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## Sexual size dimorphism and positive assortative mating in red-backed shrike *Lanius collurio*: an adaptive value?

Received: July 28, 2004 / Accepted: December 9, 2004 / Published online: February 5, 2005

**Abstract** During field studies in 1997–1999 in South Bohemia (Czech Republic), we found significant differences in size between the sexes in a local breeding population of red-backed shrike *Lanius collurio*. Males were significantly larger than females for wing length and tarsus length, but had smaller body mass than females. However, there was considerable overlap in the ranges of these parameters between the sexes. Interestingly, pairs were formed at random with respect to wing length and tarsus length, but assortative mating was significant for body mass/body condition. Among tested variables, only male wing length correlated significantly with nestling body mass at day 7. However, clutch size and the number of fledglings strongly depended on differences in tarsus length between mates, but not on body size of mates. Individual improvements in foraging skills and/or courtship feeding rates are proposed as possible explanations for these findings.

**Key words** Assortative mating · Body condition · Czech Republic · *Lanius collurio* · Measurements · Red-backed shrike · Sex specific differences

### Introduction

Sexual size dimorphism, hereafter SSD, has been linked to sexual selection, food preferences, responses to density-dependent processes and competition (Przybylo 1995; Blondel et al. 2002). Natural selection can affect SSD in a bird pair and may favour it especially when food abundance is less than optimal (Van Valen 1965; Przybylo 1995).

On the other hand, assortative mating, defined as non-random mating with respect to some phenotypic character, may be indicative of active mate choice. Assortative mating may be based on, as well as constrained by, several factors, such as sensory biases (Ryan 1998), search costs for prospecting females (Alatalo et al. 1988; Slagsvold et al. 1988), or partner's age (review in Reid 1988). In particular, mate preferences apparently based on age are known in some bird species, resulting in positive age-assortative mating, i.e. birds of about the same age are more likely to become paired. However, most data on assortative mating is limited to birds that are highly sexually dimorphic in size, such as raptors, waders or geese, with only few examples for passerines (Potti 2000; Delestrade 2001). Many authors have documented the existence of assortative mating by correlation analysis but have not focussed on the ecological consequences. An exception is Potti (2000), but his analysis was limited to age-assortative pairing.

Selective pressures can therefore result in both extremes of size similarity between partners in a bird pair, i.e. strong dissimilarity, and hence a tendency to increase SSD, and strong similarity, expressed as positive assortative mating. Within such selective pressures, natural selection may act on both SSD and assortative mating, and effects may be either positive or negative depending on environmental and other conditions. In harsh environs, SSD may positively influence offspring condition and breeding success because parents can exploit different dietary niches. In contrast, in good conditions, selection on positive assortative mating should be stronger, to eliminate potential incompatibility between mates. It should be present mainly by selection on larger body size in both sexes, because many fitness traits are generally positively correlated with larger size (Gibson and Langen 1996; Widemo and Saether 1999; but see Jonsson 1987).

We describe sexual size differences, assortative pairing and their consequences in a local breeding red-backed shrike *Lanius collurio* population. The red-backed shrike is a small (body mass ca. 28–32 g), socially monogamous, passerine bird with conspicuous sexual dichromatism, widely distributed throughout Europe. The species is a long-distance

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migrant with wintering grounds in southern and southeastern Africa. It is a good subject for a study of the influence of SSD and assortative mating on breeding parameters for several reasons. Firstly, there is no evidence that pair formation occurs away from the breeding grounds, i.e. in winter or on the migration route, (e.g. Herremans 1997; Harris and Franklin 2000; Tryjanowski and Yosef 2002; Votýpka et al. 2003). Secondly, because red-backed shrike populations are frequently subjected to food stress (Leugger-Eggimann 1997; Tryjanowski et al. 2003), evolutionary factors linked with foraging differences between the sexes may be evident. And thirdly, in an earlier paper (Votýpka et al. 2003), we found a bias in pair formation related to parasite status which was suggestive of assortative mating. However, because the blood samples were collected after pair-formation, this evidence was suggestive at best; here we pay special attention to the period of actual pair formation.

