Evolution of sexual size dimorphism in birds: test of hypotheses using blue tits in contrasted Mediterranean habitats

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Abstract

Many hypotheses, either sex-related or environment-related, have been proposed to explain sexual size dimorphism in birds. Two populations of blue tits provide an interesting case study for testing these hypotheses because they live in contrasting environments in continental France and in Corsica and exhibit different degree of sexual size dimorphism. Contrary to several predictions, the insular population is less dimorphic than the continental one but neither the sexual selection hypothesis nor the niche variation hypothesis explain the observed patterns. In the mainland population it is advantageous for both sexes to be large, and males are larger than females. In Corsica, however, reproductive success was greater for pairs in which the male was relatively small, i.e. pairs in which sexual size dimorphism is reduced. The most likely explanation is that interpopulation differences in sexual size dimorphism are determined not by sex-related factors, but by differences in sex-specific reproductive roles and responses to environmental factors. Because of environmental stress on the island as a result of food shortage and high parasite infestations, the share of parents in caring for young favours small size in males so that a reduced sexual size dimorphism is not the target of selection but a by-product of mechanisms that operate at the level of individual sexes.

Introduction

During the past three decades, evolutionary biologists have developed a large body of theory for explaining the evolution of sexual size dimorphism (hereafter SSD) in terms of sex-specific differences in the selection of mates, in food preference, or in response to environmental factors including competition and population density (Hedrick & Temeles, 1989; Björklund & Linden, 1993). Following the development of evolutionary quantitative genetic models in the 80 s (e.g. Lande, 1980; Roff, 1997), the focus of studies on the evolution of SSD somewhat shifted from traditional, ecological hypotheses to other hypotheses aiming to elucidate proximate factors underlying the evolution and maintenance of SSD (Fairbairn, 1990; Shine, 1990; Badyaev *et al.*, 2001; Reeve & Fairbairn, 2001). Theoretical and empirical work indicates that SSD can evolve and be maintained when selection acts to maintain size differences between sexes, provided that variation in the trait of interest has a heritable component, and the genetic correlation between the sexes is less than one (Lande, 1980; Slatkin, 1984; Lande & Arnold, 1985; Reeve & Fairbairn, 1996; Merilä *et al.*, 1998). In addition, SSD, which is usually measured in adults, can result from differences between sexes in growth patterns or selection pressures during ontogeny (e.g. Teather & Weatherhead, 1994; Merilä *et al.*, 1997; Badyaev *et al.*, 2001). Thus, detailed knowledge of genetic and ontogenetic variation is essential for understanding how male and female traits will respond to selection. Moreover, it is also necessary to examine the nature and the strength of selection in adult males and females, and how it may vary among populations, to

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assess the relative importance of various evolutionary pressures and constraints in the evolution of SSD (Lande, 1980; Price, 1984; Hedrick & Temeles, 1989; Badyaev *et al*., 2000; Badyaev & Martin, 2000; Preziosi & Fairbairn, 2000). Thus, sexual size dimorphism may be approached from two main perspectives: evolutionary genetics, mostly based on quantitative genetics, and life history evolution, mostly based on the investigation of contemporary selection pressures. In this paper, we will mostly consider the second perspective. Among the various hypotheses that have been formulated in relation to selective factors, two broad categories can be distinguished: sex-related and environment-related theories (see Table 1). In the first category, the 'Sexual Selection Hypothesis' (SSH) has long been preferred because of parsimony and predictive value (Ghiselin, 1974; Jehl & Murray, 1986; Shine, 1989; Andersson, 1994). The argument is that large size evolved in males because of the advantages of large size in male–male competition for access to breeding territories and mates, and its genetic and behavioural correlates in terms of fitness (Selander, 1972; Clutton-Brock *et al*., 1977; Shine, 1989; Andersson, 1994). Ghiselin (1974) argued that sexual selection favouring large males is more likely to occur in species or populations that evolved at high densities because of frequent encounters among competing males (the bigger, the stronger). A second hypothesis that sits in this category is the 'Territorial Defence Hypothesis' (TDH) which involves behavioural shifts such as reduced aggressiveness in relation to population density as often observed in insular vertebrates. Changes in social behaviour in populations with reduced male–male competition should be accompanied by a reduction in male size relative to female size (Stamps & Buechner, 1985), i.e. a reduction in SSD.

