



Consistency over time of spatial patterns of fibre diameter and staple length variation over sheep fleeces



R.M. Rodríguez Iglesias^{a,b,*}, D.A. Pevsner^a, C.A. Rosas^a

^a Departamento de Agronomía, Universidad Nacional del Sur, 8000 Bahía Blanca, Argentina

^b Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

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ABSTRACT

Macro-patterns of wool variation over sheep fleeces are markedly diverse among individuals. Assessing the *consistency over time* (i.e. repeatability) of those patterns would be relevant for sampling, individual selection, and raw wool classing, but there are no canonical procedures available to estimate the repeatability of 2D traits. We devised an approach to evaluate consistency over time as a proxy for repeatability in a 2D domain and applied it to a dataset of fibre diameter (FD) and staple length (SL) measurements. Data were collected over a regular grid of 128 sampling points from 10 Corriedale ewes sampled before shearing in two consecutive years. We scaled down the dimensionality of the data set from 128D to 2D, projected the new synthetic data ($n = 20$, one per animal per year) on principal coordinate axes, extracted all relevant Euclidean distances between pairs of data points, and applied an *ad hoc* coefficient (C_{sp}) designed to assess consistency of spatial patterns over time in a scale from zero (random dispersion independent of individual animal origin) to one (perfect overlapping of data points from the same animals in different years). Point estimates of C_{sp} (\pm bootstrap-estimated SE) were 0.78 ± 0.06 and 0.64 ± 0.08 for FD and SL, respectively. Estimated 95% confidence intervals excluded zero for both traits, FD: [0.60, 0.84]; SL: [0.43, 0.75]. Contributions of individual animals to overall C_{sp} coefficients were independent between traits ($r = -0.11$, $P = 0.76$). Main conclusions were that considering the spatial variability of wool traits over fleeces may help avoiding biases of phenotyping, estimation of genetic and phenotypic parameters, and selection decisions, that spatial patterns of variation of FD and SL over sheep fleeces are similarly repeatable across years, and that FD and SL pattern expressions may be independently regulated.

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1. Introduction

The fibre coat of sheep is produced by a population of epithelial appendages replicated according to a periodic pattern, a highly conserved trait in amniotes (Chung and Homberger, 2003). Morphogenetic mechanisms, strikingly similar across taxa, have already determined the

micro-structure of the spatial pattern of wool follicles over the skin by the time animals are born (Rogers, 2006). From then on, variation of raw wool traits over fleeces will depend upon (epi)genetic and environmental factors interacting at the wool follicle level; spatial *macro-patterns* will eventually emerge and presumably stabilize as individuals mature.

Macro-pattern features, such as gradients of variation over fleeces and regionalization of trait values, have been documented for a number of raw wool traits in different fibre-producing species (e.g., Angora goats: Newman and Paterson, 1999; alpaca: McGregor et al., 2012; sheep: Fish

* Corresponding author at: Departamento de Agronomía, Universidad Nacional del Sur, 8000 Bahía Blanca, Argentina. Tel.: +54 291 4595102; fax: +54 291 4595127.

E-mail address: cerodri@criba.edu.ar (R.M. Rodríguez Iglesias).

et al., 2002). We recently reported that when densely sampled at the scale of wool staples, fibre diameter (FD) and staple length (SL) show bilaterally symmetric spatial patterns characterized by non-linear trends over fleeces and ample variation among individuals, a result with possible implications for wool sampling, selection, and wool classing (Rodríguez Iglesias et al., 2009a,b, 2013). We also showed that sample point estimates of the repeatability of raw wool traits vary considerably over fleeces and that attributes of the spatial variation, such as the inter-sample distance required to ensure spatial independence of repeated measures, are also repeatable (Rodríguez Iglesias et al., 2013). In this study, instead of looking at the variation of the repeatability of raw wool traits over fleeces, we focused on estimating the consistency over time of the spatial macro-patterns themselves.

