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A tale of two tails: asymmetry in Great Grey Shrike (*Lanius excubitor*)

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Abstract

Background: Asymmetry in the wild is a controversial, and to date, unresolved subject. Fluctuating asymmetry (FA) is the developmental instability (intra-individual variation) while, directional asymmetry (DA) expresses the asymmetry of the population mean.

Methods: We analysed 63 Great Grey Shrike (*Lanius excubitor*) skins at the Naturalis Biodiversity Center, Leiden, the Netherlands. The black markings on the tails were digitized in order to evaluate the symmetry of the two sides of each shrike. Ptilochronology helped understand if nutritional condition affected symmetry.

Results: ANOVA revealed no significant differences in size of the tail between sexes ($F = 1.67, p > 0.05$). However, there was significant difference in the shape of the black area in feathers between the sexes ($F = 2.14, p < 0.05$), and males had more elongated and slender black areas. Further, DA was observed only in males, but FA was noted in both sexes. Spearman correlation showed no significant association between FA score and tail features in both the sexes. However, in females, we observed a negative significant correlation between the number of fault and growth bars. The shape of the black area in the tail displayed no statistically significant association with the tail features in both sexes although growth bars influenced tail shape more than the number of fault bars.

Conclusions: We concluded that the characteristics discovered by us need to also be checked in the field and if they can be used to sex individuals. Also, chromatic manipulative studies are required to verify if DA influences sexual selection in the Great Grey Shrike.

Keywords: *Lanius excubitor*, Ptilochronology, Geometric morphometrics, Fluctuating, Directional asymmetry

Background

In wild animals, especially avian, the tail has been ascribed a wide range of functions and capabilities. These include roles in aerodynamics (e.g., Pennycuik 1975; Mayburg et al. 2001), inter- and intra-specific communication (cf. Ortolani 1999), and sexual selection (Darwin 1871; Hamilton and Zuk 1982; Møller 1994). Thomas (1993) concluded that much of the variation in the level of fluctuating asymmetry (FA) in the tail can be explained by natural selection for aerodynamic efficiency. Further, Balmford et al. (1993) summarized their study by saying that patterns of FA in long tails may often be better understood in a context of natural rather than sexual

selection, and that natural selection favored symmetrical wings and tails in birds. In addition to the morphology of the tail, the coloration and markings are also found to be important signals that can influence individual fitness (cf. Endler 2000).

The subject of asymmetry in the wild is a very controversial, and to date, unresolved subject (e.g., Markow and Clarke 1997; Palmer 1999, 2000). Fluctuating asymmetry is described as developmental instability (intra-individual variation) while directional asymmetry (DA) expresses the asymmetry of the population mean (e.g. Mitteroecker and Gunz 2009). Several reviews have tried to address the subject of how FA could be influenced by genetic and environmental factors, and its ultimate influence on the fitness of an individual or a population (e.g., Møller and Thornhill 1997; Vøllestad et al. 1999; Swaddle 2003). Many studies have succeeded in demonstrating

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the adaptive significance and influence of asymmetry on evolutionary paradigms, such as sexual selection (e.g., Møller and Höglund 1991; Andersson 1994; Møller et al. 1998; Gonzalez-Jaramillo and de La Cueva 2010).

Swaddle (2003) compiled some of the studies which demonstrated relationships between fitness and asymmetry and which decreased competitive (Sneddon and Swaddle 1999) and mating ability (Blackenhorn et al. 1998), or predation (Swaddle 1997). But asymmetry has also been shown to affect sexual selection (Swaddle and Cuthill 1994; Morris and Casey 1998; Shykoff and Møller 1999). Swaddle (2003) summarised that environmental factors, including stress, could determine the expressions of FA and suggested that it has little or no genetic origin. A non-invasive technique to determine relative stress in individuals is ptilochronology (e.g., Yosef and Grubb 1994).