In the environment-related theories, SSD results from differences between sexes in their response to environmental characters and constraints. First, the intersexual niche differentiation hypothesis or 'Niche Variation Hypothesis' (NVH) states that an increase in the diversity of food resources used by a population leads to an increase of SSD resulting from differences between sexes in resource utilization (Van Valen, 1965; Selander, 1966, 1972; Schoener, 1967; Ebenman & Nilsson, 1982; Partridge & Green, 1985; Shine, 1989, 1990). Sex differences in size reduce intersexual competition when both sexes forage in the same microhabitat, allowing birds to decrease diet overlap, especially if food is scarce and population density is high (Van Valen, 1965; Schoener, 1967, 1982; Selander, 1972; Ebenman, 1986; Shine, 1989, 1990; Przybylo & Merilä, 2000). In this hypothesis, intersexual foraging competition can select for SSD with males being usually larger and exploiting larger and more diverse food items than females. However tests of the importance of the intersexual niche differentiation hypothesis, which has been a favourite theme in island biology for explaining the widening of the trophic niche of many organisms, provided equivocal results (Przybylo, 1995; Przybylo & Merilä, 2000), including on islands (Grant, 1979; Grant & Price, 1981; Dennison & Baker, 1991).

The second environment-related hypothesis is the 'Ecological Causation Hypothesis' (ECH) (Shine, 1989) which states that size differences between the sexes result from their different roles in reproduction. Differences in the share of parental care such as food provisioning, nest sanitation and antiparasite defence may lead to size differences between sexes irrespective of sexual selection or intersexual or intrasexual competition. Females may have advantage to be large because large females produce more and larger eggs, have better brooding aptitude (Selander, 1972), and can cope with longer fasting periods. On the other hand, males may have an advantage to be small because reduced size increases agility and manoeuvrability, allowing smaller birds to expend less energy during foraging bouts, and hence increase their foraging efficiency (Mosher & Matray, 1974; Andersson & Norberg, 1981). When males play the principal role in provisioning the family, forcing them to fly more than

Table 1 Main hypotheses explaining sexual size dimorphism (SSD) in passerine birds and their predictions for differences in SSD between Corsican and mainland blue tits.

Hypotheses	Prediction	Target trait	Sexual size dimorphism
Sex-related hypotheses			
1. Sexual selection (SSH)	More intense in Corsica because of high density	Overall size	Corsica > mainland
2. Territorial defence (TDH)	Lower aggressiveness and weak territorial defence in insular birds	Body mass	Corsica < mainland
Environment-related hypotheses			
3. Niche variation (NVH)	Stronger inter- and intra-sexual competition for food in Corsica	Bill size and shape, tarsus	Corsica > mainland
4. Ecological causation (ECH)	Food and parasite constraints in Corsica favours small males (small male hypothesis)	Body mass	Corsica < mainland
5. Environmental stress (ESH)	Males more sensitive than females to environmental stress, especially parasitism	Body mass and size	Corsica < mainland

females, flight energetics might explain the reversed SSD whereby males are smaller than females ('energetic efficiency hypothesis', Andersson, 1994).

Finally, the 'Environmental Stress Hypothesis' (ESH) states that sexes differ in their sensitivity to environmental stress with males being more sensitive than females to adverse environmental conditions such as poor habitat quality, intrabrood competition (Sheldon *et al*., 1998) and especially parasitism and disease (Williams, 1975; Trivers, 1985; Zuk, 1990; Møller & Saino, 1994; Potti & Merino, 1996; Møller *et al*., 1998; Badyaev *et al*., 2001). Thus, this hypothesis predicts a smaller SSD in populations confronted to environmental stress, e.g. experiencing strong parasite pressures.

