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Marine biology

Consistency pays: sex differences and fitness consequences of behavioural specialization in a wide-ranging seabird

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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 specialization between the sexes. Here, we examine spatial and temporal niche width (intraindividual variability in aspects of foraging behaviour) of male and female black-browed albatrosses (*Thalassarche melanophrys*), 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 specialization is adaptive in both sexes. These results demonstrate that while there are sex differences in niche width, the fitness benefit of specialization in spatial distribution is strong in this wide-ranging seabird.

1. 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, specialization is thought to be the evolutionary response to habitat stability, allowing individuals to optimize their behaviour and repeatedly exploit persistent resources [8]. Furthermore, there is evidence of density-dependent specialization, 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 specialization [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.

The widespread occurrence of specialization is often reported in stable environments, such as the patchy, yet predictable oceanic waters [9]. Here,

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). Deviance information criterion (DIC) estimates are given for models with and without a heterogenous variance structure for the four groups. Credibility intervals are given in brackets and models with the lowest DIC are highlighted in bold font.

| spatial or temporal niche metric | group (<i>N</i> individuals) | niche width (group variance) estimates | niche width (group variance) DIC |
|----------------------------------|----------------------------------|---|---|
| maximum range (km) | SuFs (14) | 9516 (5700–14 024) | with heterogeneous variance = 2542.61 ; |
| | UnSuF (11) | 31 776 (15 870–51 465) | without heterogeneous variance = 2598.61 |
| | SuMs (33) | 3347 (2340–4482) | |
| | UnSuMs (15) | 6669 (1660–11 647) | |
| 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) | without heterogeneous variance = 615.59 |
| | SuMs (33) | 0.6916 (0.4794–0.9248) | |
| | UnSuMs (15) | 0.5111 (0.2363–0.8554) | |
| longitude at terminal point (°) | SuFs (14) | 1.148 (0.6748–1.716) | with heterogenous variance = 804.80 ; |
| | UnSuF (11) | 6.168 (2.9154–9.98) | without heterogenous variance = 828.89 |
| | SuMs (33) | 1.645 (1.117–2.236) | |
| | 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) | without heterogeneous variance = 3323.63 |
| | SuMs (33) | 1015.7 (656.6–1401.8) | |
| | UnSuMs (15) | 2506.6 (1168.5–3989.3) | |

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 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 specialization.

While niche width, and hence specialization, is commonly reported to confer a fitness advantage (e.g. [13–15]), 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 specialization may also vary [17], offering some explanation for differences between populations. Extending this prediction, if males and females experience different environmental heterogeneity, selection for specialization would be predicted to be asymmetrical between the sexes. As such, a system like this would offer an ideal opportunity to study sex-specific specialization 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 (*Thalassarche melanophrys*). 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), and (ii) specialist males but generalist females will have higher fitness within the year studied.

2. Material and methods

Data were collected at the colony of Canon de Sourdils Noirs, Kerguelen (48.4° S, 68.4° E), in December 2011–January 2012 (see [12] for full details). In brief, GPS loggers (Igot-U 120, Mobile Action Technology) were attached to the backs of 91 adult black-browed albatross, using Tesa tape. This species has reduced sexual size dimorphism [4] and we confirmed this in our population (see the electronic supplementary material). We used only tracks collected during chick guarding for reproductive events of known outcome ($N = 73$) as there is significant variation in foraging behaviour between incubation and guarding [12]. From these trips, we calculated three classic metrics of spatial foraging niche and two that are linked to trip duration: (1) maximum 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 the electronic supplementary material, table S1.

We divided the data into four groups: (i) females that successfully fledged a chick (SuF), (ii) females that 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 group variances to differ (niche width), with individual variance nested within group. Deviance information criterion (DIC) 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 fewer than four levels are not recommended [20].

3. Results

Summary data are given in the electronic supplementary material, table S1. 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 and 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 (maximum 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 and figure 1), but as above, the heterogeneous variance between groups was only supported for spatial behaviours.

