J Ornithol
DOI 10.1007/s10336-006-0091-3

ORIGINAL ARTICLE

Do melanin-based tail patterns predict individual quality and sex in Lesser Grey Shrikes *Lanius minor*?

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Received: 23 November 2005 / Revised: 24 May 2006 / Accepted: 24 May 2006

Abstract In many bird species, males display colourful, usually carotenoid or structurally based plumage ornaments. On the other hand, there are many bird species and entire avian genera that are achromatic, i.e. with predominantly white, grey and black plumage colours. Achromatic plumage is a typical feature in many shrikes for example. In this study, we examine the importance of an achromatic plumage pattern, namely, the black tail spots on the two outermost tail feathers (T6 and T5) of Lesser Grey Shrikes (LGS) for sex discrimination and as an indicator of individual quality. Our results suggest that the black tail patterns, especially spots on T5, are important for sex discrimination, but only in combination with other melanin-based or morphological features. The presence of black tail spots on T5 is also an indicator of male age. However, there is no indication that presence, size and asymmetry of these black spots are indicators of individual quality of both sexes in the terms of breeding performances.

Communicated by F. Bairlein

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Keywords Plumage colouration · Achromatism · Sex recognition · Breeding success · Shrikes

Introduction

In many bird species, males possess colourful, usually carotenoid or structurally based plumage ornaments (see Anderson 1994; Gray 1996), frequently in the tail (Fitzpatrick 1998). These plumage patterns are explained by their importance in sexual selection (Anderson 1994; Keyser and Hill 2000; Mennill et al. 2003; Doucet et al. 2005), sex, species or age recognition (Bub 1981; Schön 1994; Siefferman et al. 2005). On the other hand, there are many birds and entire avian genera that are achromatic, i.e. with predominantly white, grey and black plumage colours. There is a relationship between sexual dimorphism and carotenoids, but not achromatism (Gray 1996). Many achromatic species are, in fact, sexual monomorphic. A common feature of many, especially achromatic shrike species, is the existence of characteristic black and white plumage patterns and sexes are usually very similar in colouration (about 90% of all species). An apparent colour difference between the sexes occurs only in a few species (i.e. *Lanius collurio*, *L. gubernator* and *L. bucephalus*; see Lefranc and Worfolk 1997). However, the lack of any obvious sexual dichromatism does not necessarily mean that achromatic plumage traits cannot be used as an indicator of quality or condition. In fact, several studies (Mennill et al. 2003; Török et al. 2003; Doucet et al. 2005) found achromatic plumage traits to be important in mate choice and in establishing dominance hierarchies.

The Lesser Grey Shrike (*Lanius minor*, further LGS), is an achromatic species with no apparent plumage differences between the sexes (Cramp et al. 1993; Glutz von Blotzheim and Bauer 1993; Lefranc and Worfolk 1997). Colour ornaments like the black forehead mask have been shown to be too variable for an accurate sex determination (Busse 1984; Cramp et al. 1993; Lefranc and Worfolk 1997). Since males and females display their tail feathers during courtship, it might well be that the black tail spots play a role in courtship behaviour and mate choice of these species (Panov 1983; Cramp et al. 1993; Glutz von Blotzheim and Bauer 1993). Furthermore, several authors (Pajewski in Iljitshew 1976; Bub 1981; Busse 1984) mentioned these black spots as a possible trait for sex identification. However, no proper quantitative data have been available to test their importance for sex discrimination or whether they may serve as a quality indicator for mate choice.

In Great Grey Shrikes *Lanius excubitor*, black tail patterns are a proper indicator of sex (Eck 1973; Dohmann 1980; Schön 1994). In Red-backed Shrikes *L. collurio*, black tail patterns have been found to be a quality indicator for males (Votypka et al. 2003). In this study, we investigated the importance of the black tail spots (presence, size and symmetry) as an indicator for individual quality and sex in LGS. As a determinant of individual quality, we considered other morphological variables, body mass, start of egg laying, breeding success, age and return rate as a rough measure for survival (see Sanz 2001).