In an animal breeding context, repeatabilities of one-dimensional variables have precise meaning and associated estimation methods (e.g. Becker, 1992). That is not the case for traits expressing themselves in a higher-dimensional space, like fleece patterns. In particular, we are not aware of any general method of assessing the repeatability in time of unspecific 2D or 3D patterns. In this study we attempt to circumvent this limitation by first reducing the dimensionality of the problem, and then applying an *ad hoc* estimator of spatial consistency over time as a proxy of the repeatability of spatial patterns of wool traits over fleeces.

2. Materials and methods

2.1. Source of data

Data came from a 2-year observational field trial aimed at characterizing the spatial distribution of FD and SL over the fleece of adult Corriedale sheep. Full details on animals, sampling, and pattern visualization methods are offered in Rodríguez Iglesias et al. (2013). Briefly, following a regular grid pattern over the fleece, we collected 128 wool staples from the same 10 adult Corriedale ewes in two consecutive years. After allowing for ~340 d of growth, we removed staples (~1.5 cm of basal diameter) from the 120 intersection points of a rectangular grid of 10 longitudinal by 12 transverse lines plus 2 more sampling points from the upper part of each leg and aligned with the grid. We then determined FD in μm using an Optical Fibre Diameter Analyser (OFDA2000, Baxter et al., 1992) and assessed SL to the nearest 0.5 cm with the help of a ruler; both measurements were expressed as deviations from over-the-fleece means before analyses. Thus, for each trait the dataset consisted of 10 temporally correlated pairs of sets of 128 spatially correlated samples.

2.2. Visualization of spatial patterns

Using *ordinary kriging* for interpolation (Wackernagel, 2003) we mapped the spatial variation of each trait over the fleece for each individual in each year (Figs. 1 and 2). Kriging is an exact spatial interpolator routinely applied in many fields for mapping spatially referenced data collected in two or three dimensions. Maps are composed by producing massive interpolated predictions for unobserved locations using the original data while accounting for the spatial covariance between sampled points (as assessed by an experimental *variogram*) and their relative orientation. A moving neighbourhood of a minimum of 12 and a maximum of 24 samples was allowed to influence each point prediction. Maps consisted of 20,293 kriged points spread within a boundary shaped after a sheep pelt (Figs. 1 and 2). Predictions were generated using the VESPER software (Minasny et al., 2005) and plotted with S-Plus 2000 (MathSoft, 2000).

2.3. Assessment of pattern consistency over time

Apparently, there is no standard method for assessing the repeatability in time of unspecific spatial patterns. We reasoned that by reducing our 128D problem down to a 2D problem it would be possible to evaluate similarity in the same domain in which wool spatial patterns express themselves (i.e. wool follicles are arranged on a surface). For reducing dimensionality we applied a *metric multidimensional scaling* procedure (Johnson and Wichern, 2007). From a set of $n(n-1)/2$ measures of (dis)similarity between n items, multidimensional scaling generates a representation in few dimensions that attempts to match original (dis)similarities between items as closely as possible. For the sake of simplicity, we chose Euclidean distance as surrogate for similarity. When plotted on the 2D space determined by the first two *principal component* axes extracted from the original data, points corresponding to the 20 instances of spatial patterns for each trait (i.e. 10 animals by 2 years) would be expected to scatter according to whatever similarity was preserved through the scaling process.

If successive expressions of individual spatial patterns were consistently similar (i.e. repeatable in some sense), points corresponding to observations recorded on the same animal in consecutive years would be expected to lie closer to each other than to the rest of data points in the 2D domain. Those data pairs, in turn, would be closer to (or farther away from) other data pairs according to the (dis)similarity of patterns across animals. Following this logic, we formulated a measure of pattern consistency across years on the basis of calculating two sums of distances when n animals are evaluated twice:

$$\Sigma B = \sum_{i=1}^{n-1} \sum_{j=1}^2 \sum_{k=i+1}^n \sum_{l=1}^2 d_{ij,kl}; \quad l \neq j$$

where ΣB stands for sum of distances *between* animals, $d_{ij,kl}$ indicates Euclidean distance between animal i in year j and animal k in year l , provided measurements correspond to different years (i.e. when $l \neq j$), and

$$\Sigma W = \sum_{i=1}^n d_{1,i2}$$

where ΣW stands for sum of distances *within* animals.

