**Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator**

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**SUMMARY**

Consistent intra-population variability in foraging behaviour is found among a wide range of taxa. Such foraging specialisations are common among marine vertebrates, yet it is not clear how individuals repeatedly locate prey or foraging sites at ocean-wide scales. Using GPS and time-depth loggers we studied the fine-scale foraging behaviour of central-place northern gannets *Morus bassanus* at two large colonies. First, we estimated the degree of consistency in individual foraging routes and sites across repeated trips. Second, we tested for individual differences in searching behaviour in response to environmental covariates using reaction norms, estimated from mixed effect models. Adult gannets tracked over multiple foraging trips showed repeatable between-individual differences in terminal points and departure angles of foraging trips, but low repeatability in trip duration and trip length. Importantly, individual birds showed highly repeatable dive locations, with consistently different environmental conditions (such as copepod abundance), suggesting a high degree of foraging site specialisation. Gannets also showed between-individual differences in searching behaviour along environmental gradients, such that individuals intensified searching under different conditions. Together these results suggest that widespread individual foraging consistency may represent specialisation and be linked with individual responses to environmental conditions. Such divergent searching behaviour could provide a mechanism by which consistent foraging behaviour arises and is maintained among animals that forage across large spatial scales.

**Introduction**

There is increasing work detailing the extent of intra-population variation and individual specialisation in traits, including diet and foraging (Araujo et al. 2007; Bolnick et al. 2003). While such foraging specialisations are often determined by ontogenetic or sex differences (e.g. Shine 1989; Shine 1991; van de Pol et al. 2009), individual-level specialisations independent of these factors are also common. Consistent individual differences in foraging site and diet are prevalent among marine vertebrates (See Appendix Table S1), which live in an environment where oceanic fronts, upwellings and other sub-surface features often lead to temporally and spatially predictable prey patches (Weimerskirch et al. 2007). Moreover, as these species breed in dense aggregations, intra-specific competition is high, which may lead to strong frequency dependent selection for divergent foraging strategies (Araujo et al. 2007).

When air-breathing marine vertebrates are constrained to forage from a central place, they may repeatedly cover huge distances between breeding sites and foraging grounds. However, how consistent individual behaviours arise and are maintained is not known. There is evidence that these animals alter searching intensity in response to biotic and abiotic cues (Hamer et al. 2009), indicating that they use such environmental proxies to locate prey (Pinaud and Weimerskirch 2005; Votier et al. 2010). Furthermore, subsections of the population differ in the scale of their search response to environmental conditions, such as sea surface temperature and chlorophyll concentration (Pinaud and Weimerskirch 2005), demonstrating a degree of individual divergence in searching behaviour. However, the possibility that individuals increase searching under different environmental conditions has not been tested. The spatial consistency previously reported could arise from individuals searching in different locations for the same environmental conditions or for different environmental conditions at different locations. To test these hypotheses requires high-resolution data on the spatial movement of species and accurate measures of the environmental conditions over which they forage.

Bio-logging technology has been deployed extensively on marine vertebrates, resulting in some of the best data sets on fine scale foraging movements (Wilson et al. 2002). From these, it is possible to pin-point not only foraging locations, but also changes in searching behaviour which precede these events. In this study, we used a combination of GPS and time-depth loggers, in tandem with data on marine environmental conditions, to investigate fine-scale foraging behaviour in a medium-ranging central place predator, the northern gannet (*Morus bassanus*, hereafter gannet) at two large colonies in different water masses. We used repeatability measures to examine consistency in foraging routes, site fidelity and dive characteristics, and also investigate the environmental conditions under which gannets dive. These consistently divergent behaviours could themselves be termed foraging specialisations, as they demonstrate that individual niche width is considerably narrower than the population niche (Previously described for trophic niche; Bolnick et al. 2003). However, as other definitions of specialisation involve a restriction in individual behaviour (Bolnick et al. 2003) which we did not test in this paper, we report consistency and divergence in our data and discuss the potential implications for specialisation. We used reaction norms, estimated from mixed effect models (Nussey et al. 2005; Dingemanse et al. 2010) to measure the change in individual search behaviour along three environmental gradients, indicative of biotic and abiotic proxies for resource availability in the marine environment. While these models, commonly applied in evolutionary biology, have been advocated to help understand both seabird responses to environmental conditions (Gremillet and Charmantier 2010) and changes in behaviour at the individual level (Dingemanse et al. 2010), they have yet to be used to study changes in individual foraging behaviour in a wide-ranging marine predator.