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## Materials and methods

The study area (15 km<sup>2</sup>) was located in South Bohemia northeast of the town of Písek (49°19'N, 14°15'E). Different aspects of the breeding ecology of the red-backed shrike have been studied in this area over the period 1989–1999. The mean population density was 3.5 pairs/km<sup>2</sup>. However, sufficient numbers of adults for this study were trapped only in 1997–1999. In total, 79 adult males and 79 adult females, i.e. 79 mated pairs, were trapped during different stages of their breeding cycle. For more details about the study area and the local red-backed shrike population, see Šimek (2001).

In the local population, the red-backed shrikes arrived from African wintering grounds in early May, and after some days start to pairing and to continue other breeding activities. During that time, birds were attracted by mealworms inserted as a lure and trapped by using bowl-traps or mist-nets (Šimek 2001). Individuals were ringed, sexed and aged according to Svensson (1992), and then basic body measurements were taken. For each individual, we measured the length of the right wing (maximum chord, with an accuracy of ±0.5 mm) with a metric ruler, the length of the right tarsus (with an accuracy of ±0.05 mm) with callipers, and body mass (±0.1 g) with a spring balance. We estimated body condition index as residuals from a regression of body mass on tarsus length (for more details on index computation and their significance, see Tryjanowski et al. 2004). Because of a significant decrease in the female body mass (and therefore body condition index) during the breeding cycle (Takagi 2002; J. Šimek, unpublished data), the body mass of each female was adjusted by regression analysis to that at the time the first egg was laid. All morphological parameters and reproductive measurements were made by one person (J. Šimek).

For measuring SSD, we used the absolute differences between linear traits (wing length and tarsus length) in each pair. We did not use principal component analysis, an alternative and commonly used method, e.g. Blondel et al.

(2002), because wing length and tarsus length relate to different type of foraging used by shrikes (e.g. hovering flight and sit-and-wait) and thus selection may work independently on these traits (Leugger-Eggimann 1997; Hromada et al. 2003).

To find potential relationships between morphological differences in the red-backed-shrike pairs and reproductive parameters, only data for first (non-replacement) breeding attempts were included in the analyses. The timing of breeding was established separately for all 3 years and was expressed relative to the median value, which was set at 0, for the breeding population as a whole in each year. As a measure of breeding success, we counted the number of fledglings in each nest. Nestlings (in 41 nests) were individually marked (colour points on the body, rings). They were also weighed to the nearest 0.1 g at age 6–9 days (day of hatch = 0) and body mass was then recalculated by regression to give mean nestling body mass at day 7.

We measured the power of assortative mating using correlation analysis. However, we did not test age-assortative mating, because of insufficient data (Šimek 2001). After the first winter, exact age cannot be determined by plumage features (Svensson 1992) and, despite reasonably high local recruitment, the numbers of known-age ringed birds was too small for analysis (Šimek 2001).

Effects of body size and of differences between mates within pairs were tested using forward model selection in multiple regression analysis, keeping only variables and interaction terms in the models with significance of  $P < 0.1$ . Statistics were performed using SPSS for Windows following Zar (1999), and all tests were two-tailed. Data are presented as means ± SD. Although neither body measurements nor reproductive traits differed significantly between years ( $P > 0.25$  in all comparisons), effect of year was controlled in all analyses. Sample sizes differed slightly among analyses because not all measurements were available for all individuals.

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## Results

### Sexual size dimorphism

Significant differences occurred between the sexes for all measurements (Table 1). Thus, in adult red-backed shrikes, females were on average heavier than males. On the other hand, in the case of both linear traits, males were on average larger than females. Thus, females, during the start of breeding, were in better condition than their mates (body condition index  $1.39 \pm 0.16$  vs  $1.19 \pm 0.07$ , females vs males, respectively,  $U$ -test,  $Z = -7.63$ ,  $P < 0.0001$ ).

