Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference

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Summary

1. There is widespread evidence that within populations, specialists and generalists can coexist and this is particularly prevalent in marine ecosystems, where foraging specialisations are evident.

2. While individuals may limit niche overlap by consistently foraging in specific areas, site fidelity may also emerge as an artefact of habitat choice, but both drivers and fitness consequences of site fidelity are poorly understood.

3. Here, we examine an individual metric of site and habitat fidelity, using tracking data collected over 11 years for black-browed albatrosses (*Thalassarche melanophris*). Fidelity was calculated as the similarity between pairs of foraging zones, quantifying measures for within and between years. Foraging areas were identified using area-restricted search, defined as periods during which birds decrease speed and increase turning.

4. Our results demonstrate that birds were considerably more specialised in the habitat in which they forage than the exact location they use within years, and there was a similar pattern between years. However, despite this, it was site fidelity that explained reproductive success. Within a single year, females which were more faithful to a specific location had higher reproductive success than non-specialists, and between years there was a tendency for both sexes.

5. Our results suggest that black-browed albatrosses are highly faithful in their foraging habitat but it is rather site fidelity that is more clearly associated with reproductive success.

Key-words: black-browed albatross, foraging niche width, generalist, intra-individual variability, seabirds

Introduction

Individuals within populations can show extensive niche variation, leading to ecologically significant differences in resource use (Bolnick *et al*. 2003, 2011; Araújo, Bolnick & Layman 2011). A large body of this work has focused on diet and foraging behaviour, revealing that individuals differ in their degree of specialisation or variability in traits (reviewed by Bolnick *et al*. 2003). Spatial site fidelity is a specific type of niche segregation, whereby individuals show two-dimensional habitat partitioning (Switzer 1993; Piper 2011). While individuals gain information from previous experience and may use this to select future sites (Zach & Falls 1979; Cain, Gerin & Moller 1994; Shanks

2002; Brown, Brown & Brazeal 2008; Piper 2011), competition at the population level may drive individual divergence in space use, resulting in specialisation or site fidelity (Birt *et al*. 1987; Bolnick *et al*. 2003). However, the proximate cues individuals use to develop and maintain site fidelity, and its associated fitness consequences, are not well understood (Piper 2011).

The emergence of site fidelity, where individuals repeatedly visit the same location, can be explained by three main hypotheses (Switzer 1993). First, if resources are spatiotemporally correlated, a 'win-stay, lose-shift' tactic should be optimal (Switzer 1993; Schmidt 2001; Piper 2011; Spencer 2012), such that site fidelity is associated with prior success. Second, populations may be made up of a series of specialists, all of whom benefit from decreased competition through niche partitioning and

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have equal fitness at equilibrium (Roughgarden 1974; Wilson & Yoshimura 1994). Finally, individuals may display varying levels of site fidelity, with generalists and specialists coexisting in the population as the diversity in foraging tactics could itself reduce niche overlap or be under fluctuating selection (Roughgarden 1974; Wilson & Yoshimura 1994). Empirical studies attempting to test these hypotheses are needed and require estimates of the fitness consequences of site fidelity to disentangle them.

While density-dependent selection may drive spatiotemporal partitioning of niches, site fidelity can also arise as a consequence of habitat choice if prey are highly clumped. Individual resource or habitat choice in heterogeneous landscapes will be associated with spatial consistency if prey distribution is predictable (Switzer 1993; Barraquand & Benhamou 2008). Habitat selection and space use can be decoupled as fidelity to habitat type can occur both by returning to the same location (=site fidelity) within a year and/or between different years, and using a variety of locations with the same habitat conditions. Therefore, examining the persistent use of space and habitat simultaneously is necessary to understand the mechanisms through which site fidelity emerges.