Ptilochronology (Grubb 1989) is based on the evaluation of the width of feather growth bars during each 24-h period at the time of moult and depends on the amount of energy and nutrients invested by an individual into the regeneration process, which at the same time depends on the nutritional condition and quality of an individual (Grubb 1989, 2006). Growth bar width indicates an individual's relative nutritional condition. Other indices of nutritional condition, such as total body mass or fat percentages, are more commonly applied (Grubb 1989, 2006). Age and sex have also been proved to influence width of growth bars, and the total length and mass of both an induced feather and the original feather grown from the same follicle during the preceding pre-basic molt varied significantly with the age and sex of Northern Cardinals (*Cardinalis cardinalis*; Grubb et al. 1991). However, the interpretation of these traditional indices is often questioned. In certain circumstances, the highest body mass or fat percent does not correspond with the highest nutritional condition of an individual (Grubb 1995). Feather growth as an index of the nutritional condition is based on natural selection, which forces birds to regenerate lost feathers as rapidly as possible. Therefore, birds in better nutritional condition regenerate feathers much faster than individuals in poor condition (Grubb et al. 1991; Grubb 2006). Thus, feather quality is a relatively accurate indicator of an individual's quality.

Also, we took into account the fact that Prentice et al. (2008) found no relationship between the occurrence of fault bars and degree of bilateral asymmetry, and concluded that FA and fault bar occurrence should not be used interchangeably as bio-indicators. Hence, we ignored the data pertaining to fault bars on the feathers and only considered a combination of the study of the asymmetry of the tail feathers of Great Grey Shrike (*Lanius excubitor*) combined with ptilochronology to

allow us to elucidate a possible relationship between these two states that are determined simultaneously during the growth of the feather. That is why, the first aim of the study was to analyse relationship between DA and FA of the black markings on both sides of the tail, and their related nutritional condition. We wished to understand whether the two parameters could be influenced by nutritional stress at the time of moult. Although the only paper on shrike that we found that studied the effects of the melanin-based tail patterns on individual quality was in Lesser Grey Shrikes (*L. minor*; Krištin et al. 2006), the relative number of skins in the museum available for analyses and the similarity between the two species convinced us to study the tail patterns of Great Grey Shrike (also see Hromada et al. 2003b). Also, the Great Grey Shrike is a relatively well-studied species of True Shrike (Laniidae spp., Dylewski et al. 2017). Aspects of sexual selection (Yosef and Pinshow 1989; Votypka et al. 2003), courtship (Tryjanowski and Hromada 2005), reproduction (Degen et al. 1992), parasites (Szczykutowicz et al. 2006), foraging niche (Hromada et al. 2003a), and a wide range of other subjects (e.g., Lorenz et al. 1968; Yosef and Pinshow 2005) have been studied in this species. Hence, our second aim was to try to assess if there are differences in tail patterns and coloration between the sexes. We hoped that if indeed we are able to find differences, this might help explain the function of these different markings.

Methods

The species is of special interest to Martin Brandsma (MB; www.martinbrandsma.nl), an artist who uses the species extensively as a focal subject for his exhibitions worldwide. One of his projects is to meticulously draw the black markings on the tails of Great Grey Shrikes in museum collections. Upon bringing this to our attention we devised a study wherein, in order to better understand asymmetry in the study species, we decided to apply in parallel a comparative technique which represents the nutritional condition of the bird in the form of growth bars known as ptilochronology (Grubb 1989).

MB and Reuven Yosef (RY) met at the Naturalis Biodiversity Center at Leiden, the Netherlands, in August 2014 and evaluated 324 skins of Great Grey Shrike. One of the main purposes was to analyse relationship between the tail shape and its features (growth and fault bars) using geometric morphometrics. This method is very strict in terms of the number of landmarks (each analyzed shape must contain the same number of landmarks) therefore, we could carry out analyses only on tails with all preserved feathers. That is the reason, due to varying states of preservation, and excluding those with missing feathers and pulli, only 198 (61.1%) were considered to be in

acceptable shape and were included in the study, but owing to other considerations the final analyses were done on 63 (19.4%) tails.

The skins analysed were collected between the years 1844 and 1983 and were collected one (1.6%) each from Canada, Czech Republic, Kyrgyzstan, Romania; two (3.2%) each from Switzerland and Italy; three (4.8%) each from China, France, and Russia; and 52 (82.5%) were collected in the Netherlands.

RY first conducted the ptilochronology evaluation and then MB photographed the tails of the skins. In order to respect the protocols of a blind test, independently of each other, RY marked the growth bars on the feathers on index cards at the museum but measured the growth bars at home in Israel while MB traced the black markings on the complete tail of the Great Grey Shrike skins in his studio (Fig. 1). On each feather, 10 growth bars centred on the point two-thirds of the distance toward the tip of the feather were measured by RY, who served as a blind test (e.g., Grubb and Yosef 1994; Gombobaatar et al. 2009; Bujoczek et al. 2011).