**2. MATERIALS AND METHODS**

***(a) Data collection***

Fieldwork was conducted on Grassholm Island, Wales, UK (51o 43’ N, 05o 28’ W) and Ile Rouzic, Brittany, France (48° 54’ N, 3° 26’ W). Data from multiple foraging trips were collected during chick-rearing from 1st – 10th June 2010 (Rouzic) and 3rd - 21st July 2010 (Grassholm), for pairs with chicks aged 4 - 6 weeks. Birds on Rouzic bred ca. one month earlier than those on Grassholm (S. Patrick, unpublished data). On Grassholm about 40,000 pairs of gannets breed annually and here 26 individuals were fitted with i-gotu GPS loggers (Mobile Action Technology; mass 30g), and programmed to record locations every two minutes. All the loggers were recovered and 18 had useable data. In addition, G5 time-depth recorders (TDRs; CEFAS technology, 6g) were deployed on ten of these birds, recording depth every 0.1 seconds when submerged. GPS devices were attached at the base of the tail and TDRs under the central two tail feathers using Tesa tape and previous work suggests that loggers such as these have no adverse effects on breeding gannets (Garthe et al. 2007; Hamer et al. 2009; Hamer et al. 2007). On Rouzic about 20,000 pairs of gannets breed and here 19 individuals were fitted with GPS loggers (Earth & Ocean Technologies and Technosmart; mass 60g), attached using TESA tape and programmed to collect location fixes every 1 second. These data were then re-sampled to a resolution of 2 minutes to allow direct comparisons between colonies and of the 16 recovered, 13 of these loggers had useable data. No dive data were collected from Rouzic.

***(b) Measuring environmental gradients***

Spring 2010 sea-surface temperature (SST, oC; <http://modis.gsfc.nasa.gov/>), spring 2010 chlorophyll-a concentration (Chl-a, mgm-3; <http://modis.gsfc.nasa.gov/>) and copepod biomass averaged over the period of 50 years (m-3, Continuous plankton recorder (CPR), Sir Alistaier Hardy Foundation for Ocean Science) were estimated at a resolution of 30 km by 30 km (Figure 1; See electronic supplementary material for detailed methods). These environmental covariates are thought to be proxies for prey abundance and have been shown to be important predictors of foraging behaviour (Votier et al. 2010). We selected this spatial scale as the resolution of CPR data prohibits a finer resolution of copepod abundance being estimated. While fluctuations in SST and Chl-a can be estimated on a finer temporal scale (Votier et al. 2010), there was incomplete coverage across our study area during the study period. Lower sea surface temperatures are typically associated with higher primary productivity (chlorophyll concentration; Figure 1). Copepods feed on phytoplankton and as such there is a positive relationship between chlorophyll and copepod levels in our study system (Figure 1). While the abundance and distribution of fish is unknown in this area, small fish which prey on copepods may be expected to have a positive relationship with copepod levels. The relationship between copepods and large piscivorous fish is unclear, as the spatial and temporal lag may lead to a mismatch between hotspots. As such, variation in the levels of these environmental covariates may demonstrate individual differences in prey choice. However, while we can predict the relationships between these environmental covariates, different oceanographic processes, temporal and spatial lags, and variation in diet among copepods and fish make the exact relationships very difficult to ascertain. All environmental covariates were population mean-centred to enable us to compare slopes among the population (van de Pol & Wright 2009).

***(c) Individual foraging consistency***

First, we measured repeatability in foraging behaviour using seven variables. For each GPS track, we calculated: (1) trip duration (hours), (2) total distance travelled (km), (3) departure angle from the colony (by averaging the first five bearings >10 km from the colony to remove the influence of nest site location, degrees) and (4) the furthest location from the colony (longitude and latitude at terminal point). Using TDR dive data from Grassholm gannets we also determined (5) maximum dive depth (m) and (6) dive profile shape, indicative of different foraging strategies (V shaped: bottom time < 3 seconds, U shaped: bottom time > 3 seconds; (Garthe et al. 2000) and by combining GPS and TDR data we estimated (7) location of all dives. Grassholm GPS data was interpolated to a resolution of 1 second using a cubic spline interpolation to identify locations of dives and the environmental conditions at these sites extracted using ArcGIS 9.1. The repeatability (r) of each index and its associated standard error and p-value were estimated in the R package: rptR (Nakagawa and Schielzeth 2010). For departure angles, which are circular measures, bounded by 0 and 360, we used a circular ANOVA (R package; circular) and calculated the repeatability using Lessels & Boag (1987) and their standard errors using Becker (1984). P-values are not available using this latter method. Individual colonies were analysed separately as they had different foraging ranges.