Individual-level foraging site fidelity has been widely reported in the marine environment (Patrick *et al.* 2014; Ceia & Ramos 2015), perhaps owing to the advent of biologging devices which provide abundant high-resolution spatial data (Ropert-Coudert & Wilson 2005). There is now a large body of work demonstrating that individual seabirds show short-term consistent spatial movements (reviewed by Patrick *et al.* 2014; Ceia & Ramos 2015), and this has been supported by evidence of consistent habitat use (Patrick & Weimerskirch 2014a; Patrick *et al.* 2014; Wakefield *et al.* 2015). However, most of these studies have examined population consistency in site fidelity (i.e. repeatability; Nakagawa & Schielzeth 2010). Individual behavioural specialisation, a behavioural analogue to dietary specialisation (Dall *et al.* 2012), where individuals each have a value of variability, has rarely been considered in seabirds (but see Potier *et al.* 2015; Wakefield *et al.* 2015), and as such, the stability of these behaviours over time is also poorly understood. A recent study examined habitat and space use within and between years in individual gannets and revealed high site fidelity but little habitat fidelity across breeding seasons (Wakefield *et al.* 2015). This is one of the first studies to examine site and habitat fidelity across breeding seasons, which is important to decouple the effects of short-term persistence of prey patches and genuine specialisation at the individual level. While hot spots of productivity may persist between years, the winter migration of birds ensures that there are changes in behaviour throughout the winter. As a result, a consistent behaviour between seasons provides a stronger test of intrinsic differences in fidelity. Second, this study raises interesting questions surrounding the individual fitness consequences of such fidelity. Therefore, using biologging data collected over 11 years, with repeated observations from individuals within and between years, we measured the level of site and habitat fidelity and linked this to reproductive success over time. From this, we make the following predictions:

- Birds will differ in the level of fidelity, demonstrating the existence of specialists and generalists.
- Fidelity will be stronger within years, but with individual ranked differences persisting between years.
- Site and habitat fidelity will be strongly correlated and equally strong within individuals.
- Generalists and specialists will persist in the population due to niche segregation as they have equal reproductive success within and between years.

Materials and methods

STUDY SPECIES

This study was conducted at Cañon de Sourcils Noirs, Kerguelen Islands (48·4°S, 68·4°E). Black-browed albatrosses (*Thalassarche melanophris*) are known to be highly susceptible to environmental conditions and persistently use the shelf region to forage during chick brooding (Weimerskirch, Mougey & Hindermeyer 1997; Cherel, Weimerskirch & Trouve 2000; Patrick & Weimerskirch 2014a,b). Given the shelf edge surrounds this island and space and habitat do not vary linearly (Fig. S1, Supporting Information), this offers an ideal test of the respective importance of habitat and site fidelity. Black-browed albatrosses are annual breeders, with strong monogamous pair bonds. They commence breeding in October, with chicks hatching in late December. The pair shares both incubation and provisioning roles and brood the chick for around 3–4 weeks. This colony has been studied since 1967, and all adults and chicks in the study population are ringed with a unique metal band. This allows individuals to be monitored across their lifetime. Nests are checked in early April for fledging success and fledglings ringed. From these successive controls of nests, reproductive success is calculated.

DATA COLLECTION

Between December 2004 and February 2015, adult black-browed albatrosses were equipped with miniaturised GPS loggers (Technosmart GPS, Igot U 120 or 600) during chick brooding. These devices weighed between 20 and 35 g, which is less than 2% of the mean black-browed albatross body mass of 3740 ± 450 g (Weimerskirch, Zotier & Jouventin 1989), and there was no evidence of any effect on reproductive success or survival (S. Patrick, unpublished data). Adults were caught on the nest, and the device was attached to their lower back feathers with Tesa tape. The devices recorded positional data every 2 min and were left on the birds for up to 3 weeks. Birds were selected at random initially, and then, since 2011, birds which had been tracked previously were targeted (17 individuals). In total, 61 (40 male; 21 female) individuals were used in the within-year comparison and 17 (15 male; 2 female) in between-year comparisons.

QUANTIFYING BEHAVIOUR

Albatrosses use area-restricted search (ARS) to locate prey, and these areas are associated with searching and prey capture

(Pinaud & Weimerskirch 2005, 2007; Weimerskirch *et al.* 2007). We used this method to identify areas with a high probability of representing foraging zones, as this species has rapid commuting behaviour followed by intense searching (Pinaud & Weimerskirch 2005, 2007; Weimerskirch *et al.* 2007). ARS zones were identified using peaks in first passage time (FPT). First, all points where birds were sitting on the water were removed using a speed filter (<10 km h^{-1}), as birds cannot actively search for food when on the water, and tracks were spatially interpolated so all points were 1 km apart. First passage time is the time taken to travel across a circle of given radius, and peaks in FPT show changes from straight to tortuous movement (full details can be found in Fauchald & Tveraa 2003). We estimated FPT using circles of varying radii (2–200 km) and identified the scale at which maximum FPT occurred. Once this scale had been identified, segments were identified using Lavielle segmentation (Barraquand & Benhamou 2008) implemented in the R package adehabitatLT (Calenge 2006). This divided each track into periods of ARS and non-ARS. Location data were extracted from each zone of ARS. For each period of ARS, we identified a central point, based on time, and extracted the longitude and latitude of this point and a measure of bathymetry at this point (depth, metres). Bathymetry is an important predictor of habitat choice in this species (Waugh *et al.* 1999; Wakefield *et al.* 2011) and more widely in seabird species in general (Bost *et al.* 2009). This is thought to be because changes in slope of the ocean floor create upwellings, associated with peaks in productivity and hence prey abundance (Constable, Nicol & Strutton 2003).