As in all museum skins, the tails were closed, and required each rectrix to be transferred separately. All black areas on the tail feathers, including the shaft, were transferred with a sharp pencil in two steps: (a) with points (through the feather) and (b) connecting the points in contour lines. This transfer was done on a fixed standardized template of the rectrices (Additional file 1: Figure S1) because not all feathers are of the same size. The next step was to fill all parts within the contour lines in 'black fields' (with Photoshop CS 6). Under each image the collection number of the relevant skin was noted.

Of the 198 tails whose black markings were traced, we included in our final analyses only 63 Great Grey Shrike tails (19.4%; 28 females and 35 males) where all 12 of the rectrix feathers were intact and the markings sharpest. We also verified that the skins included in our study were collected in regions that are today recognised as the geographic distribution of *L. excubitor* and not that of others

that were later recognised as separate species (e.g., *L. meridionalis*; Hernandez et al. 2004; but see Olsson et al. 2010). For each tail, 72 landmarks were distributed on the black area of the feathers using tpsDig2 software (Fig. 1; Rohlf 2010). A maximum number of landmarks was established in order to reconstruct the tail markings as completely as possible. Six landmarks were digitised on each black area of the feather, three on the proximal and three on the distal end. One of the main purposes of our study was to analyse DA and FA of the black sections of the shrike's tail. Thus, the landmarks were digitised twice on each individual. Double distribution was also used to estimate measurement error in the landmarks' position.

Statistical analysis

Before statistical analysis, a Generalised Procrustes Analysis (GPA) was used for landmark superimposition, and centroid size was employed as the size measurement. Centroid size was calculated as the sum of the squared distances among all pairs of landmarks (e.g. Zelditch et al. 2004). In order to obtain the measurement error associated with landmark digitisation, Procrustes ANOVA test was carried out to analyse whether the variation between double distributions of landmarks on the same individual's tail was greater than that between samples. Since size effects can be an important component of shape variation in biological studies (Outomuro and Johansson 2017), the association between the tail shape and centroid size was analysed using regression analysis.

To analyse the significance of the differences in tail shape between sexes, the Procrustes ANOVA test was also carried out. We used principal components analysis (PCA) to describe major trends in shape variation within the sample. The PCA was conducted taking sex into account.

Based on Klingenberg (2011), in order to detect the existence of DA and FA in tails, the Procrustes ANOVA was conducted separately for females and males. Directional asymmetry is a measure of the mean difference between the original and mirrored copy of each individual. In turn, FA shows the dispersion of left–right differences within individuals. One of the main purposes of this study was to analyse whether a tail's features (growth and fault bars) are associated with FA scores. Hence, individual levels of FA were conducted in Mahalanobis distances using MorphoJ (Klingenberg 2011). We used the Mahalanobis distance to characterise the FA of each individual because this approach takes into account that some shape features are more variable than others (Klingenberg 2015). In order to find the association between FA score and the tail's features a Spearman correlation was conducted. Further, in order to analyse whether

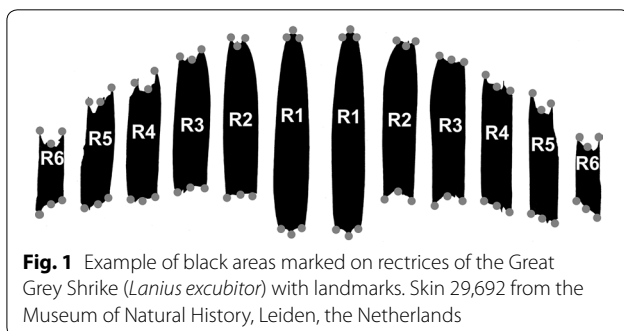


Fig. 1 Example of black areas marked on rectrices of the Great Grey Shrike (*Lanius excubitor*) with landmarks. Skin 29,692 from the Museum of Natural History, Leiden, the Netherlands

individual FA levels differ between sexes, the Mahalanobis distances were analysed using ANOVA test.

Two-block partial least-squares (PLS) were calculated to study the relationships between FA of the tail shape and sets of tail's features (growth and fault bars). This is a test which enables the calculation of covariation between two or more blocks of variables (Slice 2007; Mitteroecker and Gunz 2009). The purpose of the PLS is to link the two blocks using the fewest dimensions possible (for more details see McIntosh et al. 1996). Moreover, this test shows which variable, in our case the tail features, has the greatest influence on the shape of the shrike's tail. The statistical significance of the PLS analysis was run for each sex separately and tested using a permutation test of 10,000 randomisation rounds.