A measure of *spatial pattern consistency* (C_{sp} , our surrogate for repeatability) was then synthesized on the basis of contrasting the average distance between repeated expressions of the spatial patterns of the same animals (i.e. *within* animals, $\Sigma W/n$) against the average distance between expressions of spatial patterns of different animals in different years (i.e. *between* animals, $\Sigma B/2C_2^n$) and expressing the difference relative to this latter term:

$$C_{sp} = \frac{\Sigma B/2C_2^n - \Sigma W/n}{\Sigma B/2C_2^n}$$

This C_{sp} coefficient will be equal to one when data points within animals across years superimpose exactly (i.e. when $\Sigma W=0$) and it will be equal to zero when the average distance *within* animals equals the average distance *between* animals (i.e., $\Sigma W/n = \Sigma B/2C_2^n$). Negative estimates are mathematically possible, i.e. when the average distance *within* animals turns out to be larger than the average distance *between* them, but biologically unreasonable. It would be hard to imagine any systematic biological process inducing less average similarity among instances of spatial patterns coming from the same rather than from different animals. In other words,

$$\text{if } 0 \leq \Sigma W/n \leq \Sigma B/2C_2^n \text{ then } 0 \leq C_{sp} \leq 1$$

for any biologically reasonable data set.

As it could be expected, C_{sp} will tend towards zero as the distribution of data points in the 2D domain approaches randomness in spite of the common origin (same animal) of individual points within data pairs. Although for very low n random samples may occasionally render small negative estimates of C_{sp} (simply due to sampling variation), estimates tend quickly towards zero as n increases (Rodríguez Iglesias et al., unpublished simulation results) thus ensuring a non-negative parameter space for any reasonable n .

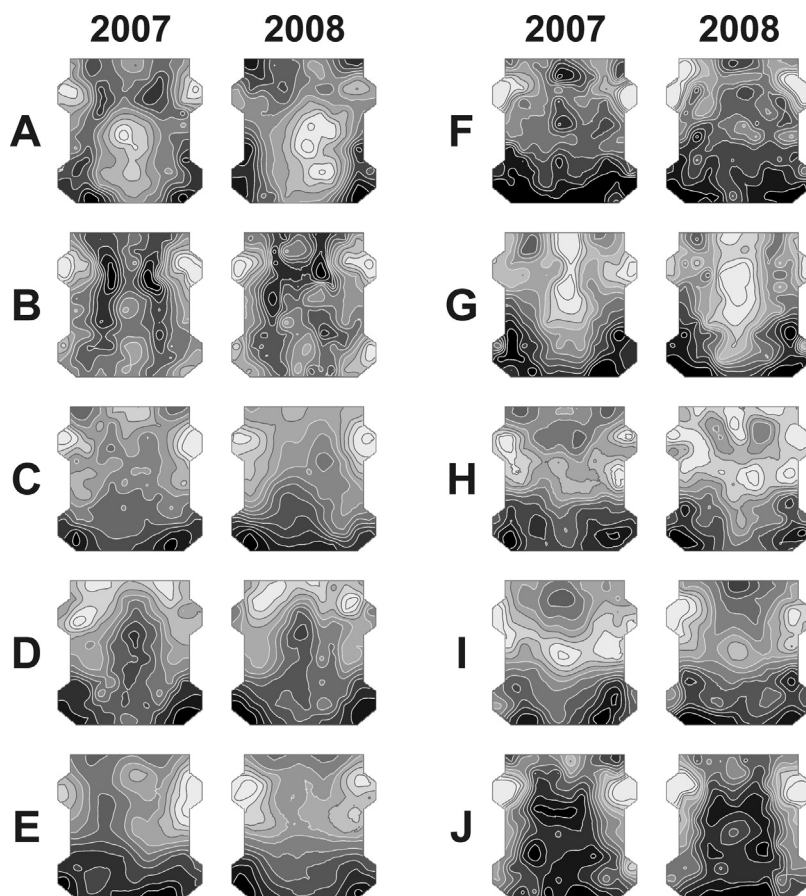


Fig. 1. Kriging predictions of fibre diameter deviations from overall fleece means ($n=128$ samples per ewe) for 10 ewes (A–J) in two consecutive years (2007 and 2008). Lightest areas correspond to finest wool, darkest to strongest.