In detail, we address the following questions: (1) is the presence and size of black subterminal spots in the first and second outermost tail feathers (T6 and T5) a useful trait for distinguishing the sexes in LGS?; (2) consequently, we also want to know whether there is a relationship between the size and symmetry of black spots and other morphological variables, i.e. forehead height and body size in terms of wing and tail length, which have been previously mentioned as being important in sexing LGS (Bub 1981; Busse 1984); (3) is there a combination of morphological factors, including black tail patterns, which improves sex determination in this species?; (4) to understand whether black tail spots are an indicator for individual quality or condition, we try to correlate different breeding parameters and age with occurrence, size and symmetry of black tail spots.

Materials and methods

Species

The LGS is highly endangered and is declining throughout Europe. Its range is contracting from the Northwest to the Southeast during the last century (see Lefranc and Worfolk 1997). It is a long-distance migrant, over-wintering in South Africa (8,000–10,000 km from our study area), showing high breeding site fidelity for such a long-distant migrant (40% males and 25% of females, Krištín et al. 1999). LGS belongs to the sexually monomorphic and achromatic group of shrikes (*Laniidae*) with characteristic black and white plumage patterns (Bub 1981; Panov 1983; Lefranc and Worfolk 1997). It is socially monogamous with biparental care (Valera et al. 2003). It is a foraging specialist, dependent on larger insects (Lefranc and Worfolk 1997; Hoi et al. 2004) and prefers a high diversity of traditionally managed habitats (Wirtitsch et al. 2001).

Study area

The study was conducted in a 20-km^2 plot in Central Slovakia (40°35′–38′N, 19°18′–22′E, 450–850 m a.s.l.) on the southern slopes of Polana Mts. Biosphere Reserve. The study area consisted of an extensively managed agricultural landscape, characterised by a high diversity of habitats (meadows, fields, bare grounds and orchards with plenty of high trees, see Wirtitsch et al. 2001). This area supports one of the last stable and dense populations of the LGS in Central Europe (65–85 breeding pairs/20 km^2; for details, see Krištín et al. 2000).

Data collection

Data were collected from May to July 1996–2000. We examined the presence of a black spot in the first (T6) and second (T5) outermost tail feather on both sides in 72 females and 97 males (see Table 1). In 48 females and 29 males of all individuals possessing black spots, we also measured their size (length in mm following the axis of the feather) on both T5s. For the analyses, we considered only birds with the full number of tail feathers. Additionally, to relate the size of the black tail spots to other morphological parameters, we also measured wing, tarsus, bill and tail length, forehead height and body mass according to Svensson (1984). All plumage and morphological variables were measured using callipers within ±0.1 mm. To relate the size of the black tail spots to other morphological parameters and to compare it between sexes, we used only the right T5 (Table 2). We did not use the left or the mean of the left and right T5 spots because one, more frequently, the left T5, was missing. There is no difference in the size of the right or left tail spots (paired *t*-test for males and females, for both P>0.4, n=48 females, 29 males).

Table 1 Occurrence of black spots in female and male Lesser Grey Shrikes *Lanius minor* in T5 feathers in 1996–2000

	Female							Male						
Year	1996	1997	1998	1999	2000	*n*	*n*%	1996	1997	1998	1999	2000	*n*	*n*%
N	11	28	20	11	2	72		10	32	25	20	10	97	
0 black sp		2	2	1		5	6.9	9	21	13	13	10	66	68.1
1 black sp		1		3		4	5.4	1	6	1	3		11	11.3
2 black sp	11	25	18	7	2	63	87.5		5	11	4		20	20.6

0 black sp=no black spots in T5 feathers, 1 black sp=a black spot on the right or left T5 feather; 2 black sp=a black spot on both T5 feathers

Table 2 (Upper) Three morphological parameters which significantly followed a stepwise discriminant function model to separate males and females. (Lower) Three morphological parameters which significantly followed a stepwise discriminant function model to separate males and females when including only individuals with black spots in at least one T5 feather