We used fledging success values from 2004 to 2015 as a measure of reproductive success for each bird. All reproductive success measures per year are binary estimates of chick fledging. For within-year analyses, this measure was used for the specific year. For between-year measures, we used an average reproductive success between 2004 and 2015, which estimates to a Gaussian distribution. The sex of at least one pair member was determined using genetic sexing.

STATISTICAL ANALYSES

For all ARS zones, we calculated an estimate of similarity, in both space and depth, with all other ARS zones (hereafter 'zones') from the same bird, and the wider population. This was performed in a pairwise fashion, examining two zones from the same individual ('focal zone' and 'paired zone') and calculating the distance between these two locations (site) and the difference between the depth at these locations (habitat). This was then repeated, calculating a difference (distance or depth) between the focal zone and all other zones for the 'population'. For an individual, 'paired zones' were as follows: (i) within-year estimate: a focal zone and any zone used by the same individual during that year from a different foraging trip, and (ii) between-year estimate: a focal zone and any zone by the same individual in a different year. The 'population' zones were (i) within-year estimate: all zones for all birds that year, and (ii) between-year estimate: all the zones for all birds in the year of the paired zone. For example, if we compared bird 1's zone in 2011 with one in 2013, the population zones were taken from the 2013 data set. This was repeated for all pairs of zones for an individual (Figs S2 and S3), creating a similarity index for each. Each zone was used in turn as the focal zone. The similarity index was then the proportion of zones at the population level that were more similar than the two from the same individual. Low values represent individuals that are similar to themselves and hence specialised

or faithful, and this method is an adaptation of a nearest-neighbour analysis (Freeman *et al.* 2011; Guilford *et al.* 2011).

As there were multiple measures of similarity per individual (one per pair of zones), an individual measure of similarity was estimated using a general linear model. For example, if a bird had three ARS zones, there would be six similarity indices (two comparisons per zone). We fitted a binomial GLM with Individual ID as a fixed effect, to allow parameter estimates used as a single individual similarity index. Parameter estimates are considered to be better estimates of individual behaviour than best linear unbiased predictors which can be extracted from general linear mixed models (Hadfield *et al.* 2010), and parameter estimates are regularly used in other fields of behavioural ecology (Quinn *et al.* 2009; Patrick & Weimerskirch 2014a).

Short- and long-term fidelity

We examined the strength of site and habitat fidelity by examining the similarity indices within (short-term) and between (long-term) years separately, and we present the range and median in the results. To determine whether birds were more specialised in habitat or space, we subtracted the spatial fidelity index from the habitat fidelity index and used t-tests to examine whether this was different from zero. An individual with a positive score is likely to be more habitat faithful, while individuals with negative scores are more site faithful. We also estimated the correlation between site and habitat fidelity to examine whether birds that were more site faithful were also more faithful in habitat choice. To look at the effect of sex and age on fidelity, we fitted (i) within-year site fidelity, (ii) within-year habitat fidelity, (iii) between-year site fidelity and (iv) between-year habitat fidelity as response variables, with age, sex and the interaction (where possible) between these as fixed effects in a GLM with a Gaussian error distribution.

