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Individual specialization in a shorebird population with narrow foraging niche

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ABSTRACT

Individual specialization in resource use is a widespread driver for intra-population trait variation, playing a crucial evolutionary role in free-living animals. We investigated the individual foraging specialization of Black-tailed Godwits (*Limosa limosa islandica*) during the wintering period. Godwits displayed distinct degrees of individual specialization in diet and microhabitat use, indicating the presence of both generalist and specialist birds. Females were overall more specialist than males, primarily consuming polychaetes. Specialist males consumed mainly bivalves, but some individuals also specialized on gastropods or polychaetes. Sexual dimorphism in bill length is probably important in determining the differences in specialization, as longer-billed individuals have access to deep-buried polychaetes inaccessible to most males. Different levels of specialization within the same sex, unrelated to bill length, were also found, suggesting that mechanisms other traits are involved in explaining individual specialization. Godwits specialized on bivalves achieved higher intake rates than non-specialist birds, supporting the idea that individual foraging choices or skills result in different short-term payoffs within the same population. Understanding whether short-term payoffs are good indicators of long-term fitness and how selection operates to favour the prevalence of specialist or generalist godwits is a major future challenge.

1. Introduction

Considerable intraspecific and intra-populational variation can be found in the foraging behaviour of wild animal populations. This is often attributed to individual specialization in dietary regimes, habitat use, feeding techniques or a combination of several of these factors (Sutherland et al., 1996; Durell, 2000). Individual specialization is thought to be maintained in a population by fluctuating and disruptive selection, as generalists and specialists often achieve different payoffs in response to different environmental conditions (Bolnick et al., 2003; van de Pol et al., 2010). In fact, selection towards foraging specialization can fluctuate due to temporal variation in intrinsic (e.g. density of competitors) and extrinsic (e.g. prey availability) factors (van de Pol et al., 2010). Optimal foraging theory proposes that an individual selects a particular foraging strategy in a way that maximizes its net energy intake per unit of time at the same time that minimizes other costs, such as the costs of thermoregulation and predation risk (Stephens and Krebs, 1986). The extent to which specialists achieve higher foraging success compared with non-specialists (and whether these short-term payoffs are good predictors of long-term fitness payoffs such as reproductive success or survival), is poorly known but apparently highly variable (Whitfield, 1990; Araújo and Gonzaga, 2007; Bolnick et al., 2007). Some previous studies have presented strong evidence for higher ecological performance of specialists (Golet et al., 2000; Tinker et al., 2008) whilst others showed no differences between specialists and generalists (Dornhaus, 2008; Woo et al., 2008).

There is currently extensive evidence that a large number of generalist populations are actually composed of relatively

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specialized individuals (Bolnick et al., 2007). Several studies clearly demonstrate that individual specialization in resource use or in foraging strategies does occur in a variety of taxa, such as insects (Araújo and Gonzaga, 2007), fishes (Schindler et al., 1997), birds (Goss-Custard and Durell, 1983; Woo et al., 2008) and mammals (Tinker et al., 2008; Thiemann et al., 2011). Given that niche variation might drive among-individual differences in competition, predation or parasitism risk, these findings highlight the importance of addressing individual-level variation in ecological research, namely in demographic studies, but also in conservation management and planning (Araújo et al., 2011; Bolnick et al., 2011). In spite of this, many studies either fail to focus on individuals as ecological-units and treat conspecifics as ecological equivalents without investigating potential inter-individual variation, and few have quantified the magnitude of individual specialization (Bolnick et al., 2003; Araújo et al., 2011).

Individual foraging specialization has been addressed through two complementary (but sometimes conflicting) concepts. The "niche width concept", the most widely used, classifies specialists as those individuals that consistently use a rather small subset of resources or tactics, exhibiting, in result, a much narrower niche than the population as a whole (Bolnick et al., 2002; Sargeant, 2007). The "niche overlap concept" postulates that specialists are those who mostly use rare resources or tactics, and therefore, regardless of using a small or large subset of resources, have a niche that overlaps little with the population niche (Bolnick et al., 2002; Sargeant, 2007).

