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Diet preferences as the cause of individual differences rather than the consequence

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SUMMARY

(1) Behavioural variation within a species is usually explained as the *consequence* of individual variation in physiology. However, new evidence suggests that the arrow of causality may well be in the reverse direction: behaviours such as diet preferences *cause* differences in physiological and morphological traits.

(2) Recently, diet preferences were proposed to underlie consistent differences in digestive organ mass and movement patterns (patch residence times) in red knots (*Calidris canutus islandica*). Red knots are molluscivorous and migrant shorebirds for which the size of the muscular stomach (gizzard) is critical for the food-processing rate.

(3) In this study, red knots (*C. c. canutus*, n=46) were caught at Banc d’Arguin, an intertidal flat ecosystem in Mauritania, and released with radio-tags after the measurement of gizzard mass. Using a novel tracking system (Time-Of-Arrival), patch residence times were measured over a period of three weeks. Whether or not gizzard mass determined patch

residence times was tested experimentally by offering 12 of the 46 tagged red knots soft diets prior to release; this reduced an individual's gizzard mass by 20 to 60 percent. To validate whether the observed range of patch residence times would be expected from individual diet preferences, we simulated patch residence times as a function of diet preferences via a simple departure rule.

(4) Consistent with previous empirical studies, patch residence times in the field were positively correlated with gizzard mass. The slope of this correlation, as well as the observed range of patch residence times, were in accordance with the simulated values. The 12 birds with reduced gizzard masses did not decrease patch residence times in response to the reduction in gizzard mass.

(5) These findings suggest that diet preferences can indeed *cause* the observed among-individual variation in gizzard mass and patch residence times. We discuss how early diet experiences can have cascading effects on individual expression of both behavioural and physiomorphic traits. This emphasises that, to understand the ecological consequences of individual differences, knowledge of the environment during development is required.

INTRODUCTION

Individuals are often constrained in the expression of behavioural traits relative to the overall range of expression in the population (Réale & Dingemanse 2010). Individual-specific behavioural characteristics have been captured with the terms 'behavioural syndromes' or 'animal personality' (Sih, Bell & Johnson 2004; Réale *et al.* 2010). Behaviour has often been regarded as flexible, with behavioural differences being considered to result from individual-specific physiological and morphological characteristics (Krebs & Davies 1997). Many morphological and physiological traits are highly plastic too (Pigliucci 2001), even into the adult stage (Piersma & van Gils 2011). Consequently, the causal direction of a correlation between what we will subsequently call ‘physiomorphic’ traits and behavioural traits is not self-evident (see also Stamps 2003). The two can be seen as complementary aspects of the phenotype (Dingemanse *et al.* 2010), both of which will be shaped during ontogeny in interaction with each other and the environment (Stamps 2003). Hence, behavioural syndromes may also *cause* consistent variation in others traits, be it behavioural or physiomorphic (e.g. Eklöv & Svanbäck 2006; Bijleveld *et al.* 2014; Bijleveld *et al.* 2016).

Individual diet preferences are among the best studied behaviours, and consistent differences therein have been shown to result from dietary experiences early in life (Burghardt & Hess 1966; Provenza & Balph 1987; Estes *et al.* 2003; Villalba, Provenza & Han 2004; Darmaillacq, Chichery & Dickel 2006). Hence, the early development of diet preferences may well function as the basis of individual variation in other traits later in life. Variable dietary experiences are more likely when the availability of different food sources is variable. This is the case for red knots (*Calidris canutus,* Linneaus), a medium-sized migrating shorebirds (Piersma 2007; Buehler & Piersma 2008) that primarily feed on molluscs (Prater 1972; van Gils *et al.* 2005a). The quality and diversity of the food landscape that they live in is particularly variable in space (Compton *et al.* 2013) as well as in time (Kraan *et al.* 2013; van Gils *et al.* 2013). In captive as well as free-living red knots (*C. c. islandica*), diet preferences were put forward as a possible cause of differences in movement behaviour and digestive organ mass (Bijleveld *et al.* 2014; Bijleveld *et al.* 2016). Red knots ingest their mollusc prey whole and crush them in the gizzard (Piersma, Koolhaas & Dekinga 1993), the size of which can be measured non-invasively by ultrasonography (Dietz *et al.* 1999). Gizzard mass was shown to be highly variable between- and flexible within individuals and to reflect the digestive quality of the previous diet (where prey quality is measured as ash-free dry flesh mass divided by dry shell mass; Piersma, Koolhaas & Dekinga 1993; Dekinga *et al.* 2001; van Gils *et al.* 2003a; Oudman *et al.* 2015).

In an experiment with captive red knots, gizzard mass was positively correlated with the average duration of patch visits (patch residence time) (Bijleveld *et al.* 2014). The lack of behavioural change after manipulating an individual's gizzard mass suggested that variation in digestive organ mass resulted from consistent behavioural differences, rather than the other way around. Measurements in the wild also showed that gizzard mass was negatively correlated with the average digestive quality of prey in their selected habitat (van Gils *et al.* 2005b; Bijleveld *et al.* 2016). Together, these findings suggest that individual variation in gizzard mass and differences in movement behaviour may be consequences of variation in diet preferences between individuals, and ask for an experimental test under natural conditions.