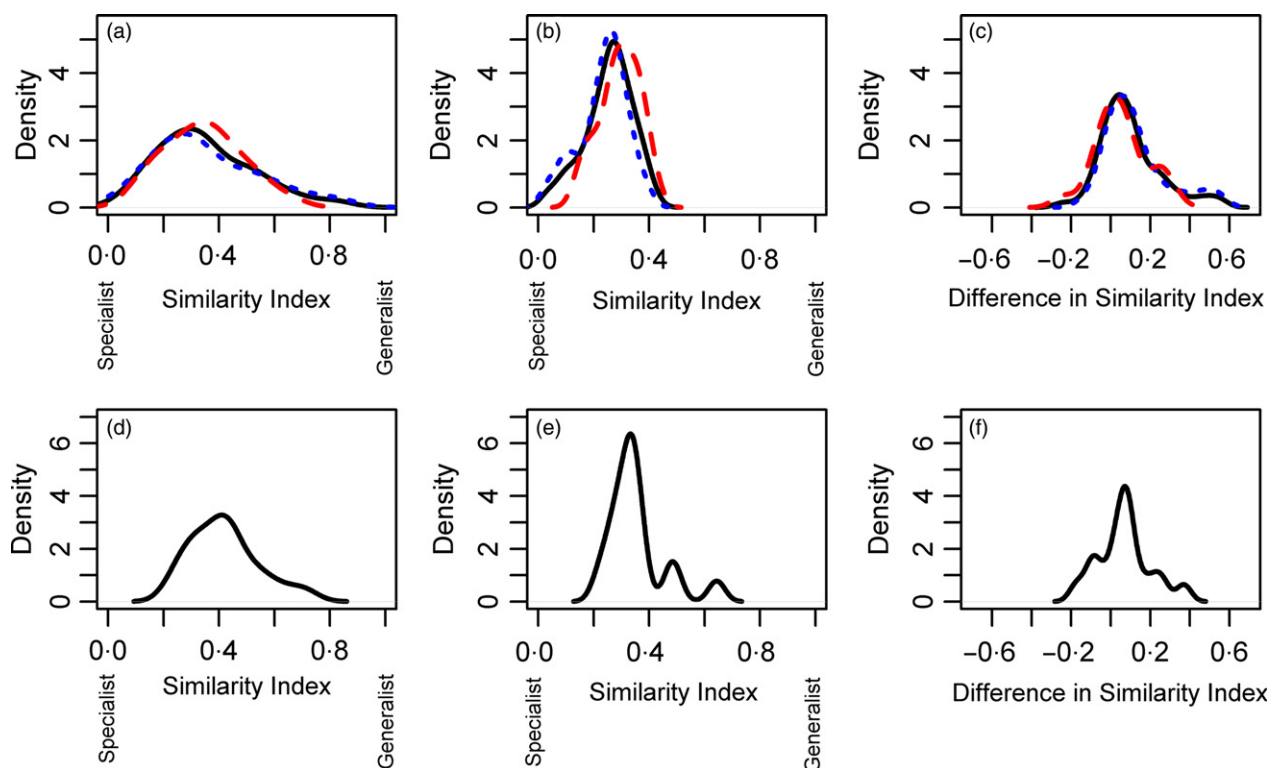### Short- and long-term fitness consequences

To examine the consequences of fidelity on reproductive success, we fitted reproductive success as the response variable with a binomial or Gaussian error distribution. (i) Within-year site fidelity, (ii) within-year habitat fidelity, (iii) between-year site fidelity and (iv) between-year habitat fidelity were fitted as fixed effects. We also fitted the interaction between these metrics and both age and sex. For the between-year analysis, there were insufficient data to fit interactions.

ANOVA model comparisons were used to compare models with and without the term of interest. All not statistically significant first-order interactions were dropped for models, but all fixed effects were maintained.

Results

SHORT-TERM FIDELITY: ARE BIRDS SITE AND HABITAT FAITHFUL?

Within a single year, birds were very variable in the level of site fidelity (range: 0·04–0·82; median = 0·32; Fig. 1a), but habitat fidelity was high (range: 0·03–0·42; median = 0·27; Fig. 1b). In total, 75% (45 of 60) of birds had stronger habitat than site fidelity ($t = 4·97$; d.f. = 60; $P < 0·001$; Fig. 1c). Within years, the site fidelity and habitat fidelity were correlated ($r = 0·46$; $P < 0·001$; Fig. 2a).

Fig. 1. The degree of site and habitat fidelity between and within years. (a) The level of site fidelity within years, where 0 = highly faithful. (b) The level of habitat fidelity within years, where 0 = highly faithful. (c) The frequency of birds that are more faithful in habitat use (positive) than site fidelity (negative) within years; $N = 61$; male $N = 40$; female $N = 21$. (d) The level of site fidelity between years, where 0 = highly faithful. (e) The level of habitat fidelity between years, where 0 = highly faithful. (f) The frequency of birds who are more habitat faithful (positive) than site faithful (negative) between years, $N = 17$. Males are shown in dotted lines (blue in colour version) and females in dashed lines (red in colour version), when displayed, and the whole population in a solid black line. [Colour figure can be viewed at wileyonlinelibrary.com]

There was no evidence of an interaction between age and sex on the degree of site fidelity ($\chi^2_1 = 0.02$; $P = 0.39$), nor an effect of age ($\chi^2_1 = 0.07$; $P = 0.12$) or sex ($\chi^2_1 = 0.01$; $P = 0.52$). We also found no interaction between age and sex on habitat fidelity ($\chi^2_1 = 0.03$; $P = 0.46$) nor age ($\chi^2_1 = 0.01$; $P = 0.19$). However, males showed stronger habitat fidelity than females ($\chi^2_1 = 0.04$; $P = 0.02$; females: 0.26 ± 0.03; males: 0.20 ± 0.03).