Parameter	Males (n = 70)	Females (n = 51)	part. Lambda	P
Black spot length in T5	3.4 ± 0.8	15.6 ± 1.1	0.78	<0.0001
Forehead height	12.9 ± 0.18	11.2 ± 0.23	0.83	<0.0006
Body mass	45.2 ± 0.38	50.6 ± 0.99	0.76	<0.0001
Parameter	Males (n = 29)	Females (n = 46)	part. Lambda	P
Black spot length in T5	11.8 ± 1.08	18.3 ± 1.3	0.86	<0.0013
Forehead height	12.7 ± 0.27	11.1 ± 0.24	0.82	<0.0006
Bill length	21.6 ± 0.16	22 ± 0.13	0.9	0.1

Given are means ± SE (in mm), partial Lambda and significance values

To correctly determine the sex of the investigated individuals, we made behavioural observations during the mating, incubation and nestling periods and measured the cloacal protuberance length and noted the presence or absence of a brood patch.

To examine the importance of melanin-based tail patterns in relation to individual quality, we examined breeding parameters, age of individuals and symmetry of their black tail spots. The following breeding parameters were examined: start of egg-laying (using the Julian calendar), clutch size and number of nestlings. To collect these breeding parameters, territories (nests) were inspected every third day during the whole breeding season (see Krištín et al. 2000).

Using recoveries, we could determine the age of 40 individuals. In retrapped birds ringed as juveniles, our age determination was precise, but in adults retrapped after 1 year, we estimated age only as older than 1 year or 2 years after ringing as >3 years old etc.).

Deviation from perfect bilateral symmetry has been shown to be an indicator of individual quality (Møller and Thornhill 1998; Barbosa et al. 2003), i.e. in reaction to environmental or genetic stress (Møller 2000; Tomkins and Kopiaho 2001). For this reason, we examined the asymmetry in the size of the black tail spots of males and females. Therefore, we determined the difference in size of the black spot between left and right T5 feathers for each individual. As a threshold for asymmetry, we used the standard error of the population mean for males and females, respectively. Thus, we considered individuals as being asymmetric if the difference between the left and right patches was bigger than double the standard error (in our case >2.6 mm for both sexes, see the Results section). Size and asymmetry have been used as independent variables since there was no intercorrelation between them (for males: r=0.01, P>0.9, n=29; for females: r=0.13, P>0.5, n=48).

Additionally, we determined the survival rate in terms of the return rate to the study area for males and females with and without black tail spots in T5.

Data analysis

Binomial tests (z) were used to examine differences in the presence/absence of black tail spots (on both or only one T5) between males and females. A Student's t-test was used to compare the size of black spots in the right T5 between males and females and differences in clutch and brood size between individuals with or without T5 black tail spots. A stepwise forward discriminant function analysis was used to search for differences in morphological variables between individuals with or without black spots. Additionally, the same analyses was used to compare males and females (1) including the size of black spots on T5 and other morphological parameters and (2) including only individuals with black tail spots present. Stepwise multiple regression analyses were used to examine the relationship between the size and asymmetry of black spots and morphology and breeding success, respectively. In the analyses, we introduced size and asymmetry of the black tail spots on T5 as independent variables and forehead size, wing, tail, bill and tarsus length and body mass (morphological variables) and clutch and brood size and start of egg-laying (breeding variables) as dependent variables, respectively.

Means and standard error (SE) in the size of the black spots in the right tail (T5, T6) and other morphological parameters are given throughout.

Results

Sex determination in relation to melanin-based tail patterns

All of the investigated males (*n*=97) had the first outermost tail feathers (T6) completely white but 9 (9.2%) of these males had dark stripes on the feather shaft. For females, all except 4 (5.5%) out of 72 had completely white T6.