This study provides (1) field measurements of the correlation between patch residence times and gizzard masses, (2) an experimental test of the causal direction of this correlation, and (3) a conceptual mechanism to explain the observed differences in patch residence times between red knots as a function of diet preferences. Using the novel Time-Of-Arrival tracking system (MacCurdy, Gabrielson & Cortopassi 2012; Piersma *et al.* 2014; Bijleveld *et al.* 2016), patch residence times were measured in 34 free-living red knots (*C. c. canutus*) on the intertidal flats of Banc d'Arguin, Mauritania. Additionally, after having been held captive for two weeks on diets of medium (6 birds) and high digestive quality (6 birds), 12 tagged red knots were released with reduced gizzard masses. To test whether this manipulation caused differences in patch residence times after release in the wild, we compared the observed relation between gizzard mass and mean patch residence time for these 12 treated birds (to be referred to as "treatment birds") with the 34 unmanipulated birds (to be referred to as "reference birds"). Finally, the observed range of patch residence times and gizzard masses were compared to simulated patch residence times where animals were assumed to have constant patch giving-up times, but differ in the minimum digestive quality of accepted prey.

METHODS

TOA tracking

Between 9 January and 13 February 2013, 46 red knots were tracked with the Time-Of-Arrival (TOA) tracking system (MacCurdy, Gabrielson & Cortopassi 2012; Piersma *et al.* 2014; Bijleveld *et al.* 2016) in the Baie d'Aouatif in Parc National du Banc d'Arguin, Mauritania, West Africa (19˚53'N, 16˚17'W) (Piersma *et al.* 2014). The birds were caught adjacent to Zira island, on the southwest entrance of the bay, using mist nets (14 birds, between 8 and 11 January) and a cannon net (32 birds, 12 January). All birds were released with a 6 g (range 5.5 - 6.5 g) tag glued to the skin of their rump with cyanoacrylate (Warnock & Warnock 1993). Gizzard mass was measured by ultrasonography (Dekinga *et al.* 2001; Oudman *et al.* 2015) within 4 hours after catch. The 34 reference birds were released within one day after catch, between 9 and 12 January, except for one bird that showed signs of illness after being caught on 12 January. It was released in a healthy condition and with a tag on 20 January and was omitted from the analyses. The 12 treatment birds were released on 23 January after 11 days of captivity.

Each tag emitted a tag-specific radio signal each second, which could be received by up to nine radio receiver stations placed in the area (Piersma *et al.* 2014 and Fig. S1). These stations then registered the time of arrival of the tag-specific signal. The differences in signal arrival times between the stations were used to calculate the tag's position (MacCurdy, Gabrielson & Cortopassi 2012). Position error estimates were produced when the signal was received by at least four stations (MacCurdy, Gabrielson & Cortopassi 2012). Signals that were received by less than four stations were not considered for the analyses, and only position estimates with an error below 125 m (the radius of residence patches, see below). For comparing the treatment group with the reference group, only data from 23 January onwards were used for the analyses, i.e. the date when the treatment birds were released.

Summarizing the tracking data into patch residence times

To calculate mean patch residence times of each bird during each low tide, the position estimates were combined into residence patches (Bijleveld *et al.* 2016) according to the method of Barraquand and Benhamou (2008). We will describe the basics only and refer to both papers for detailed methodology. First, the data was median-filtered with a 5-points sliding window to reduce error. For each position estimate (Fig 1A), the duration of the stay within 125 m of that position, without any excursions outside the radius for more than 30 s, was calculated. Subsequently, the sequence of residence times was segmented into so-called residence patches, using the penalized contrasts method described by Lavielle (2005). Finally, adjacent residence patches of which the median position was within 125 m of each other were combined (Fig. 1B). Hereafter, residence times were calculated as the interval between the first and last position estimate (Fig. 1C).

Because we were interested in low-tide (foraging) distributions, patch visits that started or ended within 2 h before or after astronomical low tide (4.5 h after Dakar, retrieved from tides.mobilegeographics.com) were selected. Patch visits that extended into the high tide (2 h before to 2 h after astronomical high tide) were removed from the analysis (80 of 3141 patches), as it was likely that birds were roosting. Patches visited shorter than 10 min were not considered (n = 167), as they might travelling indicate bouts (Bijleveld *et al.* 2016) during which birds were travelling. Finally, when not receiving signals from a tag for more than one hour, this bird during that low tide was excluded from the analysis (98 of 1019 cases). Patch residence times were log-transformed and then averaged per bird per tide. This resulted in a total of 921 mean patch residence times from 35 birds (26.3 per bird, SD = 11.5), of which 337 were from the 12 treatment birds (28.1 per bird, SD = 11.2).

Experimental treatment

Twelve red knots, caught by cannon net on 12 January, were kept for eleven days in two in-house aviaries (1.5 x 1 x 0.5 m) at the scientific station adjacent to the Baie d’Aouatif. The birds were divided at random into two treatment groups of six birds each. To reduce gizzard mass of individuals, one group received only the flesh of the bivalve *Senilia senilis* (Oudman *et al.* 2014). In an attempt to maintain original gizzard masses, the other group was additionally offered 1200 hard-shelled *Dosinia isocardia* per day. These prey were collected every day in the Baie d’Aouatif. All birds had *ad libitum* access to fresh water. Gizzard masses were measured within four hours after catch and on the evening before release. Gizzard mass of the birds on the soft diet decreased from 8.7 ± 0.5 g at the day of catch to 5.0 ± 0.5 g on the day before release (mean ± SE, t = -5.6, p = 0.0002). Gizzard mass of the birds on the partly hard-shelled diet decreased from 9.2 g ± 0.7 at catch to 6.6 g ± 0.7 before release (t = -2.8, p = 0.02); the decrease in gizzard mass did not differ significantly between treatment groups (t=1.4, p = 0.20), and the gizzard masses were not significantly different at release either (t = 1.9, p = 0.07).