Second, we measured individual differences in the environmental conditions at dive sites. Every dive along each foraging track was associated with a measure of SST, Chl-a concentration and copepod biomass, to determine whether diving behaviour changed under different environmental conditions. The repeatability of each environmental covariate at the diving sites of an individual, and associated standard errors and p-values, was calculated using rptR (as above).

***(d) Individual search behaviour***

When seabirds encounter a prey patch, they increase turning and slow down, which is associated with intensifying searching or prey intake (Pinaud and Weimerskirch 2007; Hamer et al. 2009). Previous work has shown that foraging sites can be inferred from GPS tracking data, by measuring these changes in turning and speed (Votier et al. 2010). Moreover, these measures can not only be used to highlight foraging areas, but can provide a continuous assessment of foraging intensity along foraging tracks. Using GPS tracks, we tested how changes in flight speed and path tortuosity of individual gannets varied with environmental conditions (see *(b) Measuring environmental gradients* above). This was modelled using reaction norms, fitted in random slope mixed models (see Dingemanse et al. 2010 for more details). We modelled (i) straightness: the shortest straight line distance across a circle of 30km, offset against the actual track length across the circle, fitted with a binomial error structure (see electronic supplementary material for more details) (ii) speed: the speed across a 30km circle, fitted with a Gaussian error structure. We estimated the straightness and speed every two minutes along all foraging tracks. Individual bird identities were fitted as random slopes, that varied along SST, Chl-a and copepod gradients simultaneously (see Box 4 in Dingemanse et al. 2010 for details on fitting reaction norms along multiple environmental gradients) and individual trip and bird were fitted as random intercepts. All environmental covariates and colony were included as fixed effects. We included a random effect with one level per observation (observational level random effect) to model the additive overdispersion in binomial models and fitted models using the lmer package in R (Bates and Maechler 2010).

As such, we fit the general random intercept and slope model:

Yij ~ (μ + δi ) + (β + Δi)Xij + eij

Where:

 μ = population average intercept ;

δi =deviation from population average intercept for individual i;

β = population average slope;

Δi =deviation from population average intercept for individual i;

eij = residual variation.

For analyses we fitted:

Yijk ~ (μ + c + bi + tj) + (β1 + β2+ β3 +β1i + β2i + β3i)Xijk + eijk

i = individuals;

j = observations grouped by individual trips

c = deviation from population intercept as a result of colony differences

bi = deviation from population intercept as a result of variation between birds

tj  = deviation from population intercept as a result of variation between trips

eijk = residual variation

β1 = population slope as a result of chlorophyll concentration

β1i = deviation from population average chlorophyll concentration for individual i

β2 = population slope as a result of SST

β2i = deviation from population average SST for individual i

β3 = population slope as a result of copepod concentration

β3i = deviation from population average copepod concentration for individual i

The significance of variables was estimated by comparing models with and without the term of interest, using likelihood ratio tests (LRTs) where:

2log(L2/L1) = 2[log(L2) - log(L1)]

L1 = the likelihood of the full model

L2 = the likelihood of the restricted model

The LRT follows a chi-squared distribution, with the difference in the number of parameters between the models used as the number of degrees of freedom (Pinheiro and Bates 2000)

Model comparisons with different random effect structures were fitted using *REML* (restricted maximum likelihood)and those comparing models with different fixed effect structures were fitted using *ML (*maximum likelihood)*.* While there are some concerns regarding the use of LRTs to test fixed effects in mixed models (Pinheiro and Bates 2000), these are thought to apply only to studies with small sample sizes (Fitzmaurice et al. 2004). In full models, an unstructured variance covariance matrix was fitted. However, to test for the significance of random effects, we constrained the covariance of the effect of interest to zero to ensure we tested the significance of the effect and not the combined significance of the effect and its covariance. The variation explained by each model was calculated using a Nagelkerke pseudo R2 (Nagelkerke 1991), comparing the chosen model to a null model (with only a dummy random intercept). Random slopes were estimated using a full fixed effect structure. The estimates for fixed effects were extracted after removing non-significant random terms. All analyses were carried out in Matlab (R2009b, Mathworks), R 2.11.1 (R Development Core Team 2010) and ArcGIS 9.3 (ESRI, USA).