### Assortative mating

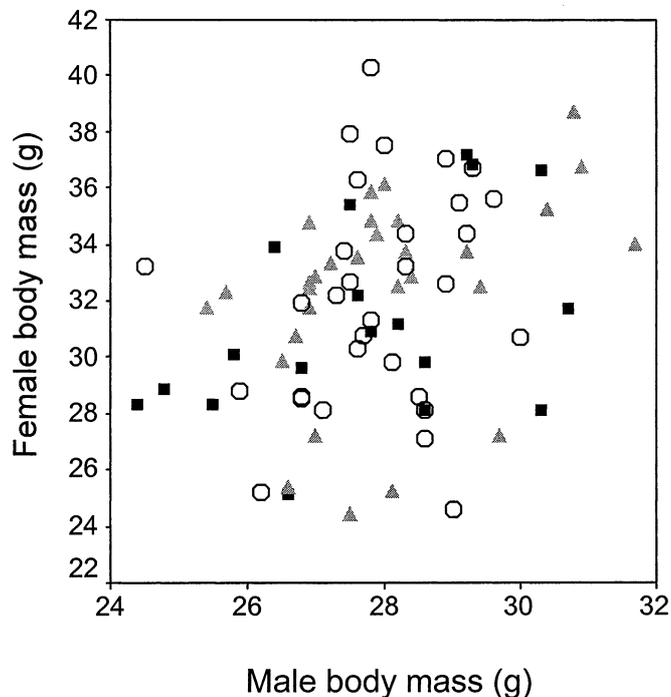
Pair mates did not resemble each other in wing length ( $r = 0.08$ ,  $N = 78$ ,  $P = 0.48$ ) or tarsus length ( $r = 0.13$ ,  $N = 74$ ,  $P = 0.26$ ). However, there were strong positive relationships between mates in both body mass ( $r = 0.33$ ,  $N = 79$ ,

**Table 1.** Differences in body measurements between the sexes for red-backed shrikes *Lanius collurio*. Sample size was 77–79 females and 75–78 males in following analyses (see Materials and methods for details). *DI* dimorphism index = (mean females/mean males) × 100. Effect of year was controlled in all analyses (ANCOVA, effect of year at  $P > 0.2$  in all cases). Differences in body mass and wing length were also statistically significant after sequential Bonferroni method for multiple tests

Variables	Mean ± SD		DI	F	P
	Females	Males			
Body mass (g)	32.0 ± 3.6	27.9 ± 1.5	114.8	87.70	<0.001
Wing length (mm)	93.1 ± 2.5	94.2 ± 2.1	98.8	8.78	0.004
Tarsus length (mm)	23.18 ± 0.62	23.43 ± 0.66	98.9	6.31	0.013

**Table 2.** Effects of measured body traits and of differences in body measurements between the sexes (SSD) on various reproductive traits of red-backed shrikes. Only variables with significant effects are shown, but effect of year is given in all cases. Note that there is no significant effect for laying date. However, after sequential Bonferroni correction to multiple tests only affect male wing on the body mass of nestlings was statistically significant

	<i>df</i>	$R^2$	F	P
Clutch size				
SSD tarsus	1, 45	0.10	4.77	0.034
Year	2, 45		0.24	0.781
Number of fledglings				
SSD tarsus	1, 64	0.12	4.17	0.045
Year	2, 64		1.93	0.154
Body mass of nestlings at day 7				
Male wing	1, 37	0.25	9.87	0.003
Year	2, 37		0.57	0.569



**Fig. 1.** Relationship between body masses of red-backed shrike *Lanius collurio* mates ( $r = 0.33$ ,  $N = 79$ ,  $P = 0.003$ ). Effect of year (circles 1997, triangles 1998, squares 1999) was controlled in partial correlation

$P = 0.003$ ) and body condition ( $r = 0.35$ ,  $N = 75$ ,  $P = 0.002$ ). Thus, there was no evidence for assortative mating based on linear measurements, but there was for overall body mass (Fig. 1) and body condition.

#### Effect of body size and SSD on reproductive traits

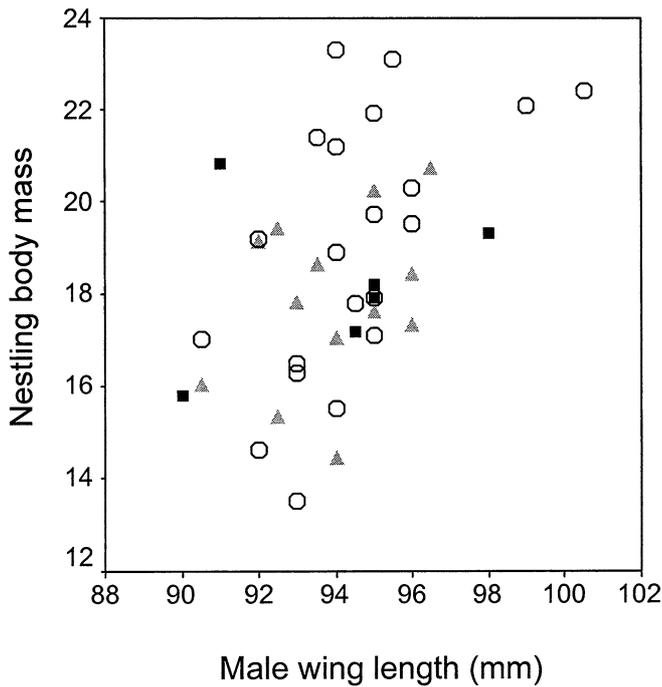
Clutch size and fledgling number decreased significantly as the breeding season progressed (respectively:  $r = -0.43$ ,  $N = 40$ ,  $P = 0.006$  and  $r = -0.40$ ,  $N = 48$ ,  $P = 0.005$ ). In contrast, average nestling body mass at 7 days of age was not influenced by the timing of breeding ( $r = 0.04$ ,  $N = 36$ ,  $P = 0.816$ ).