Approximate standard errors and 95% confidence intervals for the estimated coefficient for each trait were generated by bootstrapping with replacement the 2D coordinates of the 10 data pairs 5000 times (Efron and Tibshirani, 1993). Bootstrapping is one of a number of techniques that generates an approximate distribution for the parameter of interest (C_{sp} in our case) by massive random resampling of the original data set.

2.4. Statistical analyses

A possible association between traits regarding pair matching was quantified by correlating individual animal versions of the C_{sp} coefficient for both traits across ewes. For this purpose, and keeping the same C_{sp} definition, we limited both ΣW and the first sum in the ΣB expression to just the term corresponding to each target animal. In other words, for each animal we determined its individual contribution to departures from perfect consistency for both traits and then assessed the correlation between those two variables. A significant and relevant correlation would suggest possible interdependence between traits in the genesis of spatial patterns. We applied standard routines in the S-Plus package (MathSoft, 2000) for all calculations, analyses, and graphics.

3. Results

After reducing the dimensionality of the response variables from 128D to 2D, each data point in Fig. 3 synthesizes the particular over-the-fleece variation observed for each ewe in a given year and for each trait. By inspecting the loadings of the principal components axes (i.e. the

contribution of each of the original 128 variables to the variability expressed along each axis; results not shown) it was reckoned that, for FD, axis 1 basically contrasted fineness over the back (from neck to hip) against the rest of sampled locations whereas axis 2 contrasted fineness of wool covering rump and hind legs vs. the rest. First and second axes for SL contrasted anterior (neck, chest, shoulders) vs. posterior areas, and anterior area plus laterals vs. the rest, respectively.

Distances between pairs of points coming from the same ewes in different years assess the similarity of spatial patterns among animals within traits, i.e. the closer two sets of points from two different ewes, the more similar their spatial patterns. Those distances varied widely for both FD and SL (Fig. 3). Another noticeable feature was the relatively peripheral arrangement of points corresponding to particular ewes, which was more evident in FD (ewes A, B, D, G and J) than in SL (only ewe A) with the remaining ewes rather tightly clustered in FD but considerably scattered in SL.

The C_{sp} coefficients estimated for FD and SL were 0.78 ± 0.06 (estimate \pm bootstrap-estimated SE) and 0.64 ± 0.08 , respectively, with corresponding 95% confidence intervals of [0.60, 0.84] and [0.43, 0.75]. The estimated biases of bootstrap estimators were -0.026 and