This list of hypotheses is certainly not exhaustive and several of them probably work together reinforcing or reducing SSD depending on how selection on body size, or certain components of body size, operate on each sex. All the potentially acting factors make the causation of SSD particularly hard to explain because different causes can produce similar (or opposite) evolutionary trajectories for SSD. Except for the Sexual Selection Hypothesis that has been successful in explaining SSD in many species of birds and mammals (Jehl & Murray, 1986; Andersson, 1994), support for other hypotheses is scanty, including the intersexual niche differentiation hypothesis for which there is only very weak evidence (Shine, 1989; Przybylo, 1995; Przybylo & Merilä, 2000).

In birds, in spite of a vast literature, most studies on the adaptive significance of SSD focused on a few hypotheses only, mainly the SSH or the intersexual niche differentiation hypothesis, whereas very few tried to disentangle which is (or are) the most likely to explain patterns of SSD in a given species-specific situation. Two approaches for testing which hypothesis best explains SSD are (1) to manipulate environmental factors such as the food demand (e.g. Przybylo & Merilä, 2000) or parasitic loads, and (2) to compare populations living in habitats which differ in environmental factors of crucial importance for reproduction. We chose this latter approach and studied two populations of blue tits (*Parus caeruleus*) living in sharply contrasting Mediterranean environments, one located in mainland France, the other in the island of Corsica. Compared with the mainland population, the Corsican population differs in several aspects which are of importance for this study. First, population density is twice as high in Corsica as on the mainland [1.35 ± 0.19 (SD) and 0.70 ± 0.18 pairs ha^{-1} for the years 1991–1999 in Corsica and on the mainland, respectively, $F_{1,16} = 56.2$, $P < 0.0001$]. Secondly, the Corsican population is confronted to two sets of severe environmental constraints (see Blondel *et al*., 1993, 1998, 1999): (1) Trophic constraints because leaf-eating arthropods, mainly caterpillars that blue tits prefer as prey, are rarely abundant and occur late in the season (Zandt *et al*., 1990; Blondel *et al*., 1991, 1999; Banbura *et al*., 1994) (2) Parasitic constraints because of extremely high infestation rates by blood-sucking larvae of *Protocalliphora* spp. blowflies (Hurtrez-Boussès *et al*., 1997, 1998).

In an attempt to explain to which extent these differences in environmental factors have an effect on body size and SSD, we first examined whether SSD could be proximately determined at the nestling stage as a result of differential growth patterns of the two sexes. Then we made three predictions from the hypotheses stated above (Table 1), keeping in mind that (1) it is not possible to test all the hypotheses potentially explaining SSD, and (2) several hypotheses are not mutually exclusive and may predict similar (i.e. reinforcing) or opposite evolutionary trajectories for SSD. Our predictions were: (1) If sexual selection favours large males at high population densities, we predict a larger SSD in Corsica than on the mainland. (2) If intersexual food competition is likely to occur in a context of high population density and low food resources in the species-poor insular population as predicted by the niche variation hypothesis, again SSD should be larger in Corsica than on the mainland. (3) If the combination of low food resources and high parasite loads in Corsica makes the share of parents in caring young more unbalanced in Corsica than on the mainland with females spending more time and energy to nest sanitation and males in feeding the young, ECH predicts a larger size reduction in males than in females, hence a smaller SSD in Corsica.

Our focus in this paper is on sexual size dimorphism, i.e. body size of one sex relative to that of the other, but not on the differences in absolute size between the two populations because the *c*. 15% reduction in size of the Corsican subspecies of blue tit (*P. caeruleus ogliastrae*) is probably because of other causes than those studied in this paper. We will first compare the patterns of variation in SSD between the two populations. Then, we will assess the relative contribution of body size and sexual size dimorphism to fitness components. Thus, a first set of analyses refers to interpopulation differences in SSD, i.e. patterns; and a second set of analyses refers on how variation in SSD affects fitness components, i.e. processes.