LONG-TERM FIDELITY: ARE BIRDS SITE AND HABITAT FAITHFUL?

Between years, birds again showed a greater range of site fidelity (range: 0.25–0.71; median = 0.42; Fig. 1d), whereas habitat fidelity was consistently strong (range: 0.22–0.64; median = 0.34; Fig. 1e). In total, 76% (13 of 17) of birds had stronger habitat fidelity which is similar to results from within-year analysis ($t = 2.05$; d.f. = 16; $P = 0.057$; Fig. 1f). However, site fidelity and habitat fidelity were not strongly correlated between years ($r = 0.30$; $P = 0.25$; Fig. 2b), showing that birds which were site faithful did not also have high habitat fidelity. We found no sex effects on site ($\chi^2_1 = 0.00$; $P = 0.96$) nor habitat fidelity ($\chi^2_1 = 0.00$; $P = 0.96$). There were also no age

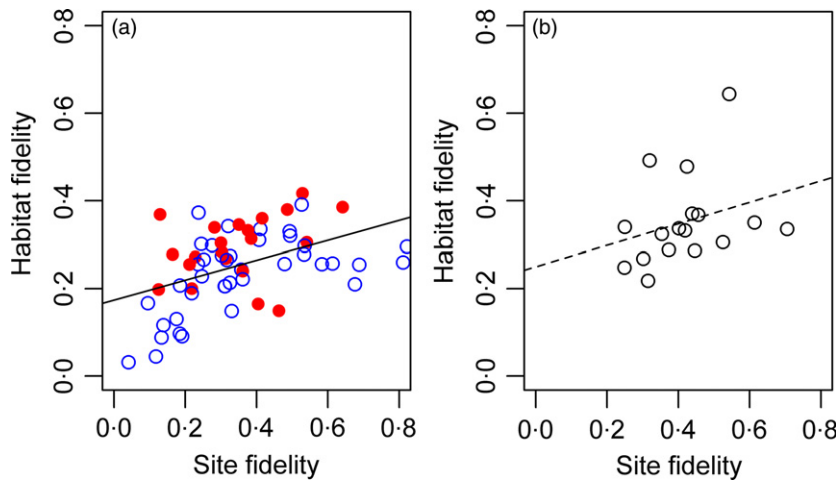effects on site ($\chi^2_1 = 0.01$; $P = 0.46$) or habitat fidelity ($\chi^2_1 = 0.00$; $P = 0.58$).

SHORT-TERM FITNESS CONSEQUENCES: DOES SITE OR HABITAT FIDELITY PREDICT REPRODUCTIVE SUCCESS?

There was an interaction between sex and within-year site fidelity on reproductive success ($\chi^2_1 = 4.27$; $P = 0.039$; Fig. 3a), which suggests that being site faithful was correlated with higher reproductive success in females, with a weaker effect in males. There was no interaction between site fidelity and age ($\chi^2_1 = 0.80$; $P = 0.37$), but older birds had higher reproductive success ($\chi^2_1 = 5.05$; $P = 0.025$).

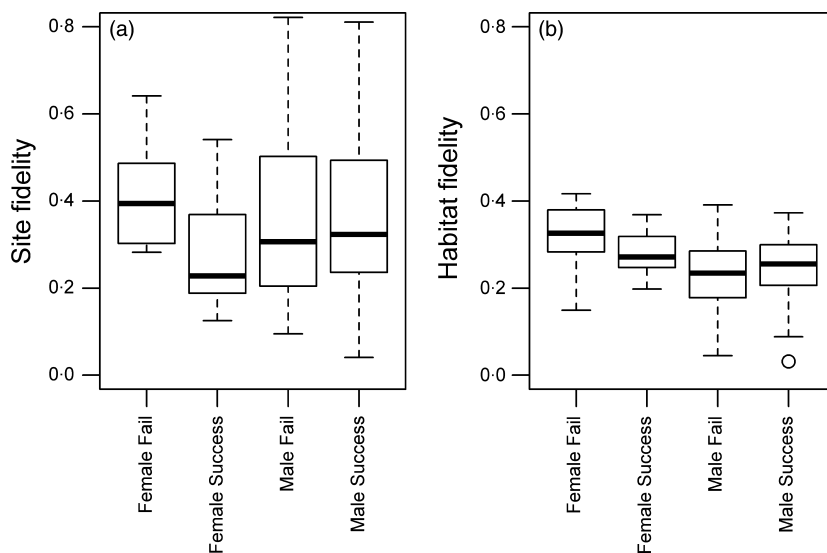There was no interaction between within-year habitat fidelity and sex ($\chi^2_1 = 0.69$; $P = 0.41$; Fig. 3b), nor habitat fidelity and age ($\chi^2_1 = 0.00$; $P = 0.96$) on reproductive success. Sex did not affect reproductive success ($\chi^2_1 = 2.78$; $P = 0.10$), nor did habitat fidelity ($\chi^2_1 = 0.26$; $P = 0.61$), but as reported above, older birds had higher reproductive success ($\chi^2_1 = 4.28$; $P = 0.039$).