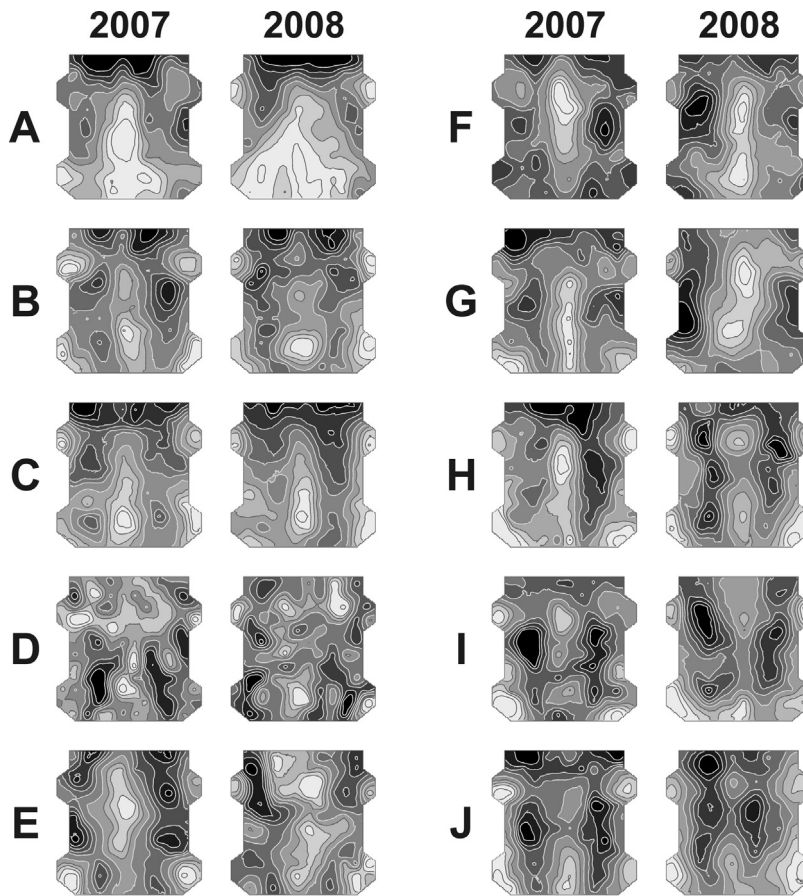


Fig. 2. Kriging predictions of staple length deviations from overall fleece means ($n = 128$ samples per ewe) for 10 ewes (A–J) in two consecutive years (2007 and 2008). Lightest areas correspond to shortest wool, darkest to longest.

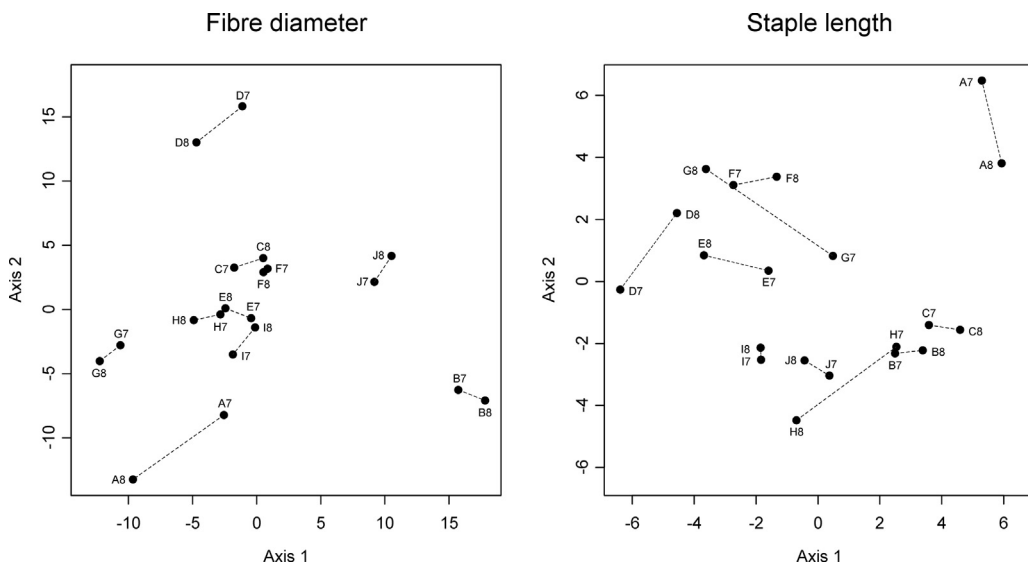


Fig. 3. Data points represent spatial patterns of fibre diameter and staple length of individual ewes (capital letters from A to J in point IDs) in a given year (Arabic numerals in point IDs stand for last digit of year of observation, 2007 or 2008) when 128 over-the-fleece measurements are projected onto a 2D space of principal coordinate axes. Dashed lines link spatial fleece patterns on the same ewe in different years.

–0.028 for FD and SL, respectively. We did not detect association between traits in the contributions of individual animals to overall C_{sp} coefficients ($r = -0.11$, $P = 0.76$).