Materials and methods

The Corsican study site is a forest of Mediterranean evergreen holm oak (*Quercus ilex*) at an altitude of 100–130 m, near Calvi (42°34′N/08°44′E, hereafter called Pirio) where blue tits have been studied since 1976 (see Blondel *et al*., 1993 for details on the habitats). The study area (*c*. 60 ha) is situated on siliceous soil poor in nutrients and the densities of leaf-eating caterpillars in the evergreen holm oaks are low in comparison with those of deciduous forests (Zandt *et al*., 1990). The mainland site (*c*. 60 ha) is a deciduous forest of downy oak (*Q. humilis*) near Montpellier

(43°40′N/03°40′E, hereafter called Rouvière). One hundred and thirty nestboxes have been evenly distributed in the two habitats at a density of *c.* 2 nestboxes ha^{-1} since 1990.

The blue tit is a small (9–12 g) insectivorous passerine whose favourite habitat is oak forest at low and mid altitudes. The female incubates alone and is regularly fed by the male during the incubation period (Nilsson & Smith, 1988). Both sexes feed the nestlings for 20–22 days. Breeding performance (laying date, clutch size, hatching and fledging success) of the birds was assessed through routine inspection of the nest-boxes at least once a week each year in 1991–1999 (a total of 316 and 301 pairs at Pirio and Rouvière, respectively, have been included in this study). As a measure of breeding success we counted the number of fledglings in each nest. Nestlings were individually marked and weighed to the nearest 0.1 g at 15 days. Tarsometatarsus (hereafter called tarsus) length was measured to the nearest 0.1 mm when the young were 15 days old. Tarsus of fledglings is the best estimate of structural size because it is the only available morphometric measurement which has reached adult length in the prefledgling stage of the blue tit (Merilä & Fry, 1998). Tarsus length did not significantly differ between their prefledging and adult stage in samples of 158 and 114 chicks (males and females combined) that have been recruited in the Pirio and Rouvière populations (paired *t*-test, $n = 272$, $t = 0.381$, $P = 0.704$; tarsus length = 16.30 ± 0.54 vs. 16.20 ± 0.51 and 16.88 ± 0.46 vs. 16.97 ± 0.39 for fledging and recruit males at Pirio and Rouvière, respectively; similar values for females are 15.56 ± 0.52 vs. 15.56 ± 0.46 and 16.42 ± 0.64 vs. 16.47 ± 0.49). Offspring condition, which is positively correlated with survival prospects (Pettifor, 1993; Blondel *et al.*, 1998; Merilä *et al.*, 1999), was defined as the residuals from the regression of body mass of the 15-day young on their tarsus length (Linden *et al.*, 1992). Parents were routinely trapped in the nest-box when feeding 9–12 days nestlings, marked with individual number rings, aged (yearling or adult), weighed and measured (wing, tarsus, culmen). Adult survival and the number of offspring recruited in the breeding population were determined by catching the breeding birds within the study area in subsequent years. For nests that produced at least one fledgling we identified 97.3% of the females and 89.0% of the males. All measurements (individuals, observers) were highly repeatable (Costes & Lecouturier, 1993). Therefore, to minimize measurement error, we used the average of all yearly measurements for every individual. Individuals with missing values were not included in the analysis. To avoid pseudoreplication, we randomly chose in the analyses only one observation for individuals which had several breeding records.

We used the first axis of a Principal Component Analysis from the correlation matrix of measurements of the four morphological traits (mass, wing, tarsus, culmen) as an estimate of body size. PC1 has the highest degree of correlation with the univariate morphometric measurements (Dennison & Baker, 1991) and has the advantage to exclude much of the measurement error in the traits (Gauch, 1982). PC1 was extracted from separate analyses for males and females to calculate a body size index (BSI). The first PCA axis accounted for 52.04% of the total variance at Pirio and 49.05% at Rouvière. In the two regions morphometric traits were strongly correlated to BSI ($r = 0.75$ and 0.77 for wing length, 0.84 and 0.78 for body mass, 0.73 and 0.64 for tarsus length at Pirio [$n = 316$] and Rouvière [$n = 301$], respectively); unless specified these sample sizes are the same throughout the whole paper. The correlation was weaker, although still significant, for bill length ($r = 0.22$ and 0.40, $P < 0.0001$ at Pirio and Rouvière, respectively) which scored on the second axis of PCA (eigenvectors = 0.96 and 0.87 on PC2 at Pirio and Rouvière, respectively).