Prey density, prey quality and giving-up times

The study area was systematically searched for tagged red knots. On 44 occasions, tagged birds were filmed from a distance of ~200 m. Excluding cases in which birds were obviously disturbed by the observers, 12 giving-up times were measured, where giving-up time is defined as the time between last prey encounter and take-off. At each of the 44 locations, next to where the bird left traces (footprints, droppings or probing holes), eight sites were marked with small pegs and sampled for prey availability within the following week. Each sample was taken with a PVC-core (diameter 15 cm) to a depth of 20 cm in the sediment. The top 4 cm (coinciding with the average bill length of red knots) was separated and sieved over a 1 mm mesh. All molluscs were sorted in the field station and brought to NIOZ (the Netherlands) in a 4% formaldehyde solution, where they were identified to genus level and measured to the nearest 0.1 mm. Mollusc density was calculated by dividing the summed number of observed molluscs by the summed sampled surface per location ($0.14\ m^2$, n = 8). Only prey of ingestible sizes were considered (Zwarts & Blomert 1992).

To determine dry flesh mass and dry shell mass (DM_{shell}), flesh and shell were separated for a subset of all bivalves and the gastropod *Bulla* sp., dried at 60°C for 3 days, and weighed (mg). Flesh was then incinerated for 5 h at 560°C and weighed again to determine ash-free dry flesh mass ($AFDM_{flesh}$). Flesh and shell could not be separated in gastropods other than *Bulla*. These gastropods were incinerated whole, assuming that 12.5% of organic matter resides in the shell (Dekker 1979). By linear regression on log-transformed values, $AFDM_{flesh}$ and DM_{shell} were estimated as a function of shell length for each species separately. Based on these regressions, digestive quality was estimated for each individual prey by dividing $AFDM_{flesh}$ by DM_{shell} (van Gils *et al.* 2005a). To arrive at the estimated prey quality distribution to be used in the simulations, the observed variation in digestive quality was taken into account by adding to the estimates a value drawn randomly from the normal distribution (Gaussian noise), with the standard deviation as measured for the concerning prey species.

Statistics

Firstly, the slope of the correlation between gizzard mass and patch residence times was tested in the reference birds. Secondly, we determined whether the treatment birds adjusted their patch residence times as a consequence of the change in gizzard mass. We did this by testing whether the treatment birds obeyed this observed relationship given their gizzard mass at release, and whether there was a difference in the response of the two treatment groups. Thirdly, we tested whether the treatment birds obeyed the observed correlation given their gizzard mass at catch, which would alternatively suggest that the treatment birds did not adjust patch residence times to their manipulated gizzard mass.

The correlation between patch residence time and gizzard mass in the reference birds was tested by comparing linear mixed effects models (function “lmer” in R package “lme4”; Bates *et al.* 2015; R Core Team 2015), including low-tide-ID and bird-ID as random effects. Patch residence times and gizzard mass were log-transformed before the analysis. In addition to gizzard mass, time-of-day and low-tide water level were included as explanatory variables. When astronomical low tide was within 2 h before sunrise and 2 h after sunset, the low tide period was classified as “Day”, and otherwise as “Night”. All possible combinations of variables were compared, including all interactions between two variables, but not more than two, resulting in 14 different candidate models. Model selection was performed by calculating AIC_c-weights of all the candidate models (Burnham & Anderson 2002). Models were regarded as competitive to the best model (the model with lowest AIC_c-score) if the cumulative AIC-weight was below 0.95 and did not contain uninformative parameters (parameters that did not decrease AICc-score when added to the model; Arnold 2010).

Because the duration of each low tide is fixed, mean patch residence time per tide was negatively collinear with the number of patches visited per tide and did not follow a normal distribution, nor any other parametric distribution. However, a histogram of the model residuals and a plot of the residual values against the fitted values did not show strong violation of normality assumptions. An alternative analysis was performed on the number of patches visited per tide instead of mean patch residence time. Although this alternative procedure gave the same results and conclusions (not shown), this method was not preferred because 234 out of 584 data points had to be removed, since the number of patch visits could not be accurately assessed when birds were out of range of the receiver stations during parts of the low tide period.

Because patch residence times could not be measured in the treatment birds before they underwent the treatment, we assumed that the relation between patch residence times and gizzard mass before treatment was the same as in the reference birds. Hence, if the treatment had no effect, patch residence times after the treatment should have the same relation with gizzard mass *at catch* as found for the reference birds. On the other hand, if the treatment birds adjusted patch residence times to their gizzard mass after treatment, the relation between gizzard mass *at release* and patch residence times should be the same as observed in the reference birds. This was tested by comparing the explanatory power of linear mixed effects models with and without including a treatment parameter, fitted on the data of both the reference birds and the treatment birds, using either gizzard mass *at catch* or gizzard mass *at release*. The coefficients for the model intercept and log-transformed gizzard mass were constrained to the values that were estimated for the reference birds alone (by specifying an "offset" in the function "lmer"). Additional models were added to test for an effect of diet on patch residence times within the treatment birds, even though no effect of diet group on gizzard mass was found. To reveal a potential treatment effect that wore off after a few days in the field, which may be masked in the analysis of the full three weeks after release of the treatment birds, an additional analysis was performed with only the data of the first two days after the day of release.

A simulation to explain differences in patch residence times from diet preferences.

Foragers may individually differ in the minimum prey quality that they accept. Given that the decision of a foraging animal to leave a patch should be related to the encounter rate of acceptable prey at that patch, this is likely to affect average patch residence time (Charnov 1976). Red knots foraging on mollusc prey were shown to increase acceptance probability for prey of higher quality (van Gils *et al.* 2005a). Diet quality was expressed in terms of digestibility, measured as the amount of ash-free flesh mass per unit of dry shell mass. In red knots, gizzard masses were shown to reflect the digestive quality of the previous diet (Dekinga *et al.* 2001). Hence, if birds maintain the minimum gizzard mass that is needed to fulfil energy demands on prey of minimum acceptable digestive quality (at an ash-free dry flesh intake rate of 0.2 mg/s; van Gils *et al.* 2009), gizzard mass and patch residence time are expected to correlate. This expectation was formalized in a simulation.

