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Consistency pays: Sex differences and fitness consequences of behavioural specialisation in a wide ranging seabird

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Abstract

Specialists and generalists often coexist within a single population but the biological drivers of individual strategies are not fully resolved. When sexes differ in their foraging strategy, this can lead them to different environmental conditions and stability across their habitat range.   As such, sexual segregation, combined with dominance, may lead to varying levels of specialisation between the sexes. Here we examine spatial and temporal niche width (Intra-individual variability in aspects of foraging behaviour) of male and female black browed albatrosses, and its consequences for fitness. We show that females, where maximum foraging range is under fluctuating selection, exhibit more variable behaviours and appear more generalist than males, who are under directional selection to forage close to the colony. However within each sex, successful birds had a much narrower niche width across most behaviours, suggesting some specialisation is adaptive in both sexes.   These results

demonstrate that while there are sex differences in niche width, the fitness benefit of specialisation in spatial distribution is strong in this wide ranging seabird.

Introduction

There is increasing evidence that individuals within the same population may use different resources (1,2). This variation in niche is thought to be adaptive as it limits the overlap, and therefore the competition, between conspecifics (1,2). Differences in niche are often explained by ontogenetic or sex differences (3) attributed to variation in competitive ability (4), foraging efficiency (5) or nutrient requirements among the groups (6).

Individuals may differ from one another because of the frequency with which they use resources (niche) or because of the variation in resource use they exhibit (niche width). Generalist strategies, with large niche width, are predicted to persist when there is a lack of stability in the environment (7). Such generalism allows individuals to exploit resources that fluctuate in time and space but this may come at a cost; "the jack of all trades, master of none hypothesis". Conversely specialisation is thought to be the evolutionary response to habitat stability, allowing individuals to optimise their behaviour, and repeatedly exploit persistent resources (8). Furthermore, there is evidence of density-dependent specialisation, where individuals can reduce competition by niche divergence. However, uncertainty in the environment, and associated fluctuations in resource abundance or location, can result in costs to specialisation (8). While early theory predicted that populations should consist mainly of generalists, there is pervasive evidence that populations are regularly composed of specialist individuals (1,2), raising questions surrounding the ecological drivers of such individual strategies.

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The widespread occurrence of specialisation is often reported in stable environments, such as the patchy, yet predictable oceanic waters (9). Here individual divergence in niche is widely reported, particularly between the sexes (4,10,11) where it is often thought to arise as a result of sexual size dimorphism (11), differences in nutritional demands (e.g. 10) or competitive ability (e.g. 12). Sex-specific foraging strategies can often lead the sexes to forage in dramatically different areas (4) and differences in competitive ability may affect the stability of these strategies between years (12). As such, the sexes may exhibit very different levels of specialisation.

While niche width, and hence specialisation, is commonly reported to confer a fitness advantage (e.g. 13,14,15), results are not conclusive, suggesting under some conditions, generalists are favoured (15,16). Theoretical predictions infer that if groups experience different levels of environmental heterogeneity, the selective pressures favouring specialisation may also vary (17), offering some explanation for differences between populations. Extending this prediction, if males and females experience different environmental heterogeneity, selection for specialisation would be predicted to be asymmetrical between the sexes. As such, a system like this would offer an ideal opportunity to study sex-specific specialisation and its fitness consequences.

Here we quantify such variation, examining the sex differences in spatial niche width, using high resolution GPS tracking data in black browed albatrosses. Male albatrosses forage close to the colony and this is under directional selection (12). Foraging range is under fluctuating selection in females, such that females should forage close to the colony when food is abundant but far when food is scarce (12). Therefore we test the hypotheses that i) females

will be more variable in their spatial and temporal niche width within a single year

(generalists) ii) specialist males but generalist females will have higher fitness within the year

studied.