Examining black tail spots on the second outermost tail feather (T5), we found significant differences between males and females (Table 1). Almost all females show black tail patterns T5 (67 out of 72 females, 93.1%). In contrast, most males have no spots (66 out of 97 males, 68.1%) (binomial test: z=– 7.8, P<0.00001), but there is still a fraction of 31.9% (31/97) males having at least one T5 with black tail patterns. Hence, this trait cannot be used to significantly discriminate between the sexes in LGS. There is also a small proportion of individuals with an asymmetric trait, i.e. a black pattern in only one T5 (left or right) (Table 1), but the proportion of asymmetric individuals does not differ between sexes (binomial test: z=1.3, P>0.1).

On average, the extension of the black tail patterns in female T6 was 10.4 mm ±7.1 (*n*=4), but we found no spots in male T6 (*n*=30). In female T5, the black tail spot was, on average, 19.1 mm ± 1.3 (*n*=48) and was significantly smaller in males, 7.7 mm ± 1.3 (*n*=29) (*t*-test, t=5.6, P<0.0001). According to our results, adult individuals, at least in our breeding population, having black spots longer than 24 mm can be considered as females. However, there is still a high proportion of overlap in the size of this trait (Fig. 1). Examining the degree of asymmetry in the extension of T5 spots within an individual, we found that significantly more males (20 of 29=69%) revealed a strong asymmetry (asymmetry>double the SE of the mean, see the Materials and methods section) than females (19 of 48=39.6%; binomial test: z=2.5, P=0.012).

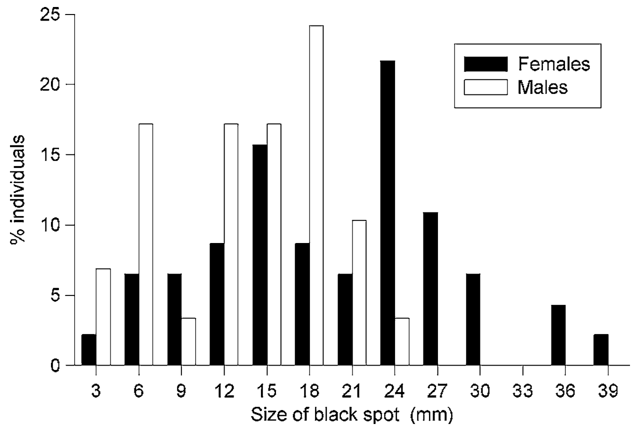

Fig. 1 Size distribution of black spots on the second outermost tail feather (T5) for male and female Lesser Grey Shrikes (*n*=29 males and 46 females). Spot length is separated into 3-mm intervals

Also including other morphological parameters, namely, the extension of the black forehead, wing, tarsus, tail and bill length and body mass to discriminate between males and females, a stepwise discriminant function analysis established a significant model. Three variables were used in the final model (Wilks' Lambda=0.45, $F_{3,117}$=48.6, P<0.0001) and, with these variables, the model is able to correctly classify the sex of 88.4% of the cases, whereby 92.9% males and 82.5% females were correctly classified by the model. The three variables significantly affected the model, including two melanin-based traits, namely, the presence and size of black spots on T5 and the extension of the black forehead, and body mass (Table 2a). The extension of the black forehead is bigger in males, but females more likely have spots in T5 and are also larger and significantly heavier than males.

We also obtained a significant model when examining only males and females with black spots in a stepwise discriminant function analysis. Again, three variables were used in the final model (Wilks' Lambda: 0.67, $F_{3,71}$=11.6, P<0.0001), allowing us to correctly classify the sex of 77.3% of individuals with black spots. The three variables included were again the forehead height, the size of the spots and the bill length (Table 2b). The extension of the black forehead is bigger in males, but females have bigger spots in T5 and slightly longer bills (Table 2b).

Black tail spots and their importance as a quality indicator

To examine morphological differences between individuals with or without black spots, no variable followed a stepwise discriminant function model (for males $P>0.3$ and for females $P>0.4$). Furthermore, examining the relationship between the size of the black spots and morphological variables, no variable followed a stepwise regression model at a significance level of $P<0.05$. Thus, the occurrence or size of black spots does not seem to be reflected in any other morphological trait of this species. We found no significant differences in the number of eggs and fledglings of males, respectively, females with or without black spots in both T5 feathers (Table 3). Furthermore, there is no relation in the size of the black spots of males or females and clutch size, number of fledglings or date of first egg-laying (no variable followed a stepwise multiple regression model, for males and females $P>0.1$).