For measuring SSD, we first used the residuals of a within pair regression of female body size values (PCF) on male body size values (PCM) by region as suggested by Ranta *et al.* (1994). However as the question we addressed was to analyse the effects of relative size differences between males and females of the pairs on reproductive output, the use of a ratio to express SSD is justified (Sokal & Rohlf, 1996). Therefore, we also used the dimorphism index of Storer (1966), DI = 100 * (female trait – male trait)/[0.5 * (female trait + male trait)]. For each pair we calculated SSD for each morphometric trait using this index. Then, all these indices were entered into a PCA. We used the first axis of this PCA (PC1) as an index of sexual size dimorphism (SSDI). PC1 ordinates pairs from small females with large males (negative values) to large females with small males (positive values). All analyses were done with both residuals and Storer's index and gave the same results because PCM is linearly linked to PCF by a regression line with a null intercept (intercept: $t < 0.01$, $P = 0.99$; PCF, $t = 25.15$, $P < 0.0001$), a result predicted by Ranta *et al.* (1994). Thus we will only show the results with SSD based on the index of Storer. In all the analyses we entered year and age as covariates (ancova) or as independent variables in multiple regressions.

Because environment-related hypotheses involve testing for sexual differences in diet we used a large body of data on prey items brought to nestlings in the two populations through video-recording inside the nest-boxes (Banbura *et al.*, 1994 and unpublished data). These analyses included 25 and 10 nests, and 3358 and 2259 prey items at Pirio and Rouvière, respectively. Prey items were divided into five categories according to taxon, and their size and volume were measured following Blondel *et al.* (1991).

Effects of body size and SSD were tested using generalized linear models [GLIM (NAG, 1986) and SAS (SAS Institute *et al.* 1992)]. We used forward model selection, keeping only significant variables and interactions in the models ($P < 0.1$). In all analyses, backward selection gave the same final model. All tests are two-tailed. We used Levene's tests to examine homogeneity of variances between populations because this test is preferred over traditional *F*-tests and Bartlett's test in detecting real differences in variances (Dennison & Baker, 1991).

Results

The SSD was significant in the two populations, males being larger than females in three of the four traits whereas females had larger bills than males (Table 2). The four morphological traits had smaller values in Corsica than on the mainland except female bill length which was similar in the two regions although Corsican blue tits, which belong to the subspecies *P. c. ogliastrae*, are 15% smaller than their mainland conspecifics. Absolute value of trait-specific SSD was smaller on Corsica than on the mainland for body mass and tarsus length and larger for wing length and bill length but the differences were significant for tarsus length only. Absolute value of SSDI (which combines wing length, body mass and tarsus length, see Methods) was significantly smaller in Corsica than on the mainland. This means that the two sexes are more alike on the island than on the mainland and that populations differ in shape with a proportionately longer bill and larger bill dimorphism at Pirio than at Rouvière. In most cases, Levene's tests showed that morphometric traits were significantly more variable at Rouvière than at Pirio (except male body mass which was more variable at Pirio). Sexual dimorphism in morphometric traits tended also to be more variable at Rouvière than at Pirio but the interpopulation difference in trait variability was significant only for bill length (Table 2). The two populations did not differ in the variation of SSDI.

Our first test was to examine whether differences in SSD between the two populations proximately resulted from differential growth of the two sexes in the nest. One proximate cause of interpopulation differences in SSD could be because of males suffering more from parasites at Pirio than at Rouvière (Environmental stress hypothesis). We checked this possibility from experiments of parasite removal that have been conducted over several years at Pirio (see Hurtrez-Boussès *et al*., 1997). Parasites had strong detrimental effects on growth patterns of both male and female nestlings ($F_{1,999} = 4.58$, $P = 0.032$, and $F_{1,999} = 29.70$, $P < 0.0001$ for body mass and tarsus length, respectively) but these effects were not more severe in males than in females (interaction sex * parasites, $F_{1,197} = 1.82$, n.s., and $F_{1,197} = 0.824$, n.s. for body mass and tarsus length, respectively). Similar results have been obtained by Hurtrez-Boussès *et al*. (1997) on chick survival.