Methods

Data was collected at the colony of Canon de Sourcils Noirs, Kerguelen (48.4°S, 68.4°E), in

December 2011-January 2012 (See 12 for full details). In brief, 91 GPS loggers (Igot-U 120,

Mobile Action Technology) were attached to the back of adult black browed albatross, using

Tesa tape. This species has reduced sexual size dimorphism (4) and we confirmed this in our

population (See ESM). We used only tracks collected during chick guarding from

individuals where there were multiple trips per bird (N = 73) as there is significant variation

in foraging behaviour between incubation and guarding (12). Loggers were recovered after

1-7 foraging trips and for 73 birds, we had both repeated foraging trips and reproductive

success data. From these trips we calculated three classic metrics of spatial foraging niche

and two which are linked to trip duration were calculated: 1) Max range (km; distance to

point furthest from the colony), 2) Latitude at terminal point (furthest point from colony), 3)

Longitude at terminal point and 4) Total duration (hours). For summary data see Table S1.

We divided the data into four groups: i) Females that successfully fledged a chick SuF, ii)

Females which failed to fledge a chick UnSuF iii) Males who successfully fledged a chick

SuM and iv) Males who failed to fledge a chick UnSuM . Using Bayesian mixed models in

MCMCglmm (18) in R (19), we fitted the four models, one for each measure of spatial or

temporal niche. Group was included as a fixed effect to allow groups to vary in their

behavioural niche. Individual ID was fitted as a random intercept to account for repeat trips

between individuals and a heterogeneous residual variance structure was fitted allowing

individual and group variances to differ (niche width). ΔDIC values are provided as the most suitable way to compare models. Simplifying variance structure into just sex or reproductive success was not conducted as random effects with less than 4 levels are not recommended (20).

Results

Summary data is given in ESM Table S1. Groups differed in their niche width in Max range, Latitude terminal point, Longitude terminal point and Trip Duration (Table 1). Females were more variable than males in spatial niche, shown in their maximum range (Females = 80% (% of population variation accounted for by females)) and the position of the terminal point (Latitude: Females = 69%; Longitude: Females = 60%; Table 1; Figure 1). A heterogeneous variance structure was not supported for the temporal measure of trip duration (Females = 31%; Table 1)

Spatial niche width was considerably lower for all successful breeders, irrespective of sex (Max range: Successful breeders = 25% (% of population variation explained by successful breeders); Latitude: Successful breeders = 42%; Longitude: Successful breeders = 23%; Duration: Successful breeders = 28%; Table 1; Figure 1), but as above, the heterogeneous variance between groups was only supported for spatial behaviours.

Discussion

Here we show strong sex differences in behavioural niche width and fitness correlates of specialisation. Male black browed albatrosses, which are under directional selection to forage close to the colony (12) are more specialised in their distribution than females. Females have a wider spatial niche, supporting the hypothesis that fluctuating selection

between years on their foraging strategy (12) may correlate with a degree of generalisation. However successful male and female breeders had a considerably narrower niche width than unsuccessful breeders, suggesting relative specialisation is adaptive for both sexes.

Sex differences

In the year of this study, the oceanographic conditions were considered to be average, but in poor quality years female fitness is higher if they travel further from the colony and in good years the pattern is reversed (12). This may emerge as a result of the reduced sexual size dimorphism or competitive exclusion (4,12). Across years, selection should favour females who can vary their maximum range and a plastic foraging range may lead to an increased niche width. Theory supports the premise that specialisation is most likely to evolve when a single behaviour is consistently adaptive (1,2)Given that males, which forage close to the colony, always have a higher fitness (12), selection should favour individuals which undertake only short trips, leading to specialisation. Our results support this prediction, demonstrating a narrower niche width in males. Specialisation is also predicted to arise as a function of density dependence (21), and as such, because males forage nearer the colony, where competition is higher, they may be under stronger selection to specialise. To disentangle the effects of density and foraging plasticity would require substantial amounts of data, to correlate maximum range itself with specialisation. Our results also suggest that males still exhibit variation in trip duration. Many studies suggest that while seabirds are spatially consistent, they demonstrate an element of plasticity in temporal measures as this is likely to be an adaptive in response to aspects of oceanic unpredictability and variation in foraging success (12,22,23).