The positive correlation between within-year site and habitat fidelity was found in both unsuccessful ($r = 0.55$;

Fig. 2. The correlation between site and habitat fidelity. (a) There is a linear relationship between site and habitat fidelity within years. Males are shown in open circles (blue in colour version) and females in solid circles (red in colour version), $N = 61$. (b) Between years, there is no correlation between fidelity in habitat and space, and both sexes are shown in open circles (black in colour version), $N = 17$. We have included a line on our correlation plots to show the direction of the relationship. This is solid for a statistically significant correlation and dashed when the correlation is not detectable. [Colour figure can be viewed at wileyonlinelibrary.com]

Fig. 3. The fitness consequences of within-year site and habitat fidelity. (a) Within years, there is little evidence of an effect of site fidelity on male fitness; however, more site-faithful females had considerably higher fitness. (b) Within years, there is no evidence of an effect of habitat fidelity on male or female fitness. Individuals are divided into failed female breeders (female fail, $N = 10$), successful female breeders (female success; $N = 11$), failed male breeders (male fail; $N = 12$), successful male breeders (male success; $N = 28$). While reproductive success was the response variable in these models, for clarity, we used boxplots to show the difference in site fidelity among these groups.

$t = 2.96$; d.f. $= 20$; $P = 0.008$; Fig. 4a) and successful birds ($r = 0.39$; $t = 2.56$; d.f. $= 37$; $P = 0.015$; Fig. 4b).

LONG-TERM FITNESS CONSEQUENCES: DOES SITE OR HABITAT FIDELITY PREDICT REPRODUCTIVE SUCCESS?

Site fidelity between years had a tendency to affect average reproductive success ($\chi^2_1 = 0.08$; $P = 0.056$; Fig. 5a), but sex ($\chi^2_1 = 0.04$, $P = 0.21$) and age did not ($\chi^2_1 = 0.01$, $P = 0.46$). Habitat fidelity did not have a detectable effect on average reproductive success ($\chi^2_1 = 0.05$, $P = 0.15$; Fig. 5b) nor did sex ($\chi^2_1 = 0.04$, $P = 0.21$) or age ($\chi^2_1 = 0.04$, $P = 0.21$).
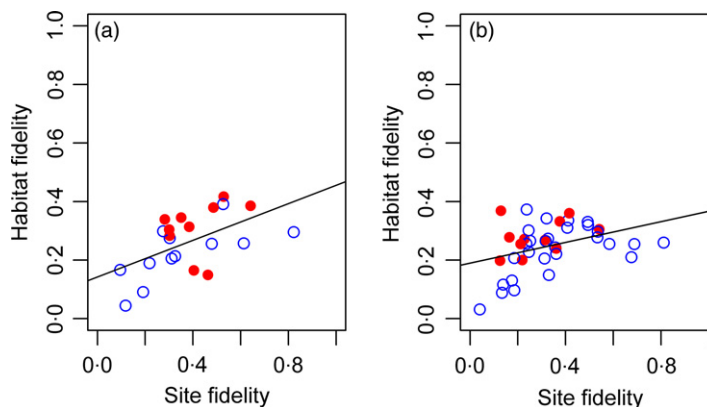
Discussion

In this study, we show that black-browed albatrosses are more specialised in the habitat in which they forage than the geographical area they use. This result