**3. RESULTS**

***(a) Summary of data***

On Grassholm, a total of 49,902 GPS locations were collected from 18 individuals, along a total track length of 31,553 km. We obtained three repeat trips from nine individuals, four repeats from eight individuals and six repeats from one individual. Individual track distances ranged from 77 km to 1782 km, travelling between 33 km and 472 km away from the colony with trip durations of 2.7 to 97.3 hours. Dive data from 23 trips were collected from 8 individuals. The deepest dive was 22.2 m and the longest lasted 37.5 seconds (Figure 1a). From Rouzic, 58,599 GPS locations were collected from 13 individuals, with a total distance of 21, 235 km travelled. We obtained two repeats from one individual, three repeats from two individuals, four repeats from seven individuals and five repeats from three individuals. The total distance travelled ranged from 68 km to 798 km with a maximum distance from the colony of 28 km to 193 km and trip durations from 14.4 to 46.5 hours (Figure 1a).

 ***(b) Individual foraging consistency***

At both colonies, individuals consistently foraged along the same paths (Figure 2) with highly repeatable terminal points (Grassholm: Latitude r = 0.54 ± 0.13; p = 0.001, Longitude r = 0.53 ± 0.13; p = 0.008; Rouzic: Latitude r = 0.57 ± 0.15; p < 0.001, Longitude r = 0.66 ± 0.13; p < 0.001) and departure angles (Grassholm: r = 0.71 ± 0.09; Rouzic: r = 0.55 ± 0.14). Individuals were not repeatable in trip duration (Grassholm: r = 0.00 ± 0.13; p = 0.70; Rouzic: r = 0.00 ± 0.07; p = 0.79) or total distance travelled (Grassholm: r = 0.06 ± 0.08; p = 0.26; Rouzic: r = 0.05 ± 0.09; p = 0.25).

At Grassholm, individual gannets showed both highly repeatable dive locations (Latitude r = 0.86 ± 0.10; p < 0.001, Longitude r = 0.84 ± 0.10; p < 0.001; Figure 2) and environmental conditions at these sites (SST: r = 0.46 ± 0.14; p < 0.001; Chl-a: r = 0.77 ± 0.15; p < 0.001; Copepods: r = 0.76 ± 0.13; p < 0.001). However birds were much less repeatable in their maximum dive depths (r = 0.18 ± 0.07; p < 0.001) and dive shape (r = 0.18 ± 0.08; p < 0.001).

***c) Individual search behaviour***

Gannet at-sea behaviour changed with environmental conditions and there was clear between-individual variation. Gannets altered their search behaviour differently according to copepods (Straightness: χ21 = 242.45, p < 0.001; Speed: χ21 = 2695.5, p < 0.001), Chl-a (Straightness: χ21 = 517.15, p < 0.001; Speed: χ21 = 4593.8, p < 0.001) and SST (Straightness: χ21= 10.34; p = 0.001; Speed: χ21 = 2418.9, p < 0.001; Table 1; Figure 3). There were strong individual differences in the strength and direction of slopes demonstrating individual responses to environmental cues. Individuals with negative slopes increased searching with increasing SST, Chl-a and Copepods. Conversely individuals with positive slopes increased searching as SST, Chl-a and copepods decreased. Straightness and speed models accounted for 50% and 55% of the data variance, respectively.

**4. DISCUSSION**

Here we report novel aspects of foraging behaviour demonstrating that individuals show strongly consistent foraging behaviours and dive under consistently different environmental conditions. These results are strengthened by analyses showing that individuals also increased searching under different conditions. Together, these data suggest that spatial foraging consistency, reported here and elsewhere, may represent individual differences in preferred foraging habitat. Furthermore, individual responses to environmental gradients may provide a mechanism through which spatial foraging specialisation could arise.