4. Discussion

A 1D phenotype may be any attribute (discrete, continuous or anything in between) evaluated at the individual animal level along a single dimension. For traits varying in 2 (e.g. any raw wool trait) or 3 dimensions (e.g. marbling, meat tenderness), phenotype assessment is routinely based on observations or samples taken at particular locations that are assumed to be representative of whole-animal phenotypic averages. But there are hidden costs in this procedure because of the implicit assumptions that spatial patterns are the same across individuals, and that the variance between individuals is the same for different sampling points across the dimensions of the patterns. If spatial patterns were not homogeneous across individuals, as it seems to be the case for both FD and SL in our study (see also Rodríguez Iglesias et al., 2013), the location of sampling points representative of over-the-fleece averages would vary among individuals. Adopting any universal sampling point would then inflate the temporary environmental component of variation (due to measurement error affecting the estimation of over-the-fleece averages) and consequently reduce the repeatability (and heritability) of the trait. On the other hand, if the between-animal variance does vary over the fleece, so does the 1D repeatability and probably also the heritability, as seems to be the case for Angora goats (McGregor and Butler, 2008). Thus, characterizing the spatial variability of multidimensional traits is relevant to quantify potential biases that may affect 1D phenotyping, estimation of genetic and phenotypic parameters, and selection decisions and outcomes.

Genotype, nutrition, photoperiod, and internal parasitic diseases are typical known factors influencing raw wool traits through *systemic*, physiological pathways (Ryder and Stephenson, 1968). However, that does not preclude those same factors from contributing to over-the-fleece variation and eventually inflate measurement error of whole-individual 1D phenotypes. In addition, other typically *non-systemic* environmental influences such as fibre tip abrasion from rubbing or UV exposure, and patchy fibre damage from ectoparasites or deposition of particulate matter on certain fleece areas, are examples of factors capable of inducing significant regionalized variation even with minimal or negligible systemic effects.

Spatial variability can also be looked at as a trait in itself, i.e. as a multidimensional attribute that could be assessed for any raw wool trait and used for classifying, ranking, or otherwise discriminating between individuals. A first step in this direction would be determining the consistency over time of that variability. According to our results, such consistency would be moderate to high for the two traits we studied.

The approach we devised to quantify consistency of fleece spatial patterns over time produced estimates within the expected parameter space for a repeatability, i.e. the interval [0,1], significantly different from zero, and comparable between traits (FD: 0.78 ± 0.06 ; SL: 0.64 ± 0.08). The

FD estimate is in line with the average of the 128 sample point repeatabilities estimated over the fleece for the same dataset (0.76 ± 0.10 ; Rodríguez Iglesias et al., 2013) but the corresponding C_{sp} assessment for SL differs considerably from the average of point repeatabilities over the fleece (0.36 ± 0.23). If C_{sp} were a reasonable proxy for the repeatability of a spatial pattern, the magnitude of the estimates would depend, in principle, on the same components determining the repeatability of any 1D attribute, i.e. genetic, permanent environmental, and temporary environmental variances. The first two components represent the temporally invariant part of the variability (from either genetic or environmental causes), the latter one is the portion of the total variability induced by environmental effects that may change from one expression of the attribute to the next. The ratio of the sum of the permanent components relative to the total variation is an estimator of the repeatability. However, in a 2D setting the total phenotypic variance resulting from adding together those three components is a 2D property which may also be affected by the regional effects of systemic factors (e.g. nutrition, photoperiod, internal parasitic diseases) as well as by non-systemic factors (e.g. rubbing, UV exposure, ectoparasites) typically inducing *regionalized* effects. Although the relative magnitudes of the variances involved is unknown for our data set, it is clear that FD and SL would be differentially affected mainly by the action of non-systemic environmental factors preferentially affecting SL. Regionalized effects induced by those factors would likely reduce the repeatability of the trait when assessed in certain sampled areas but not in others, as we observed previously in this data set (Rodríguez Iglesias et al., 2013). In contrast, the consistency across years of the SL spatial patterns themselves was much less affected, as reflected in the similar C_{sp} estimations for both traits. This suggests that characteristic features of the spatial patterns, conserved through the dimensionality reduction process, are relatively invariant to local variability at the sampling point scale. Two features that probably contributed to this behaviour were that the original set of variables shared a common scale and distribution (i.e. they were essentially the same variable sampled at 128 different locations), and that 2D is the proper domain of pattern expression for raw wool traits evaluated *in situ*. In fact, repeating the analyses in 3 to 6 dimensions did not change the estimates of C_{sp} noticeably (Rodríguez Iglesias et al., unpublished simulation results) although this may be a consequence of the limited number of data pairs relative to the number of original dimensions. With more data available, additional principal coordinates could possibly capture less noticeably details of the spatial patterns and that may or may not affect the repeatability of the patterns. For our limited data set, the extracted principal coordinates were interpreted as synthesizing differences between relatively large body regions (i.e. back, rump, sides, anterior vs. posterior regions). In other words, C_{sp} could be expected to be invariant to scale issues provided the size of the data set is commensurate with the number of principal coordinates extracted to synthesize patterns from the original 128 dimensions.