was strong within years, with a tendency between years. Despite this, it was site fidelity that correlated with differences in reproductive success, with more specialised birds having higher reproductive success within years, with a tendency between years. Interestingly, it was females, who are often suggested to be less competitive than males because of their smaller size (Weimerskirch *et al.* 1993), that appeared to benefit most from site fidelity within years. Together, these results suggest that although black-browed albatrosses are highly faithful in the habitat that they use, it is site fidelity that is associated with increased reproductive success.
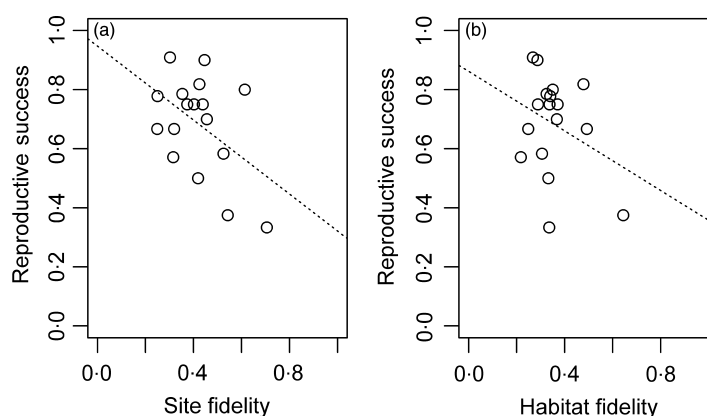
DO BIRDS SHOW STRONG FIDELITY AND HOW DOES THIS DIFFER IN THE SHORT AND LONG TERM?

In keeping with our prediction, birds varied in both their level of site and habitat fidelity. We showed that fidelity was stronger within years, but did persist between years.

Fig. 4. The within-year correlation between site and habitat fidelity between (a) unsuccessful ($N = 22$) and (b) successful ($N = 39$) birds. Males are shown in open circles (blue in colour version) and females in solid circles (red in colour version). We have included a line on our correlation plots to show the direction of the relationship. This is solid for a statistically significant correlation and dashed when the correlation is not detectable. [Colour figure can be viewed at wileyonlinelibrary.com]

Fig. 5. (a) Between years, we found across both sexes a tendency for more site-faithful birds to show a fitness advantage. (b) Between years, we found across both sexes no fitness advantage of habitat fidelity, $N = 17$.

Our results support previous single-year studies on albatrosses (Patrick & Weimerskirch 2014b), having shown that individuals differ in their level of site fidelity. We could demonstrate that this pattern also persists between breeding seasons, and this suggests that our studied albatross population is not composed of a series of site-faithful specialists with different niches (Bolnick *et al.* 2003), but instead individuals that vary in their degree of fidelity (Wilson & Yoshimura 1994). However, the extent of site and habitat fidelity differed. The individuals least faithful to their habitat were still twice as faithful as the least site-faithful individuals, suggesting that niche segregation may drive stronger habitat fidelity. This may emerge if competition for habitats is stronger than that for space.

WHY ARE BIRDS MORE SPECIALISED IN HABITAT USE?

Contrary to our prediction, birds were more faithful in the habitat they used than the site. The lack of habitat generalists suggests that the costs involved (i.e. jack of all trades, master of none; MacArthur 1972) make this tactic maladaptive (Bradshaw 1965; Vantienderen 1990). While this is often explained by environmental heterogeneity, our study specifically used static environmental proxies

for habitat to allow a comparison independent of temporal variability. Constraints on adaptations may limit the emergence of generalist habitat strategies (Vantienderen 1990), for example if birds are constrained to forage under specific habitat conditions, as a function of prey choice. Black-browed albatrosses are known to forage on very diverse prey, and there is some evidence of spatial segregation in prey types (Cherel, Weimerskirch & Trouve 2000). Individuals seeking specific prey may lead to high habitat fidelity if these prey can be found in different places with similar depth profiles. Stable isotope studies in other species have shown strong dietary specialisation in seabirds (Bearhop *et al.* 2006; Patrick *et al.* 2014; Ceia & Ramos 2015), which would only be associated with space use if prey are abundant or highly clumped, whereas black-browed albatrosses feed extensively on squid, which are often patchily distributed (Cherel, Weimerskirch & Trouve 2000). These methods could also be used to improve our models of habitat type and the association between habitat and prey abundance. It is these direct links between prey and habitat type which may drive habitat fidelity, which combined with dynamic oceanographic features, could improve our understanding of seabird habitat choice.

If competitive pressure drives specialisation, through niche divergence (Roughgarden 1974), habitat fidelity may

be a result of higher competition for habitat types rather than space. This is difficult to test specifically, as we do not know the constraints on habitat selection, but the availability of habitats seems to far exceed the demand in this species (Fig. S4), suggesting lack of suitable habitat is unlikely to be the case. However, at this site, interspecific competition with other albatross species is mainly with wandering albatrosses (*Diomedea exulans*) which are considerably larger and may displace the smaller black-browed albatrosses. Moreover, the only other study to our knowledge to compare site versus habitat fidelity found stronger support for site fidelity, particularly between years (Wakefield *et al.* 2015). This suggests that species- or site-specific parameters may mediate the type of specialisation in seabirds.