Effects of body size and SSD on reproductive traits

Body size of parents and both measurements of SSD had no effect on laying date and clutch size (Table 3). Fledging success (proportion of eggs producing fledglings) strongly depended on male body size with opposite effects between Pirio and Rouvière. Small males had a better fledging success than large males at Pirio whereas the opposite was true at Rouvière

Traits	Pirio Mean ± SD	Male vs. Female *t*-test probability	Rouvière Mean ± SD	Male vs. Female *t*-test probability	Equality of variances *P*	Pirio vs. Rouvière
Wing length (mm)						
Male	63.6 ± 1.44		66.8 ± 1.66		0.013	<0.001*
Female	60.6 ± 1.15	<0.001*	63.8 ± 1.45	<0.001*	<0.001	<0.001*
SSD	−4.82 ± 2.97		−4.51 ± 3.06		0.573	0.188*
Mass (g)						
Male	9.3 ± 0.39		11.1 ± 0.18		<0.001	<0.001*
Female	9.2 ± 0.44	0.030*	10.9 ± 0.56	<0.001*	<0.001	<0.001*
SSD	−1.42 ± 6.37		−2.32 ± 6.46		0.797	0.118*
Tarsus length (mm)						
Male	16.18 ± 0.48		16.98 ± 0.45		0.149	<0.001*
Female	15.76 ± 0.48	<0.001*	16.38 ± 0.67	<0.001*	<0.001	<0.001*
SSD	−2.62 ± 4.17		−3.65 ± 4.57		0.109	<0.001*
Bill length (mm)						
Male	9.67 ± 0.33		9.77 ± 0.41		0.004	0.004*
Female	9.85 ± 0.37	<0.001*	9.87 ± 0.50	0.062*	<0.001	0.628*
SSD	1.68 ± 4.70		0.93 ± 6.01		<0.001	0.083*
SSDI	−2.919 ± 6.67		−4.135 ± 6.79		0.750	0.025*

**t*-test probability.

Table 2 Summary statistics (mean ± 1SD) of morphometric traits, their sexual size dimorphism (SSD) and the index of sexual size dimorphism (SSDI using wing length, body mass, tarsus length and bill length) of the Corsican (Pirio) and mainland (Rouvière) populations of blue tits. Sample sizes are 316 and 301 pairs at Pirio and Rouvière, respectively. Equality of variances tested with Levene's test. Probabilities of two sample *t*-tests are given for differences between regions and between sexes within regions.

Table 3 Effects of body size (derived index from PCA) on various reproductive traits of Blue tits at Pirio and Rouvière using generalized linear models (see Methods). The models controlled for the effects of age and year on breeding performance. Only variables with significant or nearly significant effects are shown. SSD was always non significant and we show the results of adding this variable to the model.

	d.f.	Type III SS	F	P
Laying date				
Region	1	172380	3790	<0.0001
Error	604	27469.52		
SSD	1	5	0.11	0.73
Clutch size				
Region	1	1684	859.2	<0.0001
Error	604	1183		
SSD	1	1.86	0.95	0.32
Fledging success				
Region	1	102.7	24.26	<0.0001
Male size*region	2	41.25	4.87	0.008
Female size	1	12.3	2.91	0.08
Error	445	1883		
SSD	1	1.49	0.35	0.55
Recruitment				
Region	1	1.3	2.41	0.12
Female size	1	2.5	4.63	0.03
Female size*region	1	3.6	6.67	0.01
Error	446	240		
SSD	1	0.05	0.09	0.76
Offspring condition				
Region	1	4.48	4.86	0.02
Male size	1	2.94	3.19	0.07
Female size	1	7.01	7.61	0.006
Female size*region	1	2.89	3.13	0.07
Error	384	354		
SSD	1	0.16	0.18	0.67

(Table 3, Fig. 1). In the two regions, there was a slight albeit insignificant positive effect of female size on fledging success.