In relation to age, we found that juveniles sometimes have traces of darkness on T6, but on T5 dark spots are almost always present. 96.2% (300/312) of nestlings examined with an age of 13–15 days had dark spots in both T5 feathers. One fledgling we measured at 38 days also had traces of dark spots on both T6 feathers and big black spots on T5 (41-mm and 40-mm long, respectively).

In adult males, we found an age-dependent change in the occurrence of black tail spots. Sixteen out of 20 one- or two-year-old males had black spots in both T5 feathers and in four males, which we retrapped a second time (all of them being older than 2 years), we found a decline in the presence of black spots, i.e. three males lost their spot on one T5 feather and one male lost their spots on both. We did not find other males older than 2 years with black tail spots, including 40 males of known age. In females of known age, only one (more than 2 years old) out of 19 females had no black spots in their T5 feathers.

Examining the relationship between asymmetry in the extension of the T5 black spots and morphological or breeding parameters, respectively, and for males and females separately, no variable followed a stepwise multiple regression model ($P>0.6$ for all).

The survival rate in terms of the return rate to the breeding area revealed no significant variation when comparing individuals with or without black tail spots on T5 (binomial test for males: $z=0.51$, $P>0.4$; for females: $z=0.19$, $P>0.3$, Fig. 2).

Discussion

We found that black tail spots on the T5 feathers are useful for discriminating between the sexes in Lesser Grey Shrikes. The role of tail colour patterns for sex identification has already been demonstrated in other shrikes, i.e. the Great Grey Shrike (GGS, *L. excubitor*) and the Loggerhead Shrike *L. ludovicianus*, where the females have more black in the tail (Dohmann 1980; Schön 1994). For LGS, Bub (1981) and Busse (1984) suggested that the black and white patterns on the tail may be useful for sex discrimination. The comparison of these older data with our results is problematic.

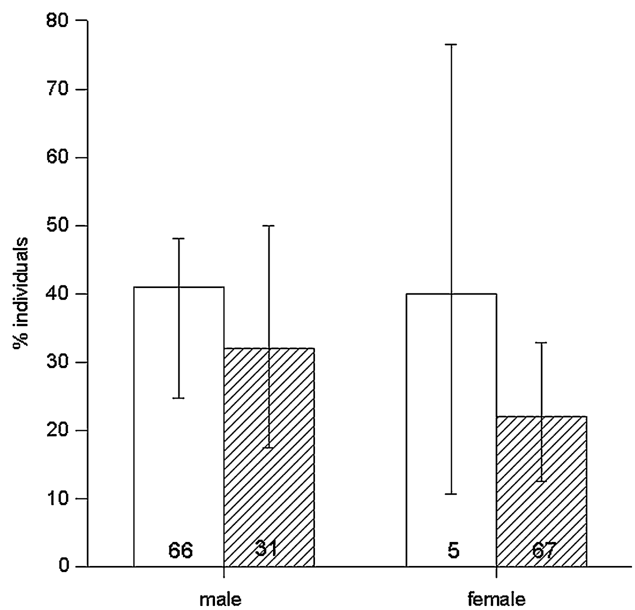

Fig. 2 Percentage of individuals (males and females) without (*open bars*) or with (*hatched bars*) at least one T5 feather with a black tail spot, which were retrapped in the following years. Given are the proportion and the 95% confidence intervals of a binomial distribution and sample size (*within bars*)

Table 3 Egg and nestling number in females and males with (BS) and without both black spots (NBS) in tail feather T5