DO HABITAT FIDELITY AND SITE FIDELITY DRIVE ONE ANOTHER?

The correlation between site and habitat fidelity within years shows that more generalist birds exhibit low relative levels of site and habitat fidelity, suggesting a syndrome of behavioural specialisation. However, between years, this correlation is not seen, suggesting it had limited temporal persistence. Consistent use of habitats may emerge as a result of site fidelity, particularly when considering static environmental parameters whose covariance with space is constant over time. We suggest that if this was the driving force, site not habitat fidelity would be stronger at the population level. Instead, our results show greater variability in site fidelity, which infers that habitat fidelity may be under selection and some level of consistent space use is a resulting behaviour.

IS HABITAT FIDELITY UNDER SELECTION?

Contrary to our prediction, site-faithful birds had higher fitness, but in keeping with our prediction, habitat fidelity did not influence fitness. Interestingly, we report no correlates of reproductive success and habitat fidelity, but site fidelity is associated with increased reproductive success. Theory behind the coexistence of specialists and generalists is often based on equal fitness (Wilson & Yoshimura 1994), but the 'win-stay, lose-shift' foraging tactic (Kamil 1983; Nowak & Sigmund 1993), where unsuccessful individuals must 'shift', could lead to increased variability in site location. This would result in a covariation between fitness and site fidelity, such that decreased fidelity correlates with decreased fitness, with generalist site fidelity strategies emerging in lower quality individuals because birds fail to repeatedly exploit prey patches successfully. Given that we find a potential fitness cost to being a generalist within years, with similar patterns between years, this explanation is the most supported by our data.

One important focus for future work should be the use of dynamic habitat features by birds. While bathymetry is a strong predictor of habitat type, this is due to the association with fronts, upwellings and zones of productivity (Bost *et al.* 2009). These are persistent in our study area but not fixed. The lack of fitness consequences of habitat fidelity shown in this study could be driven by adaptive tracking of transient hot spots. While evidence suggests these are strongly correlated with bathymetry (Bost *et al.* 2009), we do not fully understand short-term peaks in productivity, and oceanographic models should be used to map long- and short-term fronts.

SEX- AND AGE-SPECIFIC EFFECTS

The levels of fidelity were similar between the sexes, but within years, site fidelity was more important for females. It was females that had lower site fidelity that had lower reproductive success. Given that females in this population appear to travel further from the colony (Patrick & Weimerskirch 2014a), they may be more likely to 'lose-shift' when attempting to forage in areas of high competition. There is incomplete niche divergence and a large area of overlap between the sexes, with disruptive selection on foraging distance from the colony in females (Patrick & Weimerskirch 2014a), all of which may lead less successful birds to exhibit lower site fidelity. However, the results between years, which represent mainly males, support the idea that site fidelity is adaptive between years in males, but more data are needed to confirm this relationship.

Surprisingly, we found little evidence of a relationship between age and fidelity. We did show, however, that reproductive success increased with age. This may appear counter-intuitive as senescence is known to occur in this species, best described by a three-stage piecewise regression (Pardo *et al.* 2013). However, in this study, birds were equipped once they had already successfully hatched a chick and devices were mainly recovered on birds who successfully reared a chick. As a result, if older birds fail during incubation or early chick rearing, they may have been excluded from the study. This means that for the subsection of the birds we tracked, if older birds have high reproductive success during late chick guard and once the chick is left alone, this may explain the results we find here.

This study shows that birds consistently use habitat features both within and between years, suggesting high habitat fidelity. However, despite this, we show that it is site fidelity that correlates with reproductive success, which we suggest demonstrates a potential fitness cost of changing foraging sites. We show that effects on reproductive success in a single year are stronger in females that are thought to be less competitive, suggesting that it could be lower quality or subordinate individuals who are forced to switch foraging sites. The high level of habitat fidelity suggests this is a key foraging parameter and future work should focus on how this develops in individuals. Given the strong evidence that different aspects of specialisation are under selection, our study highlights the need for behavioural specialisation to be quantified at the

individual level and linked directly to fitness to help decouple the drivers of individual behaviour.

Acknowledgements

Data accessibility

Data are available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.51b25 (Patrick & Weimerskirch 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. The bathymetry surrounding the Kerguelen Islands, showing that depth is not strongly correlated with space, given the shelf edge which surrounds the islands.

Fig. S2. Comparing within individuals: Each albatross represents an area-restricted search (ARS) zone.

Fig. S3. Calculating similarity indices: Each albatross represents an area-restricted search (ARS) zone.

Fig. S4. The depth utilisation of birds and the available habitat, shown as density plots.