Individual consistency and specialisation is predicted to be important as it acts to reduce intra-specific competition (Bolnick et al. 2003). This has previously been shown to occur through spatial partitioning, whereby individuals forage in different locations or at different depths (Table 1). Here we show further evidence of consistently divergent space use between individual birds, and that this is tightly linked to consistent departure angles from the colony (see also Pettex et al. 2010). While this spatial segregation limits individual overlap in foraging area, it reveals little information on individual dietary segregation. Results from stable isotope analysis suggest that individuals forage on different prey types and that this variation persists over time (Votier et al. 2010). Here, using high resolution GPS tracking data, we link these two findings, demonstrating that spatial segregation is associated with differences in environmental conditions at foraging sites. As environmental variables are thought to be good proxies for prey type and abundance (Votier et al. 2010), our findings provide support for individual dietary specialisation (but see Votier et al. 2010; Gremillet et al. 2008).

Given that individuals increase their searching intensity before foraging (Hamer et al. 2009; Pinaud and Weimerskirch 2007), individual differences in foraging conditions should be coupled with individual differences in searching response along these gradients. Our results provide the first support for this hypothesis, demonstrating that individuals increase their searching intensity under different environmental conditions. These results together indicate that the consistent differences in foraging behaviour exhibited here and reported elsewhere may be maintained by, or may even have arisen as a consequence of, variation in individual responses to environmental gradients, driving diversification and consistency across large spatial scales. Given the short term nature of our study, we can not exclude that these consistent behaviours occur as a result of highly successful foraging grounds being repeatedly exploited and that individuals change behaviour when unsuccessful. While this seems unlikely across the population, longer term and between year comparisons would be able to exclude success as a driver of consistency.

By using population mean centred environmental covariates, we calculate a measure of plasticity in searching behaviour associated with habitat choice (Discussed in van de Pol & Wright 2009; Dingemanse et al. 2010). However recent work has suggested that these two components can be partitioned, isolating non-random association with environmental conditions and plasticity in searching response simultaneously (Dingemanse and Dochtermann 2013). As bio-logging continues to become cheaper and data sets build over time, sufficient data should exist to examine these components separately. Some definitions of foraging specialisation involve an element of constraint on behaviour (Bolnick et al. 2003) and reaction norms, used across time and contexts, could assess whether these behaviours are restricted within individuals.

We also report much less repeatable behaviours, such as trip duration and total distance travelled, suggesting that birds use different routes to arrive at foraging sites. Previous studies have also reported individual variability in certain behaviours, and it has been suggested that this flexibility allows birds to adapt to changing oceanographic or biological pressures (e.g Weimerskirch et al. 1993; Iverson and Esler 2006; Gremillet and Boulinier 2009). Fine scale weather conditions are likely to influence the most efficient route to foraging sites, and we suggest this may account for within-individual variation in trip duration and length. While learning and memory effects have been suggested to be important in locating foraging grounds, evidence that individuals use different routes to repeatedly forage at the same location suggests that individual assessment of environmental variables is likely to be important.

While we show individual differences in response to environmental variables, it is still unclear what sensory cues birds are using to assess the environment. There is evidence that Procellariiformes (Nevitt et al. 2008; Mardon et al. 2010) and penguins (Wright et al. 2011) use olfaction to locate their prey and differences in environmental gradients could potentially lead to differences in the odour landscape at sea. However there is currently no evidence for individual differences in olfactory responses and the fused nostrils of gannets suggest that odour is unlikely to facilitate prey capture. Differences in small scale tidal structures or phytoplankton blooms are potentially conspicuous visual cues (Tew Kai et al. 2009), but more work is required to determine whether such features are relevant for searching gannets and other marine predators. Furthermore, the exact relationships between environmental covariates and prey abundance and diversity are lacking but work combining stable isotope signatures with habitat preferences may be able to clarify these patterns in the future.