	Female BS (n=47)	Female NBS (n=4)	t	P	Male BS (n=29)	Male NBS (n=31)	t	P
No. of eggs	5.6 ± 1.6	5.7 ± 0.5	0.9	>0.9	5.7 ± 0.7	5.8 ± 0.4	–0.13	>0.9
No. of nestlings	5.66 ± 1.4	5.5 ± 0.5	1.1	>0.2	5.2 ± 1.0	4.9 ± 1.5	0.6	>0.5

Given are means ± SE (in mm)

Both of these older studies had no access to genetic methods and did not consider behaviour to determine the sex. Bub (1981) additionally investigated only specimens from wintering grounds, which makes a correct sex determination exclusively based on morphological parameters doubtful. However, according to our results, the tail spots on the T5 feathers alone are not sufficient. At least the extension of the black forehead and body mass must be included to accurately determine the sex in LGS (see the Results section). With these three variables, we can correctly classify males and females in almost 90% of cases (see Table 2a). In this regard, the role of body mass has to be treated with caution, as our data have been collected mainly during the early breeding season and, due to egg production, females might be heavier during that period. Alternatively, examining morphological variables in those individuals where black tail spots are present, we again found that the black forehead and the size of the black spots are important, but the bill length seemed to be an additional determinant for sex identification, with females having slightly longer bills (Table 2b). Busse (1984) already proposed to also use the length of black spots in T5 for sexing as follows: black spots longer than 17 mm are females and those shorter than 15 mm are males. In the case of spot length between 15 mm and 17 mm, he proposed to also use the forehead height: for females smaller than 10 mm, for males larger than 11 mm. Our results support this approach, but in our population, the threshold of the black spot size on T5 is about 9 mm higher (individuals with black spots smaller than 24 mm are males and those with bigger spots are females, Fig. 1). The threshold for forehead size is with 12 mm also similar (individuals with bigger black foreheads are males, Table 2).

The outermost tail feather (T6) is not very useful for sex identification, since all males and almost all females have it completely white. In contrast, the black and white pattern of these feathers vary significantly between sexes of the northern races of the GGS, but not for the Loggerhead Shrike (Schön 1994). However, in LGS, at least a small fraction of females (5.5%) show black spots on the T6 feathers, which has not been mentioned for this species (Pajewski in Iljitshew 1976; Bub 1981; Busse 1984; Cramp et al. 1993; Glutz von Blotzheim and Bauer 1993). Thus, a black spot on the T6 feathers may help to assign a female, since it does not occur in males.

Besides a female-biassed presence of black tail spots, our results also suggest an age-dependent frequency. All nestlings have black tail spots on T5 and T6. Mainly younger males (1 and 2 years) seem to have black tail spots on the T5 feathers, whereas older males (≥3 years) seem to be more likely completely white. This is, to our knowledge, the first evidence that a melanin-based trait can be an age indicator.

Age-dependent variation in black tail spots also implies that they may reflect the condition or quality of an individual (Siefferman et al. 2005). Many studies found a relationship between mating success and the expression of plumage traits. In particular, in many bird species, there is a relation between plumage colour patterns and various parameters of breeding success (e.g. Hill 1988; Anderson 1994; Griffith 2000). There is also evidence that melanin-based plumage regions are significant predictors for reproductive success (Török et al. 2003; Doucet et al. 2005) or dominance rank (Mennill et al. 2003). Melanin-based tail patterns have been found to be an indicator of parasite-resistance in the closely related Red-backed Shrike (Votypka et al. 2003). The weaker mechanical stability of white feathers and the preference of white feather parts by feather parasites also suggest a possible role of these black and white tail patterns as a quality indicator (see Kose et al. 1999). During courtship, LGS males display their spread tails towards the females and sometimes vice versa (Panov 1983; Cramp et al. 1993; Glutz von Blotzheim and Bauer 1993), which makes the tail pattern a very conspicuous trait. Thus, we expected in LGS that black and white patterns in the tail play a role in sexual selection and, consequently, influence the breeding success of an individual. In spite of that, we could not find any hint that the black and white colour pattern in the tail (specifically on the T5 feathers) reflects individual quality. We found no significant differences in the number of eggs and nestlings as well as in laying date in relation to the presence or extension of black spots in T5 feathers in males and females, hence, there is no evidence for the "good parent" hypothesis.