Whichever the concept, individual foraging specialization is mainly a result from one of four ecological causes: (1) ecological opportunity, (2) frequency-dependent selection, (3) predation or (4) phenotypic traits (Durell, 2000; Araújo et al., 2011). If resource diversity and availability – ecological opportunity – is patchily distributed, individual diet may reflect what is available in the patches used by the individual (e.g. Whitfield, 1990). For instance, when preferred resources are absent from certain patches, individuals using those patches will likely expand their niche to accept previously unutilized resources, thus decreasing individual specialization (e.g. Layman et al., 2007). On the other hand, a mixture of different individual feeding choices with equal payoffs may be maintained within the same population by frequency-dependent processes (Schindler et al., 1997). In fact, the specialization level within a species or a population, i.e., the extent to which individuals within a population vary from one another, is thought to be largely dependent on the opposite effects of intraspecific and interspecific competition, which promote diversifying and constraining forces, respectively (van Valen, 1965; Bolnick et al., 2010; Araújo et al., 2011). Thirdly, predation might affect individual specialization either through density-mediated effects (changes in prey abundance) or if prey behaviour changes in response to predation risk (Araújo et al., 2011). Finally, individual specialization may arise from different phenotypic traits. The two main sources of phenotypic variation are age and sex, and both can be strongly related with morphological differentiation (e.g. Durell et al., 1993; MacFarlane and Coulson, 2005). Nonetheless, individual dietary specializations that cannot be attributable to sex or age, or to a discrete (*a priori*) morphological group, are commonly found in several animal taxa (e.g. Araújo and Gonzaga, 2007; Tinker et al., 2008; Thiemann et al., 2011).

Shorebirds are good model organisms to address foraging specialization, as they generally occur in large numbers at their wintering grounds, and their diet and foraging behaviour are relatively easy to monitor. However, in comparison with the number of studies focused at the population level, relatively little attention has been given to the individual foraging behaviour of shorebirds, which occupy a high trophic level in estuarine systems (but see Whitfield, 1990; Goss-Custard and Durrell, 1983). This lack of knowledge is mostly due to the large difficulties in identifying individual birds and following them in the wild. Black-tailed Godwit *Limosa limosa islandica* wintering at the Tagus estuary, Portugal, forage on macroinvertebrates on the intertidal mudflats (Alves et al., 2010). Numerous wintering godwits have been individually colour-ringed at the Tagus estuary since 2006, as part of an international long-term marking program, providing a unique opportunity to identify and track individual birds throughout the winter (Gunnarsson et al., 2005; Alves et al., 2012a). Black-tailed godwits exhibit sexual dimorphism: females are overall larger and ca. 16% longer-billed than males, but within the same sex there is also considerable variability in bill length (Gunnarsson et al., 2005, 2006). Sexual segregation in diet composition has been previously reported for this godwit population (Catry et al., 2012). Larger-billed individuals presumably have access to a wider range of resources, including more deeply buried invertebrates (Zwarts and Wanink, 1993). Thus, having a long bill might allow to exploit a wider range of resources, which may be advantageous if there are temporal and spatial differences in prey profitability (generalist strategy) or, alternatively, might promote feeding upon highly profitable resources exclusively (specialist strategy). We could also expect finding individual specialization among godwits if, regardless of sexual/phenotypic traits, birds develop different skills that result in short-term payoffs, i.e. different resource use efficiency, between birds consuming variable proportions of the same prey.

In this study, we examine the foraging ecology of Black-tailed Godwits during the wintering period in the Tagus estuary, Portugal, in order to address the following main questions: (1) do individual godwits exhibit foraging specialization? (2) does specialization result from sexual and/or morphological differentiation, or can it be attributed to other factors? and (3) do specialist godwits achieve higher intake rates than non-specialists when feeding upon their preferred resources?

2. Materials and methods

2.1. Study area

The study was carried out at the Tagus estuary, Portugal (38°45′N, 09°50′W). This 97 km^2 estuary is mostly composed of mudflats with smaller areas dominated by sandy sediments, and is an internationally important site for waders, and particularly to Black-tailed Godwits (Delany et al., 2009; Catry et al., 2011). All fieldwork took place at four study sites located on the southern shore of the estuary, representing important foraging sites for godwits (Seixal, Barreiro, Moita and Montijo; see details of the study area in Catry et al., 2012).

2.2. Foraging behaviour and diet of godwits

Black-tailed Godwits were captured and individually colour-ringed in the Tagus estuary between 2006 and 2010. Although godwits of two subspecies (*limosa* and *islandica*) occur on the mudflats of the Tagus estuary, a previous study showed that 90–100% of the colour-ringed godwits at the Tagus estuary in November and December belong to the subspecies *islandica* (Alves et al., 2010). All except one of the godwits followed in this study were either captured or resighted at least once during November–December, strongly suggesting that most birds are Icelandic godwits. The sex of colour-marked birds was determined using a combination of morphological criteria (validated by genetic techniques in some cases), following Gunnarsson et al. (2006). Culmen length was also measured at time of capture. During two winter seasons, 2009/10 and 2010/11, (from January to March and