4. Discussion

Here, we show strong sex differences in behavioural niche width and fitness correlates of specialization. Male black-browed albatrosses, which are under directional selection to forage close to the colony [12], are more specialized 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 generalization. However, successful male and female breeders had a considerably narrower niche width than unsuccessful breeders, suggesting that relative specialization is adaptive for both sexes.

(a) Sex differences

In the year of this study (2011), 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 specialization is most likely to evolve when a single behaviour is consistently adaptive [12]. Given that males, which forage close to the colony, always have a higher fitness [12], selection should favour individuals that undertake only short trips, leading to specialization. Our results support this prediction, demonstrating a narrower niche width in males. Specialization 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 specialize. To disentangle, the effects of density and foraging plasticity would require substantial amounts of data in order to correlate maximum range itself with specialization. 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 response to aspects of oceanic unpredictability and variation in foraging success [12,22,23].

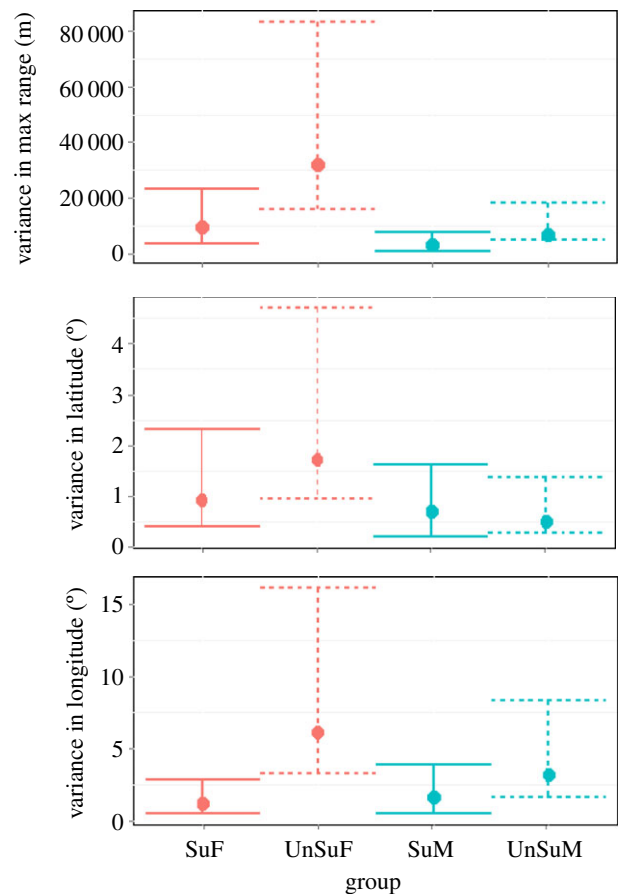


Figure 1. Estimated variance components for measures of spatial and temporal niche width. A variance estimate is shown for each sex, divided into unsuccessful and successful breeders. Filled circles show the estimated variance, and the bars show the credibility intervals around these estimates. Dashed bars show unsuccessful and solid bars successful breeders. Females are plotted on the left (in red online) and males on the right (in blue online). (a) Variance in maximum range (km); (b) variance in latitude at terminal point ($^{\circ}$) and (c) variance in longitude at terminal point ($^{\circ}$). (Online version in colour.)

(b) 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 specialization 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 specialization. This suggests that despite the greater niche width overall in females, it is still adaptive for them to specialize. 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 specialization itself and future work should address this through multi-year comparisons.

While we present strong evidence that specialization is adaptive in both sexes, our results may also be linked to aspects of individual quality. Specialization itself could emerge if competition favours high-quality birds, enabling them to repeatedly exploit a single resource. Equally, while we use a very large dataset 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 partner's, reaffirming the selective advantage to specialization.