In all statistical analyses the p value was significant at 0.05. Geometric morphometric analyses were conducted using MorphoJ software (version 1.06d; Klingenberg 2011). After that statistical analyses of FA scores were conducted using SPSS software (version 23.0.0.0).

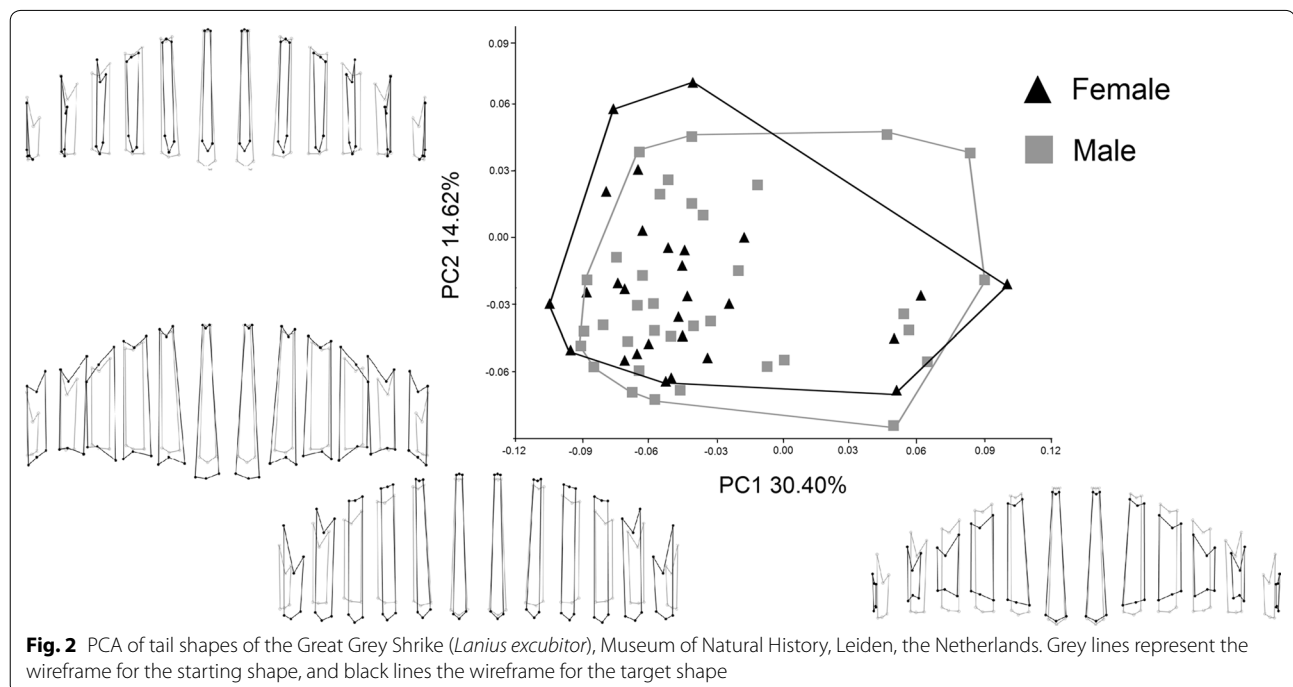
Results

The results showed that variation between samples ($MS = 9.8 \times 10^{-6}$) was much larger than that between double distributions of landmarks for both observers ($MS = 1.9 \times 10^{-7}$). Moreover, the ANOVA test showed no significant differences ($F = 1.23$, $p = 0.09$) between repeated landmark distributions; hence, high intra- and interobserver agreement was confirmed.

The regression analysis showed a significant association between tail shape and size in females (percent of predicted = 27.97%, $p < 0.0001$) and males (percent of predicted = 26.79%, $p < 0.0001$), thus the rest of the statistical analysis was conducted taking into account the centroid size of the object. The Procrustes ANOVA test revealed no significant differences in size of the tail between sexes ($F = 1.67$, $p > 0.05$) but a significant difference in the shape of the black area in feathers between females and males ($F = 2.14$, $p < 0.05$). Feathers of males were characterised by more elongated and slender black areas on the feathers than that of females.