We assumed a patchy distribution of food that varies in quality, and foragers that depart from a patch when prey of acceptable quality is not encountered within a fixed period of time (giving-up time; Krebs, Ryan & Charnov 1974). More sophisticated and perhaps more realistic behavioural rules exist (McNair 1982; Olsson & Holmgren 1998; van Gils *et al.* 2003b), but the predictions with the simple fixed giving-up time rule come reasonably close (with an approximately 10% lower encounter rate than when using more complex rules; Green 1984). Assuming that individuals do not differ in giving-up times, the predicted patch residence time is dependent on the total prey density and the prey quality distribution. Expected patch residence times were simulated for a sequence of minimum acceptable prey qualities by repeatedly drawing expected search times from an exponential distribution (Rita & Ranta 1998), where the average encounter rate (1 / search time) was defined as the average searching efficiency (de Fouw *et al.* 2016) times the density of acceptable prey. Patch residence time was then defined as the cumulative search time until search time exceeded the giving-up time, plus the cumulative handling time on all accepted prey. This procedure was repeated 100 times for each of the 44 locations where prey density and prey digestive quality were measured. A detailed description is given in Appendix S1.

RESULTS

Observed patch residence times

As expected, patch residence times of the reference birds showed a positive log-linear correlation with gizzard mass (Fig. 2, model 1.1 in Table 1). Patch residence times were longer in the night than during the day, but their correlation with gizzard mass did not differ between day and night (i.e. no interaction was observed between time-of-day and gizzard mass, Fig. 2, model 1.3 in Table 1). The low-water level did not explain any variation in patch residence times (model 1.2 in Table 1). Patch residence time estimations of the best model ranged from 67 min (95% CI: 54 to 82 min) for birds with a 5 g gizzard to 97 min (95% CI: 83 to 114 min) for birds with a 11 g gizzard during the day, and from 130 (95% CI: 96 to 174 min) to 189 min (95% CI: 146 to 244) during the night (Fig. 2, see table S1 for model 1.1 parameter estimates). The model without gizzard mass and only time-of-day showed very little support (model 1.7, AIC_c-weight = 0.05).

Patch residence times of treatment birds

The treatment birds had longer residence times than predicted on the basis of their gizzard mass at release (on average 58 min, Fig. 3A and 3C, model 3.1 in Table 1), and no effect of treatment group was observed. This suggests that the birds did not adjust patch residence time to their gizzard mass. Patch residence times was also longer than expected from gizzard mass at catch (on average 31 min, see Fig. 3B and 3D, model 2.1 in Table 1). With an AIC_c-weight of 0.06, the model without a treatment effect had little support (model 2.3 in Table 1). No difference was found between the diet groups within the treatment birds (models 2.2 and 3.3 in Table 1). Statistical summaries of the best models are given in Table S1.

Temporal trend in patch residence times of treatment birds

There was a tendency for increasing patch residence times in the treatment birds in the first week after release (Fig. 4). However, restricting the data to only the first two days after release, when mean patch residence times by the treatment birds appeared to be lower, did not change the qualitative outcome of the analysis. Even then, patch residence times remained longer than predicted from gizzard mass at release (on average 18 min, model S2.1 in Table S3, Fig. S2), and were as expected from gizzard mass at catch (on average 1 min longer, model S1.1 in Table S3, Fig. S2). Hence, although patch residence times were lower in the first days after release than thereafter, the treatment birds did not show lower patch residence times than expected from their original gizzard mass.

Explaining patch residence times from diet preferences

At the 44 identified feeding locations, average available and ingestible prey densities were 1104 molluscs m^{-2}, ranging from 0 to 9394 m^{-2} (SD = 1644). The frequency distribution of their digestive quality is given in Fig. 5A. The average giving-up time of free-living radio-tagged birds in the wild was 33 s, ranging between 3 s and 245 s. Based on the densities and prey quality distribution at the individual locations, simulations predicted that patch residence time should decrease when the minimum acceptable prey quality is increased (Fig. 5B). Repeating the simulations with giving-up times of 20, 30 and 40 s showed that expected patch residence time increases with giving-up time. Independent of the used giving-up time, the expected patch residence time decreased considerably with an increase in the minimum acceptable prey quality (Fig 5B). The range of expected patch residence times from the statistical models and the simulations are of the same order of magnitude, as are the estimated effect sizes of gizzard mass (Fig. 6).

DISCUSSION

The results of this study validate the proposed positive correlation between gizzard mass and patch residence time in free-roaming red knots (Bijleveld *et al.* 2016, Fig. 2), and show that individual diet preferences can indeed explain the observed among-individual variation in gizzard mass and patch residence time (Fig. 6). In agreement with an earlier test in captive red knots, a reduction in gizzard mass did not cause an adjustment in patch residence times of free-roaming red knots (Fig. 3A and C). These results are consistent with the suggestion that gizzard mass variation is the *consequence* rather than the *cause* of behavioural differences in red knots (Bijleveld *et al.* 2014).

Individual differences in giving-up time

Consistent differences in parameters such as searching efficiency and giving-up time may explain part of the large residual variation in a mean patch residence times (Fig 2, Table S1). Fig. 6 shows that differences in giving-up time are expected to have a large effect on patch residence time. Indeed, variation in the observed giving-up times was high, and hence these field measurements should be regarded as an indication of the order-of-magnitude rather than a precise estimate. In reality, giving-up time is expected to differ between individuals that differ in diet preferences and hence perceive a different food distribution, since giving-up time should depend on the expected prey encounter rate in the patch relative to the expected encounter rate in other patches (McNair 1982; Green 1984; van Gils *et al.* 2003b). This also may explain why the simulated values actually extended beyond the 95% confidence-interval of the mean observed patch residence times as a function of gizzard mass and time-of-day (Fig. 6). Birds with very small gizzards may in reality have higher giving-up times because their expected encounter rate may be lower in general.

