (Hunter & Caswell 2009). The simplification of the adult component of our model to analyse natal dispersal was another potential weakness of our approach. However, Gauthier *et al.* (in press) concluded that natal dispersal estimates were probably not biased by this simplification even though transition probabilities from unobservable to observable states in adults were

poorly estimated in this formulation of the model. Future methodological developments should aim at alleviating the limitations of the models used in this study.

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