Fitness correlates

Successful male breeders were half as variable as unsuccessful ones in maximum foraging range and longitude at the terminal point. While this supports the prediction that specialisation in spatial niche is adaptive for males, there is little difference between the two groups in latitude in terminal point, which we suggest arises due to limited variation in latitude in this population. Interestingly, successful females also show pronounced specialisation. This suggests that despite the greater niche width overall in females, it is still adaptive for them to specialise. These results may be explained if specialist females do well under certain environmental conditions, such as those in the year of this study. Previous work has not examined how selection acts on specialisation itself and future work should address this through multi year comparisons.

While we present strong evidence that specialisation is adaptive in both sexes, our results may also be linked to aspects of individual quality. Specialisation itself could emerge if competition favours high quality birds, enabling them to repeatedly exploit a single resource. Equally, while we use a very large data set here to assess niche width, we rarely have tracks of the two members of the same pair. Individual niche width, particularly temporally, may be tightly linked to the behaviour of a bird's partner. For example, birds who have a partner that always makes trips of the same length, will repeatedly remain on the nest for a set period of time, and therefore experience the same nutritional and energetic demands each time they go to sea. Moreover, in albatrosses, it has been shown that behaviourally synchronous pairs are more successful at feeding the chick (24). The interaction between niche width within pairs would make an interesting extension to this study and an individual's niche width may predict their partners, reaffirming the selective advantage to specialisation.

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Table 1: The parameter and variance estimates from models. Variance estimates show niche width for each group (SuF, = Females that successfully fledged a chick; UnSuF = Females which failed to fledge a chick; SuM = Males who successfully fledged a chick; UnSuM = Males who failed to fledge a chick). ΔDIC estimates are given for models with and without a heterogonous variance structure for the four groups (Allowing group niche width to vary).

Spatial or temporal niche metric	Group (N individuals)	Niche width (Group variance) Estimates	Niche width (Group variance) ΔDIC
Maximum range (km)	SuFs (14)	9516 (5700-14024)	With heterogeneous variance = **2542.61**;
	UnSuF (11)	31776 (15870-51465)	
	SuMs (33)	3347 (2340-4482)	Without heterogeneous variance = 2598.61
	UnSuMs (15)	6669 (1660-11647)	
Latitude at terminal point (°)	SuFs (14)	0.9263 (0.5305-1.3832)	With heterogeneous variance = **607.47**;
	UnSuF (11)	1.726 (0.7852-2.9711)	
	SuMs (33)	0.6916 (0.4794-0.9248)	Without heterogeneous variance = 615.59
	UnSuMs (15)	0.5111 (0.2363-0.8554)	
Longitude at terminal point (°)	SuFs (14)	1.148 (0.6748-1.716)	With heterogonous variance = **804.80**;
	UnSuF (11)	6.168 (2.9154-9.98)	
	SuMs (33)	1.645 (1.117-2.236)	Without heterogonous variance = 828.89
	UnSuMs (15)	3.219 (1.5851-5.112)	
Trip Duration (Hours)	SuFs (14)	418.2 (241.8-619.1)	With heterogeneous variance = 3317.11;
	UnSuF (11)	1128.2 (477.4-1907.7)	
	SuMs (33)	1015.7 (656.6-1401.8)	Without heterogeneous variance = **3323.63**
	UnSuMs (15)	2506.6 (1168.5-3989.3)	

Figure 1: Estimated variance components for measures of spatial and temrpoal niche width. A variance estimate is shown for each sex, divided into unsuccessful and successful breeders. Filled circles show the estimated variance, and the bars show the credibility intervals around these estimates. Dashed bars show unsuccessful and solid bars successful breeders. Females are plotted in red and males in blue. Figure 1a: Variance in maximum range (km); Figure 1b: Variance in Latitude at terminal point (°); Figure 1c: Variance in longitude at terminal point (°).