Treatment effect

Although patch residence times were lower in the first days after release than thereafter (Fig. 4), the treatment birds did not show lower patch residence times than expected from their original gizzard mass (Fig. S2). Contrarily, after a few days in the field, the treatment birds started showing a tendency for even longer patch residence times than expected from their original gizzard mass (Fig. 3B and D). This may have resulted from other potential effects of the treatment, including e.g. stress or feather damage. Furthermore, the temporary absence from the field in itself may have had short-term effects on mean patch residence times, for example by influencing up-to-date information on the environment and social status among conspecifics.

Differences between night and daytime

Interestingly, patch residence times at night were longer than in daytime (Fig. 2). Because mollusc prey are sessile and are found by touch rather than by sight (Piersma *et al.* 1995), this is unlikely caused by day-night differences in searching efficiencies. Instead, we propose that the longer patch visits during the night were a consequence of predation-avoidance behaviour. Predation risk is a factor known to influence habitat selection in general (Lima & Dill 1990), and is known to influence the spatial distribution of red knots at Banc d'Arguin (van den Hout, Spaans & Piersma 2008; van den Hout *et al.* 2014). Falcons and harriers are mainly active during the day, whereas owls are active mainly during the night (Bijlsma 1990; van den Hout *et al.* 2014). Differences in the effectiveness of escape behaviours may lead to longer patch residence times at night (Sitters *et al.* 2001; Gillings *et al.* 2005). Sitting still as a defence may be common in the night (Mouritsen 1992), whereas evasion by way of flocking flights (see van den Hout *et al.* 2009) may be more common during the day (Gillings *et al.* 2005; Conklin & Colwell 2007). Although the relative contribution of these effects remains to be studied, anti-predation behaviour is likely to have had considerable influence on the observed foraging movements (Bijleveld *et al.* 2014).

The ontogenetic development of individual variation

Since many behavioural traits are known to be influenced by experience, and diet preferences in particular (e.g. Gillingham & Bunnell 1989; Whiteside, Sage & Madden 2015), the results of this study highlight the potential cascading effect of experiences on individual trait expression in general, behavioural as well as physiomorphic. Because individual differences in trait expression are essential to take into account when estimating ecological dynamics on the population level (Araújo, Bolnick & Layman 2011; Bolnick *et al.* 2011), it is of importance to know the extent to which experience drives the expression of different traits, behavioural and physiomorphic alike. To this end, research on the ontogenetic development of traits and their consistency over the animal's lifetime is highly relevant (Stamps & Groothuis 2010). For example, the influence of the environment on expression may decrease with age in some traits, but not in others (Senner, Conklin & Piersma 2015). Comparing these developmental effects between different populations may provide knowledge on the conditions that determine them. These may include, for example, the amount of spatial or temporal heterogeneity in prey density, prey quality and predation risk (as proposed by e.g. Gabriel *et al.* 2005; Mathot *et al.* 2012).

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DATA ACCESSIBILITY

Data is available from the Dryad Digital Repository: http://ddx.doi.org/10.5061/dryad.2s8rr (Oudman *et al.* 2016)

SUPPORTING INFORMATION

The following Supporting Information is available for this article online:

Appendix S1	Simulating patch residence times
Figure S1	Map of all residence patches
Figure S2	Patch residence times of the treatment birds during daytime on the first two days after release
Table S1	Parameter estimates of the best statistical models

Table S2 AIC$_c$ comparison of statistical models testing the effect of day after release on patch residence times

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TABLES AND FIGURES

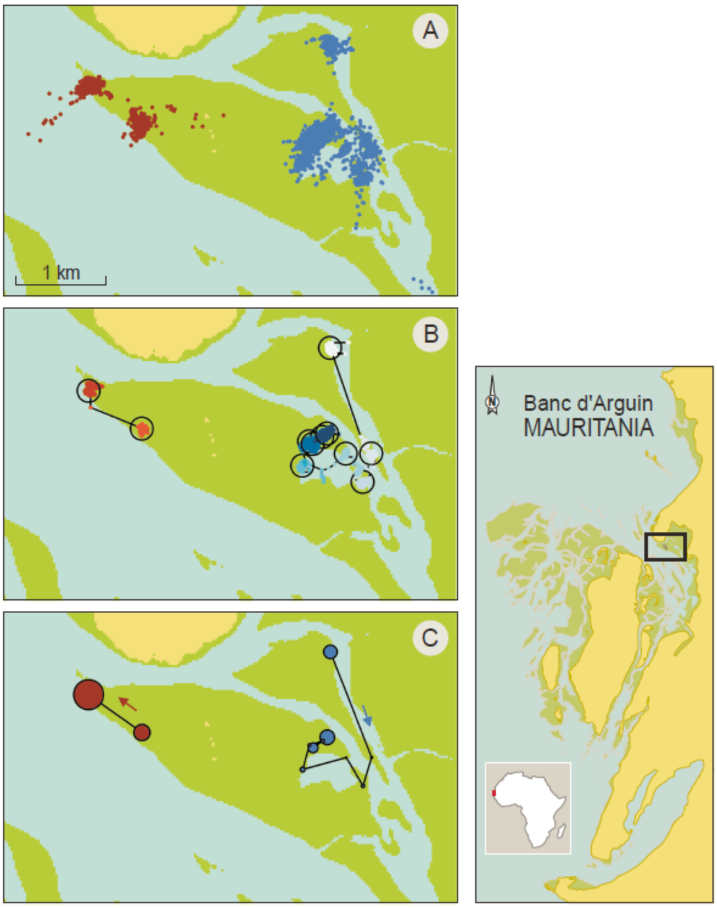

Figure 1. Example of Time-Of-Arrival (TOA) tracking data. (A) The dots show the estimated positions of two randomly chosen red knots during one low tide in the Baie d’Aouatif. The underlying map shows the mudflats that are exposed during low tide. (B) The position estimates are combined into residence time patches, shown by open circles. The median-filtered data underlying patches are shown in different shades. Subsequent positions are connected by lines. (C) Circles show the sequence of patch visits in the direction of the arrows. The size of circles show the relative duration of patch visits, i.e. patch residence times.