The PCA test was conducted with the centroid size of each individual taken into account. PC1 in both sexes explained 30.40% of the variation, in turn, PC2 in females and males was responsible for 14.62% of the variability (Fig. 2). The shrikes with positive values of PC1 are characterised by shorter black area in the tail than individuals with negative values of PC1. In turn, the positive values of PC2 are responsible for the slender black area in the shrike's tail. Individuals with negative values of PC2 have much wider and slightly elongated black area in the distal part of the tail.

The Procrustes ANOVA shape results showed that DA was observed only in males (Fig. 3), but FA was noted in both sexes of shrike (Table 1). However, there were no significant differences in Mahalanobis distance which show individual levels of FA between sexes ($F = 0.314$, $p = 0.577$).



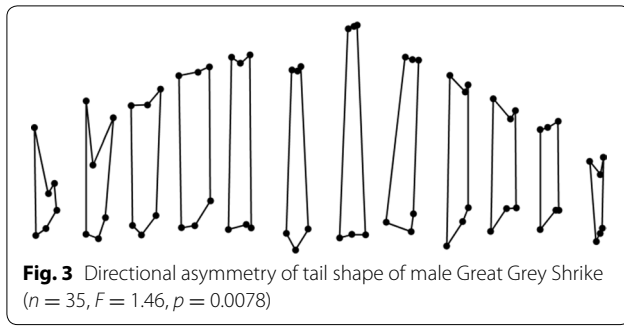


Table 1 Procrustes ANOVA for the shape of the black area in tails of Great Grey Shrikes (*Lanius excubitor*), Museum of Natural History, Leiden, the Netherlands

Effect	Sums of squares	Mean square	df	F	p
Females					
Individual ^a	0.1945	0.0001	1890	10.95	0.0001*
Side ^b	0.0008	0.0000	70	1.23	0.0997
Ind × side ^c	0.0178	0.0000	1890	4.71	0.0001*
Error ^d	0.0078	0.0000	3920		
Males					
Individual ^a	0.2670	0.0001	2380	6.36	0.0001*
Side ^b	0.0018	0.0000	70	1.46	0.0078*
Ind × side ^c	0.0420	0.0000	2380	6.74	0.0001*
Error ^d	0.0128	0.0000	4900		

*Significant differences, $p < 0.05$

^a The variation between individuals

^b Directional asymmetry

^c Fluctuating asymmetry

^d The residual variation due to measurement error

Spearman correlation showed no significant association between FA score and tail features (growth and fault bars) in either sex of the Great Grey Shrike. However, in females, we observed a negative significant correlation between the number of fault and growth bars (Table 2).

Table 2 Spearman correlation for FA score and male and female tail features of Great Grey Shrikes (*Lanius excubitor*), Museum of Natural History, Leiden, the Netherlands

Tail features	FA score	Fault bars
Females		
Fault bars	0.049	
Growth bars	-0.085	-0.376*
Males		
Fault bars	-0.029	
Growth bars	0.184	-0.180

*Significant Spearman coefficient, $p < 0.05$

The shape of the black area in the tail displayed no statistically significant association with the tail features in both sexes although in females and males, growth bars were more strongly correlated with tail shape than the number of fault bars. All PLS coefficients were positive, ranging from 0.0514 to 0.0867 (Table 3).

Discussion

The arts and the sciences are two fields which can mix but are normally kept separate, especially when it comes to scientific publications and experiments that require rigorous protocols with no tolerance for flights of imagination. The combination of art and science in this paper is an example of how an artist can highlight a phenomenon that the scientist can then research in depth.

The study of markings in natural (e.g., Yosef et al. 2012) and sexual selection in True Shrikes has been addressed in the past (e.g., Yosef and Pinshow 1989; Tryjanowski and Hromada 2005; Panov 2011) but not from the perspective of what a female could possibly read in the tail markings and asymmetry in Great Grey Shrikes (but see Panov 2011). Instinctively one assumes that symmetry would be the optimal choice but in humans while deviations from symmetry are critical perceptual units in detecting appearance of health the natural subtle asymmetry of the human face may be relatively unimportant for judgment of facial attractiveness (Zaidel et al. 2005). Similarly, Møller (1991) found that in Barn Swallows (*Hirundo rustica*) males that acquired a mate were more symmetrical in wing and outer tail length than unmated males and females with more asymmetrical tails laid eggs significantly later. He further found that males that survived were less asymmetric than non-survivors. However, one must take into account that because our study was conducted on museum skins, the idea needs to be tested in the field in a wild population and evaluated in relation to other parameters such as breeding success.