References

- Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003 The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**, 1–28. (doi:10.1086/343878)
- Araújo MS, Bolnick DI, Layman CA. 2011 The ecological causes of individual specialisation. *Ecol. Lett.* **14**, 948–958. (doi:10.1111/j.1461-0248.2011.01662.x)
- Durell S. 2000 Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biol. Rev.* **75**, 503–518. (doi:10.1111/j.1469-185X.2000.tb00053.x)
- Phillips RA, Silk JRD, Phalan B, Cattrly P, Croxall JP. 2004 Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc. R. Soc. Lond. B* **271**, 1283–1291. (doi:10.1098/rspb.2004.2718)
- Cook TR, Cherel Y, Bost C-A, Tremblay M. 2007 Chick-rearing Crozet shags (*Phalacrocorax melanogenis*) display sex-specific foraging behaviour. *Antarct. Sci.* **19**, 55–63. (doi:10.1017/S09541020070000891)
- Beck CA, Iverson SJ, Bowen WD, Blanchard W. 2007 Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *J. Anim. Ecol.* **76**, 490–502. (doi:10.1111/j.1365-2656.2007.01215.x)
- Futuyma DJ, Moreno G. 1988 The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.* **19**, 207–233. (doi:10.1146/annurev.es.19.110188.001231)
- MacArthur RH. *Geographical ecology: patterns in the distribution of species*. New York, NY: Princeton University Press.
- Weimerskirch H. 2007 Are seabirds foraging for unpredictable resources? *Deep-Sea Res. Part II-Top. Stud. Oceanogr.* **54**, 211–223. (doi:10.1016/j.dsr2.2006.11.013)
- Weimerskirch H, Corre ML, Ropert-Coudert Y, Kato A, Marsac F. 2006 Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed booby. *Oecologia* **146**, 681–691. (doi:10.1007/s00442-005-0226-x)
- Phillips RA, McGill RAR, Dawson DA, Bearhop S. 2011 Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Mar. Biol.* **158**, 2199–2208. (doi:10.1007/s00227-011-1725-4)
- Patrick SC, Weimerskirch H. 2014 Personality, foraging and fitness consequences in a long lived seabird. *PLoS ONE* **9**, e87269. (doi:10.1371/journal.pone.0087269)
- Annett CA, Pierotti R. 1990 Long-term reproductive output in Western Gulls: consequences of alternate tactics in diet choice. *Ecology* **80**, 288–297. (doi:10.1890/0012-9658(1999)080[0288:LTROIW]2.0.CO;2)
- Watanuki Y. 1992 Individual diet difference, parental care and reproductive success in Slaty-Backed Gulls. *Condor* **94**, 159–171. (doi:10.2307/1368805)
- Votier SC, Bearhop S, Ratcliffe N, Furness RW. 2004 Reproductive consequences for Great Skuas specializing as seabird predators. *Condor* **106**, 275–287. (doi:10.1650/7261)
- Woo KJ, Elliott KH, Davidson M, Gaston AJ, Davoren GK. 2008 Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *J. Anim. Ecol.* **77**, 1082–1091. (doi:10.1111/j.1365-2656.2008.01429.x)
- Montiglio P-O, Ferrari C, Réale D. 2013 Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Phil. Trans. R. Soc. B* **368**, 20120343. (doi:10.1098/rstb.2012.0343)
- Hadfield JD. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* **33**, 1–22.
- R Development Core Team. 2008 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing (<http://www.R-project.org>).
- Crawley MJ. 2012 *The R book*, 1078 p. New York, NY: John Wiley & Sons.
- Tim Tinker M, Guimarães PR, Novak M, Marquitti FMD, Bodkin JL, Staedler M, Bentall G, Estes JA. 2012 Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters: network structure of individual resource use. *Ecol. Lett.* **15**, 475–483. (doi:10.1111/j.1461-0248.2012.01760.x)
- Hamer KC, Humphreys EM, Garthe S, Hennenke J, Peters G, Gremillet D, Phillips RA, Harris MP, Wanless S. 2007 Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Mar. Ecol.-Prog. Ser.* **338**, 295–305. (doi:10.3354/meps338295)
- Patrick SC *et al.* 2014 Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* **123**, 33–40. (doi:10.1111/j.1600-0706.2013.00406.x)
- Weimerskirch H, Barbraud C, Lys P. 2000 Sex differences in parental investment and chick growth in Wandering Albatrosses: fitness consequences. *Ecology* **81**, 309–318. (doi:10.1890/0012-9658(2000)081[0309:SDIPIA]2.0.CO;2)