Notwithstanding those caveats, any inadequacy of a 2D domain to synthesize the original 128D variability

would be expected to conspire *against* chances of detecting repeatability of spatial patterns. Thus, our results demonstrate that patterns of both FD and SL variability over sheep fleeces, though quite unapparent to the naked eye, may be as permanent as the colour patterns of many mammalian species including wild sheep and some of the domesticated breeds (Sponenberg, 1997).

The two basic terms composing the C_{sp} definition may be interpreted as two different (though related) properties of the patterns: within-animal *similarity* ($\Sigma W/n$) and between-animal *distinctiveness* ($\Sigma B/2C_{sp}^2$). Distinctiveness can be best appreciated by relating relative point locations in Fig. 3 with sets of images from Fig. 1 or 2. For example, the most probable explanation for the contrasting 2D locations of FD points from ewes B and D (Fig. 3) is the essentially reversed FD patterns in those ewes (Fig. 1). Given the between-animal variability exposed in Figs. 1 and 2 and the distinctiveness of some individual patterns, probably the next important question to ask would be whether or not spatial patterns are variations of a single general motif or a sample of diverse discrete patterns. Our limited data set is inadequate to answer that question and the answer itself may be different for different raw wool traits.

The lack of association between individual ewe contributions to the C_{sp} coefficients for FD and SL suggests that the spatial patterns of the traits may be regulated rather independently of each other. This is in line with the poor phenotypic and genetic association between the traits (e.g. Atkins, 1997) although estimates derived at the population level may not be informative of the pattern of variability over fleeces within individuals.

Knowledge of the spatial distribution of trait (co)variation would be critical to interpret functional constraints in the organization of spatial patterns during the foetal period (e.g. foetal programming, Kelly et al., 2006; diameter–density relationships, Adelson et al., 2002; perinatal follicle number variations, Hocking Edwards, 1999; Toland Thompson et al., 2007). It would also be required to scale from reaction–diffusion (Nagorcka and Mooney, 1989) and other object-oriented models of wool follicle colonization of sheep skin up to fleece-level models.

Current wool phenotyping for selection purposes is blind to within-animal spatial variability. Up scaled to population level and associated with increasingly affordable on-farm measurements, spatial patterns of raw wool trait variation may yield improved models of individual wool production and better assessment and screening methods. Wool phenotyping normally relies upon results from single mid-side samples. At the population level, that information contributes towards both phenotypic and genetic parameter estimation and, ultimately, breeding value prediction. The spatial variability present in our sample and the temporal consistency of their patterns cast doubts on the idea that a single wool sample may be a representative surrogate of a fleece phenotype and the best choice to breed for better quality wool. Characterizing spatial patterns of top-tiered sires and dams and establishing the variability of phenotypic and genetic parameters over fleeces would be particularly relevant for the specialty wool industry. Phenotyping could then be concerned with assessing the amount of fibre produced from areas predicted to have

desired levels of target traits or combinations thereof. Breeding value estimation would require extending structural variance models to a 2D context, e.g. along the lines proposed by Gengler et al. (2004) for representing the temporal (i.e. 1D) heterogeneity of milking records. Covariance functions (as estimated from variogram analyses) would be key components to circumvent curse-of-dimensionality issues.

5. Conclusions

Main conclusions are that accounting for the spatial variability of multidimensional traits may be relevant to avoid biases affecting phenotyping, estimation of genetic and phenotypic parameters and selection decisions, that patterns of FD and SL variation over sheep fleeces are similarly repeatable across years, and that the lack of FD and SL association in pattern expression suggest that independent physiological regulation probably command the spatial expression of those traits.

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