Body mass of parents and their linear measurements of size differences between the sexes had no significant effect on laying date. Male wing length significantly affected nestling body mass at day 7 (Table 2 and Fig. 2). No other body size measurements nor SSD explained a significant proportion of the variance in the models ( $P = 0.11$  for female wing length, and  $P > 0.45$  for all other variables). However, clutch size and the number of fledglings were slightly influenced by the differences in tarsus length between mates (Table 2), but not by the difference in body mass of mates.

## Discussion

### Sexual size dimorphism

Red-backed shrikes were slightly sexually dimorphic in body measurements, but the degree of dimorphism was only a few percent in body measurements. This is consistent with previous reports for this and other shrike species (Collister and Wicklum 1996; Takagi 1996; Kuźniak and Tryjanowski 2003; but see Tryjanowski and Yosef 2002 for migratory red-



**Fig. 2.** Relationship between nestling body mass and male wing length ( $r = 0.47$ ,  $N = 41$ ,  $P = 0.002$ ). Explanations: see Fig. 1

backed shrikes over Israel). It should be noted that data for female body mass were collected at the start of egg laying, when females are heavier (Moreno 1989; Takagi 2002) because, among other reasons, they are fed intensively by their mates (Carlson 1989; Takagi 2002). We have no information on the effects of morphological differences on the utilisation of different dietary niches (but see suggestions in Herremans 1997). However, it is well known (including data for shrikes: Ullrich 2002; Hromada et al. 2003) that even small morphological differences can influence differences in hunting technique and food spectrum.

#### Assortative mating

While no correlative evidence (*sensu* Mueller 1995) for assortative mating based on linear measurements was found in this study, shrikes mated assortatively by body mass and condition. Both body mass and body condition are “time-dependent” traits and tend to vary strongly over the breeding season (Moreno 1989; Leugger-Eggimann 1997; Takagi 2002). Therefore, why should red-backed shrikes use this trait in mate selection? When shrikes arrive on their breeding sites, they have only several days to start breeding, and hence mate choice must be made in the same short time period in a relatively restricted area. Therefore, better quality, i.e. first arrived, males may be inclined to mate with better quality, first arrived, females. Assortative mating could be explained by differences in arrival time dependent on body measurements and body condition, as described for many passerines (Møller 1994), including other shrike species (Yosef and Tryjanowski 2002), but not red-backed

shrike, at least in the middle of migratory route (Tryjanowski and Yosef 2002).

Positive assortative mating based on structural body size was reported for some bird species, and on morphological traits such as bill length, tail length and wing length. Several potential functional explanations, for example positive assortative mating linked with foraging opportunities and/or status signalling, have also been suggested (Warkentin et al. 1992; Sandercock 1998; Wagner 1999; Delestrade 2001). Only Wagner (1999) reported for razorbills (*Alca torda*) that body mass was positively correlated between mates. However, he pointed out that body mass is generally a relatively inaccurate variable in birds because it tends to fluctuate throughout the breeding cycle, although we controlled for this effect in this study of red-backed shrikes. Morphological traits are commonly connected with age, and causes and consequences of age-assortative mating are well documented (Reid 1988; Potti 2000; Takagi 2003). In an earlier paper (Votýpka et al. 2003), we found a bias in pair formation related to parasite status suggestive of assortative mating, which could indicate a simple link between condition and parasite prevalence. However, differences in body condition between infected and uninfected birds in either females or males were not found. Mating is only a first step in the breeding cycle, and equally important questions about how body size traits and differences in their expression between the sexes influence breeding performance and, consequently, fitness, must be asked.