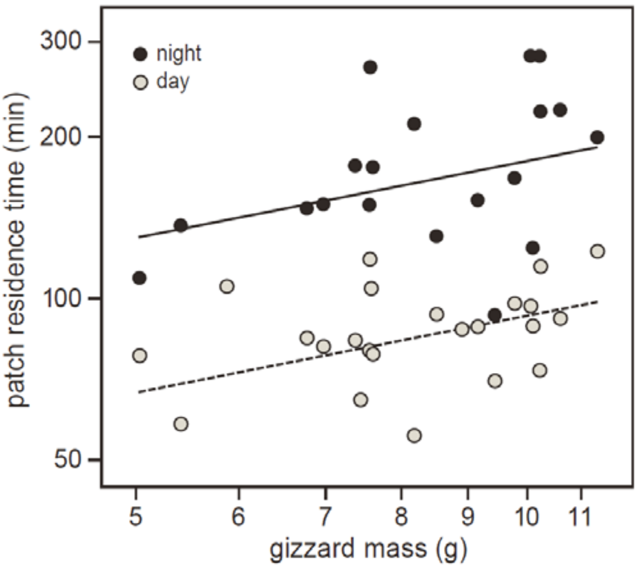

Figure 2. Patch residence times of reference birds increase with gizzard mass. Dots show the duration of patch visits per bird, averaged per low tide and then over all low tides. Regression lines show predicted values (model 1.1 in Table 1), which include differences between low-tides in the night (solid line) and during the day (dashed line). Note that the axes are log-scaled.