This study presents consistent results from two colonies, in different water masses. Given the variation in timing of breeding, oceanographic conditions and anthropogenic pressures (e.g. fishing intensity), the similarities between colonies suggest a generality in our results. We demonstrate a high degree of individual foraging consistency among central place breeding gannets. We show that individual gannets consistently differ in their at-sea movements along environmental gradients, and this intra-population variation in search behaviour may result in repeated use of different foraging locations. Therefore, we believe these individual-level responses to environmental variables in marine ecosystems may play an important role in the origin and maintenance of foraging specialisations over very large spatial scales. Moreover, we suggest that individual search responses offer a plausible underlying behavioural mechanism for widely reported individual foraging specialisations among marine vertebrates.

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***Table Legends***

Table 1: The results of models estimating the individual straightness and speed response to environmental covariates. Random slopes were estimated using a full fixed effect structure. Non-significant random slopes were dropped from the model to test the significance of fixed effect terms.

|  |  |  |  |
| --- | --- | --- | --- |
|  | **Variables** | **Tortuosity** | **Speed** |
|  | **Sample size** | Data points = 43,443; Tracks = 113; Birds = 31 |
| **Random Slopes** | **Copepods** | χ 1 = 242.45; p < 0.001 | χ 1 = 2695.5; p < 0.001  |
| **Chlorophyll**  | χ 1 = 517.15; p < 0.001 | χ 1 = 4593.8; p < 0.001 |
| **Sea surface temperature** | χ 1 = 10.34; ; p = 0.001 | χ 1 = 2418.9 ; p < 0.001 |
| **Random intercepts** | **Individual Bird** | χ 1 = 4.4; p = 0.04 | χ 1 = 146. 0; p < 0.001 |
| **Individual Track** | χ 1 = 1364.3; p < 0.001 | χ 1 = 9779.6; p < 0.001 |
| **Fixed Effects** | **Colony** | χ 1 = 13.12.; p <0.001; Grassholm: -1.49 ± 0.15Rouzic: -1.09± 0.22 | χ 1 = 1.57; p = 0.21; |
| **Copepods** | χ 1 = 12.46; p < 0.001;Estimate: 0.007 ± 0.002 | χ 1 = 5.57; p = 0.02;Estimate: 0.36 ± 0.001 |
| **Chlorophyll**  | χ 1 = 0.40; p = 0. 52; | χ 1 = 0.44; p = 0.51; |
| **Sea surface temperature** | χ 1 = 0.00; p = 1.00; | χ 1 = 1.36; p = 0.24; |

***Figure Legends***

Figure 1. Movements and environmental conditions experienced by chick rearing northern gannets. (a) GPS tracks of adult gannets from Grassholm (18 birds, 66 tracks, July and August 2010) and Rouzic (13 birds, 51 tracks, June 2010); (b) sea surface temperature; (c) chlorophyll-a concentration; (d) average copepod biomass. Environmental variables are shown at a resolution of 30x30km (white cells = no data).

Figure 2. Specialisation in gannets. (a) Example repeat tracks and dives for four birds from Grassholm (3-4 tracks per bird) are shown. Individual birds and tracks are shown in different colours and shades respectively, with dives plotted as circles in the colour applicable to the track when they occurred. The colour gradient represents increasing track numbers: Pale colours (left of box) are first tracks measured and dark tracks (right of box) are last tracks measured. (b) Example repeat tracks are shown for four Rouzic birds (3-4 tracks per bird), colour coded as above. All birds show highly repeatable departure angles and foraging locations and Grassholm birds, repeatable dive sites. All tracks are sequential repeats, separated by the time a bird spent at the colony.

Figure 3. Individual changes in searching in response to environmental gradients. Each slope shows an individual gannet’s search response to a mean centred (standardised) environmental gradient and these plots highlight the variation in direction and strength of slope between individuals, providing evidence that individuals intensify searching under different conditions. (a) Variation in individual speed response to copepod biomass. (b) Variation in individual speed response to Chl-a. (c) Variation in individual speed response to SST (d) Variation in individual path straightness response to copepod biomass. (e) Variation in individual path straightness response to Chl-a.

The following Supporting Information is available for this article online:

**Appendix 1**

**Table S1.** Individual foraging specialisation has been demonstrated in a wide-range of air-breathing marine vertebrates.

**Appendix 2:** Additional methods and analysis details

**Table S2 & S3:** The correlations between all foraging and dive parameters from the Grassholm colony (S1) and Rouzic (S2).

**Figure S1:** A schematic diagram demonstrating how path straightness was calculated.