#### The influence of size traits on reproduction

Among the analysed traits, only male wing length significantly correlated with the tested breeding variables, i.e. nestling body mass at day 7. This can be explained by two reasons. Firstly, in the red-backed shrike older males have longer wings than younger ones (Jakober and Stauber 1989). A correlation between offspring size and wing length could therefore be an effect of older birds obtaining better territories, based in part on knowledge from previous years about available breeding habitat linked to high territory fidelity (Šimek 2001). Secondly, birds with longer wings may forage more effectively, especially with respect to hovering to obtain small flying insects (Leugger-Eggimann 1997; see also predictions in Takagi 2003; Hromada et al. 2003). These types of prey, such as flies, wasps and moths, are important for nestlings during the early stages of growth (Tryjanowski et al. 2003) and thus males with longer wings may simply feed their offspring better.

#### Consequences of assortative mating for breeding traits

Variation in body traits/mating patterns per se seemed to be neutral for the pair's reproductive fitness in our study population. In contrast to positive assortative mating, we found positive relationships between differences in tarsus length between mates, which positively affected both clutch size and (correlated with this trait) the number of fledglings.

Clutch size and the number of fledglings depend on the quantity and quality of the diet, especially that delivered by the male to the female when she is laying and brooding small young (Carlson 1989; Takagi 2003). High-energy food comprises large insects (carabids, orthopterans) and, during poor weather, small vertebrates (lizards, shrews, voles) (Tryjanowski et al. 2003). To capture and handle such prey shrikes use their tarsus (Harris and Franklin 2000; Hromada et al. 2003), and therefore differences in tarsus length between the sexes may be an adaptation to avoid potential competition and broaden the prey base (see also Van Valen 1965; Przybylo 1995; Delestrade 2001).

In conclusion, explanations of assortative mating or SSD among mates could not be explained independently in an empirical field study of red-backed shrikes. Several selective factors can influence both assortative mating and size differences between mates, and there may be a balance between such pressures which are species, or even population, specific (see also Blondel et al. 2002). Hence, only experimental studies in strongly differing environmental conditions will help to clarify the causes and consequences of similarity and dissimilarity between partners.

**Acknowledgements** We are very grateful to Konrad Halupka, Piotr Zduniak, Marcin Antczak, and especially Shelley Hinsley and two anonymous referees for useful discussions and suggestions. This work was supported by the Ministry of Education (project 1131-B4) and by the Grant Agency of the Czech Republic (project 206/00/1094). During preparation of the final publication P.T. was supported by the Foundation for Polish Science.