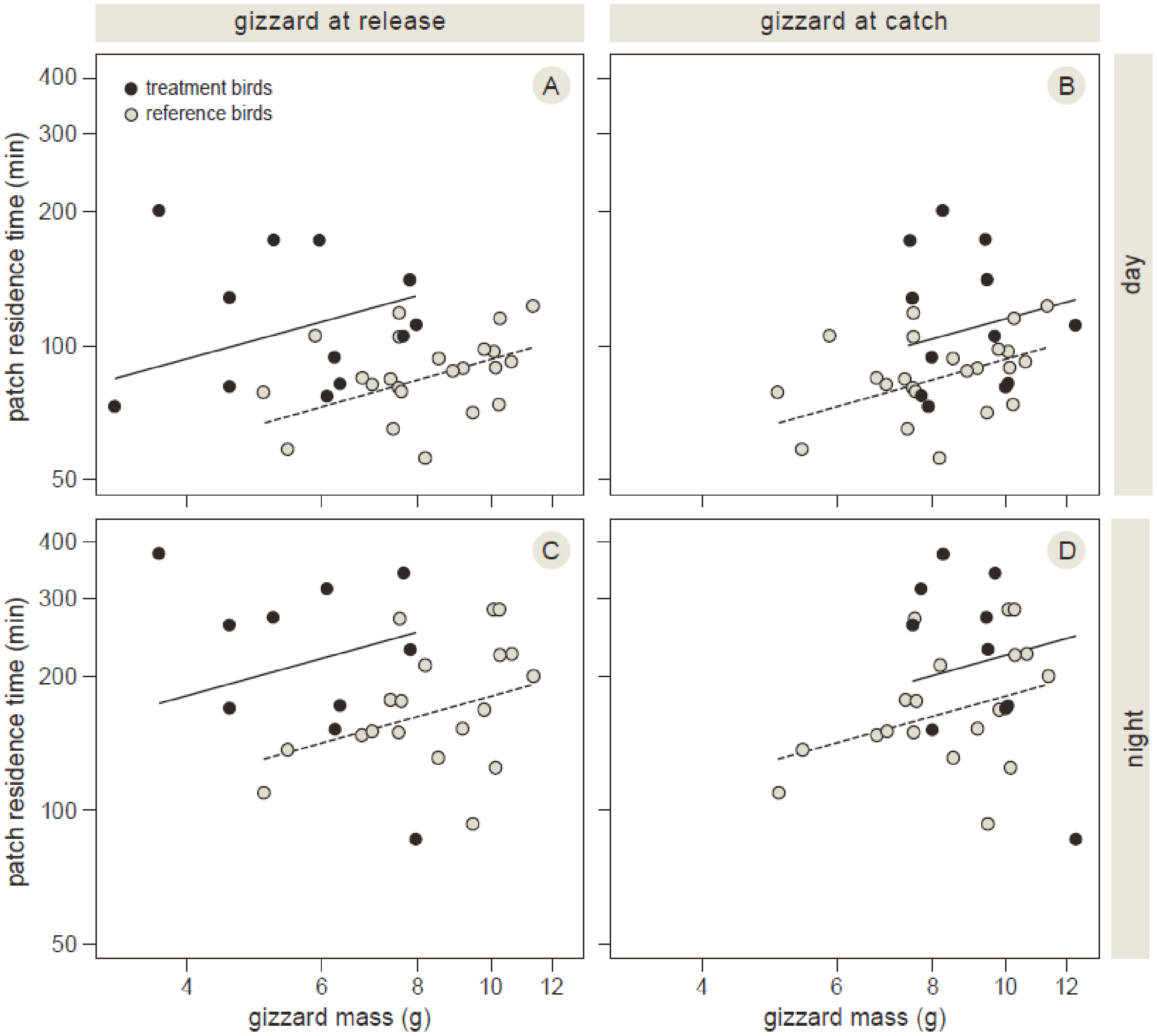

Figure 3. Patch residence time of treatment birds compared to the reference birds. Panels A and C show patch residence time as a function of gizzard mass *at release*, panels B and D show them as a function of gizzard mass *at catch*. Each dot is the mean value of one bird. Dotted lines show model predictions for the reference birds (model 1.1 in Table 1, see lines in Fig. 2). Solid lines show the treatment birds, where the slope is set equal to the dotted line (models 2.1 and 3.1 in Table 1, in which model 1.1 is used as offset). As shown by the vertical distance between the regression lines, the observed patch residence times match better with their gizzard mass *at catch* (panel B and D, models 2 in Table 1) than with their gizzard mass *at release* (panel A and C, models 3 in Table 1). Note that the axes are log-scaled.

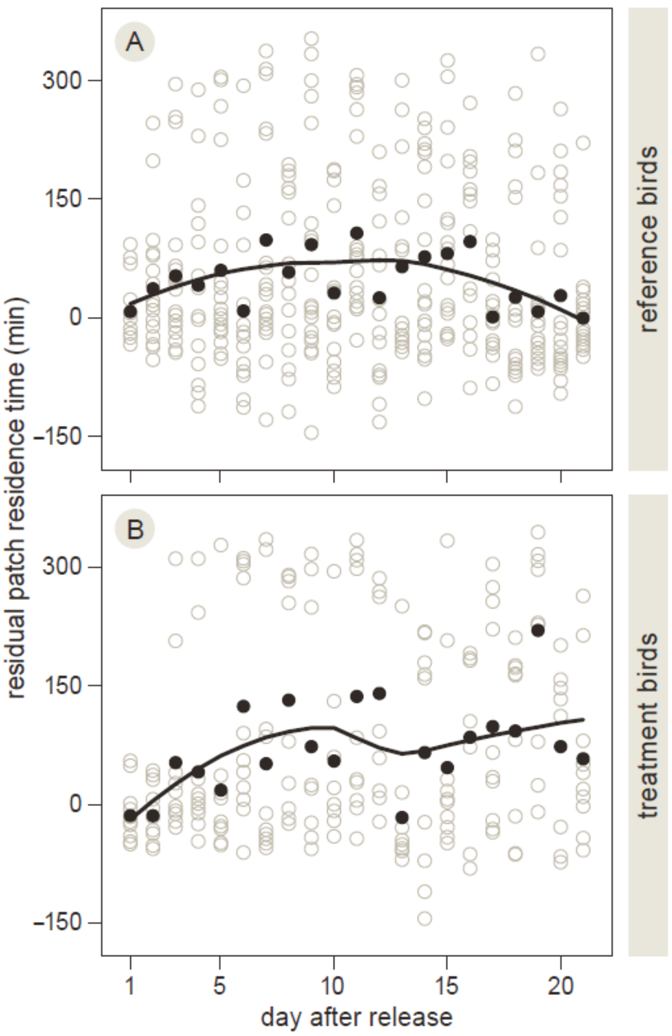

Figure 4. The effect of day-since-release on patch residence times. Shown are the residual values of model 1.1 (Table 1) against the day-since-release for the reference birds (A) and the treatment birds (B). The predicted log-transformed patch residence times are back-transformed before subtraction from the observed values. Open grey dots show the mean values per low tide averaged per bird. Black dots show the mean of those values per day-since-release. Black lines show loess-regressions (span = 0.7) on the model residuals.