The fact that shape and size of the rectrices between the sexes conform to the field data and observations that the sexes in the Great Grey Shrike are very similar (cf. Panov 2011). However, our data have shown that the

Table 3 PLS analyses between the shape of the black area in the tail and two tail and ptilochronological features of female and male Great Grey Shrikes (*Lanius excubitor*), Museum of Natural History, Leiden, the Netherlands

Shape of the black area	Tail features		n	RV	p
	Fault bars (mm)	Growth bars			
Females	0.39 ± 1.08	39.48 ± 5.75	28	0.0867	0.8475
Males	0.37 ± 1.15	36.98 ± 4.73	35	0.0514	0.0799

n denotes the number of individuals, RV the coefficient of the PLS analyses, and p the value of the permutation test

feathers of males were characterised by more elongated and slender black areas on the feathers than that of the females. It now needs to be seen if this characteristic is evident in the field and can be used to sex the individuals in the field aiding in behavioural studies where not all individuals are always marked successfully (e.g., Keynan and Yosef 2010a, b).

The above is further substantiated by the fact that our results also showed that directional asymmetry (DA) was observed only in males, but fluctuating asymmetry (FA) was noted in both sexes (Table 1). Although chromatic manipulative studies (cf. Yosef et al. 2012) are required to verify if indeed this DA may influence sexual selection in the shrikes, it has been shown to occur in other avian species (Møller 1991, 1994). However, it must be noted that in Lesser Grey Shrike Krištín et al. (2006) concluded that in spite of the fact that the black spot on T5 helped to discriminate between the sexes and was an indicator for male age, it did not reflect the quality or condition of an individual.

Grubb et al. (1991) found that in Northern Cardinals, age and sex influenced the daily growth, the total length and mass of both an induced feather and the original feather. However, owing to our inability to establish the age of the individuals based on the museum data, we were unable to evaluate if asymmetry in the tails was affected in either of the sexes.

Prentice et al. (2008) found no relationship between the occurrence of fault bars and degree of bilateral asymmetry, but concluded that FA and fault bar occurrence should not be used interchangeably as bio-indicators. Similarly, in our study ptilochronology did not statistically correlate with FA. We think that because ptilochronology shows the nutritional condition of an individual while FA shows development instability, which means that this factor is much wider than ptilochronology, and could explain why FA was not associated with growth bars.

This is of great importance because similar studies in the relatively new field of ptilochronology (Grubb 1989) are lacking and are required to establish if indeed growth bars also affect patterning of feather coloration. Lens and Eggermont (2008) concluded that given the intrinsic difficulties associated with FA analysis, ecologists need to combine information from FA with that of other individual-based biomarkers, such as growth-bar dimensions. This has been the assumption on which our study is based and that growth bars reflect symmetry in rectrices, but needs to be further studied on free-ranging individuals.

Also, because we found no significant differences between intra- and inter-observer data, we are confident that the rigorous application of the scientific and artistic

techniques by the relevant individuals was of great discipline and precision. This allows us to conclude that in spite of the fact that we have found a special marking in the male rectrix and a greater degree of symmetry, and because our study was conducted on museum skins, we remain unsure as to the importance of these findings for fitness of the Great Grey Shrikes.

Conclusions

We conclude that the characteristics discovered in this study need to also be verified in the field and if they can be used to sex individuals. Also, chromatic manipulative studies are required to verify if DA influences sexual selection in the Great Grey Shrike and in other avian species, especially the Laniidae spp., with similar tail markings.

Additional file

Additional file 1: Figure S1. Photo of black contours drawn on standardized template of Great Grey Shrike rectrices in order to control for feather size.

Authors' contributions

RY and MB formulated the ideas and conducted the experiment; AMK and PT did the statistical analyses; all authors contributed equally to the writing of the paper. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

Dataset and each of the drawings of the tail feathers will be deposited for future reference at https://www.researchgate.net/profile/Reuven_Yosef.

Consent for publication

Not applicable.

Ethics approval and consent to participate

All authors have consented with their participation. Permit of the Naturalis Museum was received prior to our being allowed to work with the skin collection.

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