## References

- Alatalo RV, Carlsson A, Lundberg A (1988) The search cost in mate choice of the pied flycatcher. *Anim Behav* 36:289–291
- Blondel J, Perret P, Anstett M-C, Thebaud C (2002) Evolution of sexual size dimorphism in birds: test of hypotheses using blue tits in contrasted Mediterranean habitats. *J Evol Biol* 15:440–450
- Carlson A (1989) Courtship feeding and clutch size in red-backed shrikes (*Lanius collurio*). *Am Nat* 133:454–457
- Collister DM, Wicklum D (1996) Intraspecific variation in loggerhead shrikes: sexual dimorphism and implication for subspecies classification. *Auk* 113:221–223
- Delestrade A (2001) Sexual size dimorphism and positive assortative mating in Alpine Choughs (*Pyrrhocorax graculus*). *Auk* 118:553–556
- Gibson RM, Langen TA (1996) How do animals choose their mates? *Trends Ecol Evol* 11:468–470
- Harris T, Franklin K (2000) Shrikes and bush-shrikes. Christopher Helm, London
- Herremans M (1997) Habitat segregation of male and female red-backed shrikes *Lanius collurio* and Lesser Grey shrikes *Lanius minor* in the Kalahari basin, Botswana. *J Avian Biol* 28:240–248
- Hromada M, Kuczyński L, Krištin A, Tryjanowski P (2003) Animals of different phenotype differentially utilise dietary niche – the case of the Great Grey shrike *Lanius excubitor*. *Ornis Fenn* 80:71–78
- Jakober H, Stauber W (1989) Beeinflussen und Alter der Ortstreue des Neuntötters (*Lanius collurio*)? *Vogelwarte* 35:32–36
- Jonsson PE (1987) Sexual size dimorphism and disassortative mating in the Dunlin *Calidris alpina schinzii* in southern Sweden. *Ornis Scand* 18:257–264
- Kuźniak S, Tryjanowski P (2003) Red-backed shrike. Wyd. KP, Świebodzin
- Leugger-Eggimann U (1997) Parental expenditure of red-backed shrikes, *Lanius collurio*, in habitats of varying farming intensity. University of Basel and Swiss Ornithological Institute, Sempach
- Møller AP (1994) Phenotype-dependent arrival time and its consequences in a migratory bird. *Behav Ecol Sociobiol* 35:115–122
- Moreno J (1989) Strategies of mass change in breeding birds. *Biol J Linn Soc* 39:297–310
- Mueller HC (1995) Correlation coefficients as evidence of female preference for size of mate. *Condor* 97:284
- Potti J (2000) Causes and consequences of age-assortative pairing in pied flycatchers (*Ficedula hypoleuca*). *Etologia* 8:29–36
- Przybylo R (1995) Intersexual niche differentiation – field data on the great tit *Parus major*. *J Avian Biol* 26:20–24
- Reid WV (1988) Age correlations within pairs of breeding birds. *Auk* 105:278–285
- Ryan MJ (1998) Receiver biases, sexual selection and the evolution of sex differences. *Science* 281:1999–2003
- Sandercocock BK (1998) Assortative mating and sexual size dimorphism in western and semipalmated sandpipers. *Auk* 115:786–791
- Šimek J (2001) Patterns of breeding fidelity in the red-backed shrike (*Lanius collurio*). *Ornis Fenn* 78:61–71
- Slagsvold T, Stenmark G, Breiehagen T (1988) On the cost of searching for a mate in female pied flycatchers *Ficedula hypoleuca*. *Anim Behav* 36:433–442
- Svensson L (1992) Identification guide to European passerines, 4th edn. Svensson, Stockholm
- Takagi M (1996) Sexual size dimorphism and sex determination of a brown shrike subspecies, *Lanius cristatus superciliosus*. *Jpn J Ornithol* 45:187–190
- Takagi M (2002) Change in body mass in relation to breeding phase in bull-headed shrikes. *Ecol Res* 17:411–414
- Takagi M (2003) Different effects of age on reproductive performance in relation to breeding stage in bull-headed shrikes. *J Ethol* 21:9–14
- Tryjanowski P, Karg MK, Karg J (2003) Food of the red-backed shrike *Lanius collurio*: a comparison of three methods of diet analysis. *Acta Ornithol* 38:59–64
- Tryjanowski P, Yosef R (2002) Differences between the spring and autumn migration of the red-backed shrike *Lanius collurio*: record from the Eilat stopover (Israel). *Acta Ornithol* 37:85–90
- Tryjanowski P, Sparks TH, Kuczyński L, Kuźniak S (2004) Should avian egg increase as a result of global warming? A case study using the red-backed shrike (*Lanius collurio*). *J Ornithol* 145:264–268
- Ullrich B (2002) Verhaltensökologische Beobachtungen am Maskenwürger, *Lanius nubicus*, im Vergleich mit anderen Würgerarten der Gattung *Lanius* unter Berücksichtigung ökomorphologischer Besonderheiten. *Okol Vogel* 24:523–558
- Van Valen L (1965) Morphological variation and width of ecological niche. *Am Nat* 104:377–399
- Votýpka J, Šimek J, Tryjanowski P (2003) Blood parasites, reproduction and sexual selection in the red-backed shrike (*Lanius collurio*). *Ann Zool Fenn* 40:431–439
- Wagner RH (1999) Sexual size dimorphism and assortative mating in razorbills (*Alca torda*). *Auk* 116:542–544
- Warkentin IG, James PC, Oliphant LW (1992) Assortative mating in urban-breeding merlins. *Condor* 94:418–426
- Widemo F, Saether SA (1999) Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends Ecol Evol* 14:26–31
- Yosef R, Tryjanowski P (2002) Migratory masked shrike, *Lanius nubicus* staging at the desert edge: phenology, and sex- and age-related differences in body mass. *Ostrich* 73:162–165
- Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, New York