Furthermore, we tested the symmetry in the colouration of T5 feathers, as it is known that deviation from perfect bilateral symmetry can reflect individual quality (Møller and Thornhill 1998; Møller 2000; Tomkins and Kopiaho 2001; Barbosa et al. 2003). However, we did not find evidence that more asymmetric individuals have significantly different breeding success and there was also no correlation with other morphological parameters and asymmetry.

Finally, we also did not find variation in the return rates depending on the black spots on T5 feathers, which does not support its importance as a predictor for survival probability (Sanz 2001).

In conclusion, the black tail spots seem to be a female trait and, on the other hand, an indicator for male age in

LGS but, besides that, it does not seem to reflect the quality or condition of an individual. For a long-distance migratory passerine, the LGS is a rather long-lived species, i.e. even an 8-year-old male has been found in our study population. Thus, there is high variation in the age of males in our breeding population and females could use tail spots to mate with an older more experienced male. However, there seems to be no obvious benefit, since females mated to older males do not fledge more offspring. Therefore, paternal quality seems unlikely to be important in mate choice. Older males could also be of superior genetic quality. The number of fledglings is probably not the best way to measure differences, due to male genetic quality. The return rate and recruitment of offspring for example, might be more appropriate indicators for the genetic quality of the father. In future studies, it remains to be investigated: (1) how important the black tail spots are for mate choice (for both sexes); (2) how important is male parental care for breeding success; and (3) which other benefits could be a result of female preference for older males. There are at least several other characteristics of these black tail spots which we have not examined yet, such as colour intensity, which could also be an important indicator for quality variation. Doucet et al. (2005) and Mennill et al. (2003) for example, found that plumage reflectance (UV-chroma) is an indicator for individual quality and breeding success.

Zusammenfassung

Sind schwarze Gefiedermuster auf den äußeren Schwanzfedern der Schwarzstirnwürger *Lanius minor* ein Geschlechtsmerkmal und Indikator für individuelle Qualität?

Bei vielen Vogelarten, sind Männchen das buntere Geschlecht, wobei die Gefiederfärbung meistens auf Karotenoid- oder Strukturfarben zurückzuführen ist. Andererseits gibt es auch viele Vogelarten und sogar ganze Gattungen mit achromatischer Gefiederfärbung (schwarz, weiß und grau). Achromatisches (basierend auf Melanin) Gefieder ist z.B. typisch für viele Würgerarten. In dieser Arbeit untersuchen wir die Bedeutung eines achromatischen Gefiedermerkmales, nämlich der schwarzen Flecken auf den zwei äußersten Steuerfedern (T6 und T5) des Schwarzstirnwürgers zur Geschlechtsbestimmung und als Anzeiger für individuelle Qualität. Unsere Ergebnisse unterstützen die Bedeutung dieser schwarzen Flecken speziell auf den T5 zur Geschlechtsbestimmung aber nur unter Berücksichtigung von anderen Gefieder- und morphologischen Merkmalen. Das Auftreten von schwarzen Flecken auf den T5 ist außerdem ein Altersmerkmal für Männchen. Es gibt aber keinen Hinweis dafür, dass das Auftreten, Größe oder Größenunterschiede der Flecken zwischen linker und rechter T5 ein Anzeiger für individuelle Qualität oder Bruterfolg dieser Art ist.

Acknowledgements We are grateful to P. Tuček, P. Kaňuch, B. Kršiak and the many enthusiastic inhabitants of our study area for field assistance and R. Hengsberger for improving our manuscript. AK and HH were funded from the bilateral exchange programme of the Slovak and Austrian Academy of Science and by a grant of the Slovak Grant Agency no. 2/5152/25, and FV by a grant from the Programa de Becas Postdoctorales de FPI del Ministerio de Educación y Cultura Español. All manipulations with birds comply with the current laws of the country in which they were performed.

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