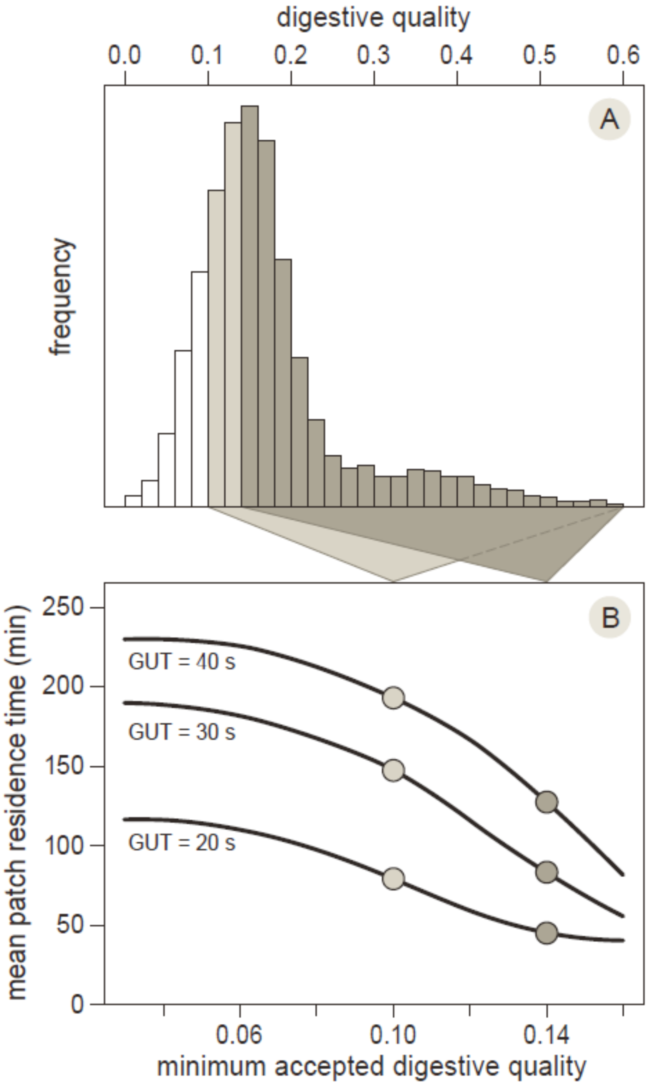

Figure 5. Proof of principle: simulating the effect of prey preferences on patch residence times using measured prey abundances. (A) Given the observed densities and frequency distribution of prey qualities, a forager that accepts all prey above a quality of e.g. 0.14 (dark grey bars) perceives a lower prey abundance than an animal that accepts all prey above a lower quality of e.g. 0.10 (light and dark grey bars combined). (B) When assuming that all animals have a fixed searching efficiency and giving-up time (GUT), the animal that accepts all prey above a quality of 0.10 is expected to depart later (light grey symbols vs. dark grey symbols). Simulations for three different giving-up time values are shown. Average measured giving-up time was 33 s.

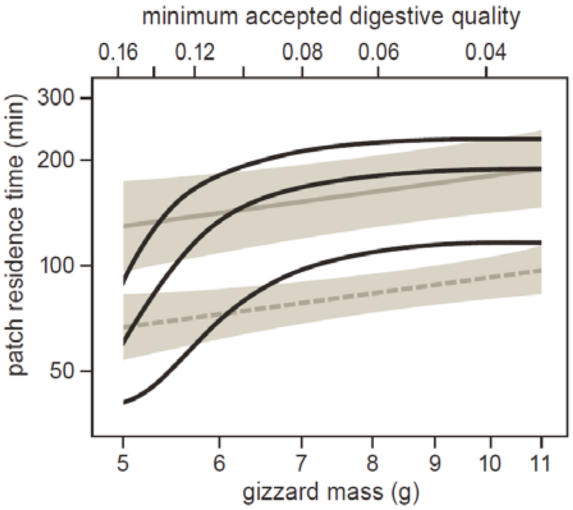

Figure 6. Predictions of the giving-up time model, compared to observed patch residence times. The black lines show simulated patch residence times as a function of gizzard mass for three giving-up time values (20, 30 and 40 s, from lower to upper line), assuming that birds maintain the gizzard capacity that is needed to fulfil energy demands on prey of the minimum accepted quality (upper x-axis). The thick grey lines show the log-linear regressions of the observed patch residence time against gizzard mass in the reference birds during the night (solid) and in daytime (dotted) (see Fig. 2). The 95% confidence intervals of the regressions are shown by the grey areas (only the uncertainty in the fixed effects of the regression model is considered). Note that the lower x-axis and the y-axis are log-scaled.

Table 1. AIC_c comparison of statistical models.

Model	Fixed effects[a]	K[b]	$\Delta\mathrm{AIC}_c$	AIC_c weight	Cum. weight	LL[c]
1.1	**Gizzard + Daytime**	**6**	**-**	**0.43**	**0.43**	**-76.1**
1.2	Gizzard + Daytime + Height	7	2.01	0.16	0.59	-76.1
1.3	Gizzard × Daytime	7	2.04	0.15	0.74	-76.1
1.4	Gizzard × Height + Daytime	8	3.49	0.07	0.81	-75.8
1.5	Gizzard × Daytime + Height	8	4.06	0.06	0.87	-76.1
1.6	Daytime × Height + Gizzard	8	4.06	0.06	0.93	-76.1
1.7	**Daytime**	**5**	**4.34**	**0.05**	**0.98**	**-79.3**
1.8	Daytime + Height	6	6.37	0.02	0.99	-79.3
1.9	Daytime × Height	7	8.42	0.01	1	-79.3
1.10	Gizzard + Height	6	17.85	0	1	-85.0
1.11	Gizzard	5	18.34	0	1	-86.3
1.12	Gizzard × Height	7	19.15	0	1	-84.7
1.13	Height	5	22.60	0	1	-88.4
1.14	1	4	22.89	0	1	-89.6
2.1	**Offset(model 1.1, giz at catch) + Treatment**	**4**	**-**	**0.69**	**0.69**	**-121.6**
2.2	Offset(model 1.1, giz at catch) + Treatment + Diet	5	2.01	0.25	0.94	-121.6
2.3	**Offset(model 1.1, giz at catch)**	**3**	**4.76**	**0.06**	**1**	**-125.0**
3.1	**Offset(model 1.1, giz at release) + Treatment**	**4**	**-**	**0.72**	**0.72**	**-122.4**
3.2	Offset(model 1.1, giz at release) + Treatment + Diet	5	1.93	0.28	1	-122.4
3.3	Offset(model 1.1, giz at release)	3	20.02	0	1	-133.4

NB. Linear mixed-effects models (function “lmer” in R package “lme4”; Bates *et al.* 2015; R Core Team 2015) with tide-ID and bird-ID as random intercepts. Best models are in bold (Burnham & Anderson 2002). Parameters were estimated by maximizing the log-likelihood. Log-transformed patch residence time is the response variable in all models, which is averaged per bird per low tide after transformation.

[a] In models 1, “Gizzard” refers to gizzard mass at catch. “Daytime” is a factor with two levels: day and night. “Height” refers to the astronomical water level at the specific low tide. To test whether the treatment birds deviate from the predictions derived from the reference bird data, the estimated coefficients of the fixed effects of model 1.1 are used as an offset in models 2 and 3. Models 2 contain gizzard masses as measured when the birds were caught, models 3 contain gizzard masses before release. Factor “Treatment” refers to whether the bird was in the treatment group or the reference group. “Diet” refers to the diet group within the treatment group (either a soft diet or a partially hard-shelled diet).

[b] The number of parameters in the model.

[c] Log-likelihood.