Female size had more effect than male size on recruitment rates (Table 3) with larger females recruiting more offspring than smaller ones at Rouvière (Fig. 2). In contrast, female size did not affect recruitment rates at Pirio (Fig. 2). Male size had no effect on recruitment rates, neither at Pirio nor at Rouvière.

Offspring condition significantly depended on female size but the effect differed between regions (Table 3). At Pirio, smaller females produced offspring of better condition while larger females produced offspring of better condition at Rouvière (Fig. 3). In both regions male body size had no effect on offspring condition in spite of a positive correlation between the scores of male parents and those of their fledglings for body mass and tarsus length at Rouvière and for body mass only at Pirio ($F_{1,177} = 8.01$, $P = 0.005$ and $F_{1,219} = 11.80$, $P = 0.0007$ at Pirio and Rouvière, respectively, for body mass, and $F_{1,219} = 29.68$, $P < 0.0001$ for tarsus length at Rouvière).

Neither SSD (Table 3) nor the residuals of the regression of body mass on tarsus length (results not shown) explained significantly more variance than body size itself in the models (Table 3). This shows that it is the parents' size and not their size differences which determine their aptitude to raise the young.

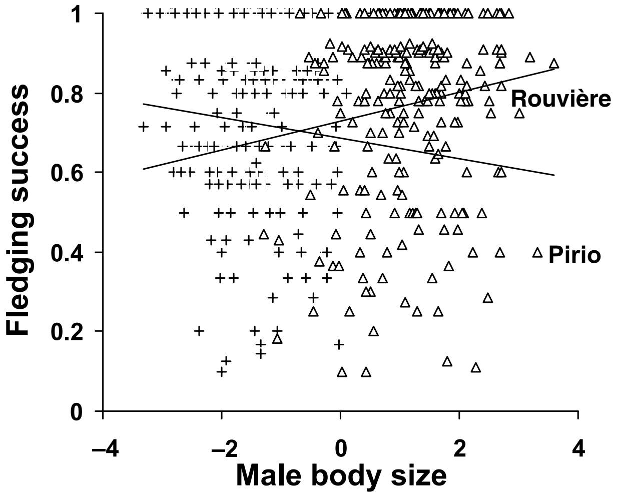

Fig. 1 Relationship between fledging success (proportion of eggs producing fledglings) and sexual size dimorphism at Pirio (crosses, thick line, $r = 0.197$, $b = 0.034$, $P < 0.001$) and Rouvière (open triangles, thin line, $r = 0.07$, $b = -0.015$, $P = 0.026$). Interaction between the slopes, $P < 0.001$.

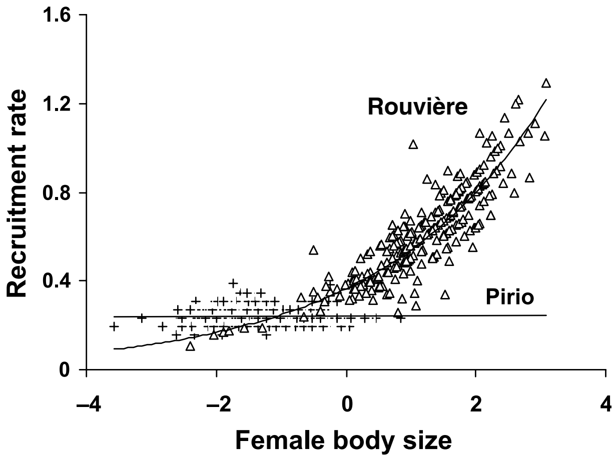

Fig. 2 Relationship between recruitment rate and female body size at Pirio (crosses, $r = 0.017$, $b = -0.003$, $P = 0.98$) and Rouvière (open triangles, $r = 0.89$, $b = 0.39$, $P < 0.001$). Interaction between the slopes, $P < 0.001$.

Fig. 3 Relationship between offspring condition (residuals of a regression of body mass on tarsus length) and female body size (Pirio, crosses, $r = -0.096$, $b = 0.108$, $P = 0.039$, Rouvière, $r = 0.20$, $b = 0.132$, $P < 0.001$). Interaction between the slopes, $P < 0.001$.

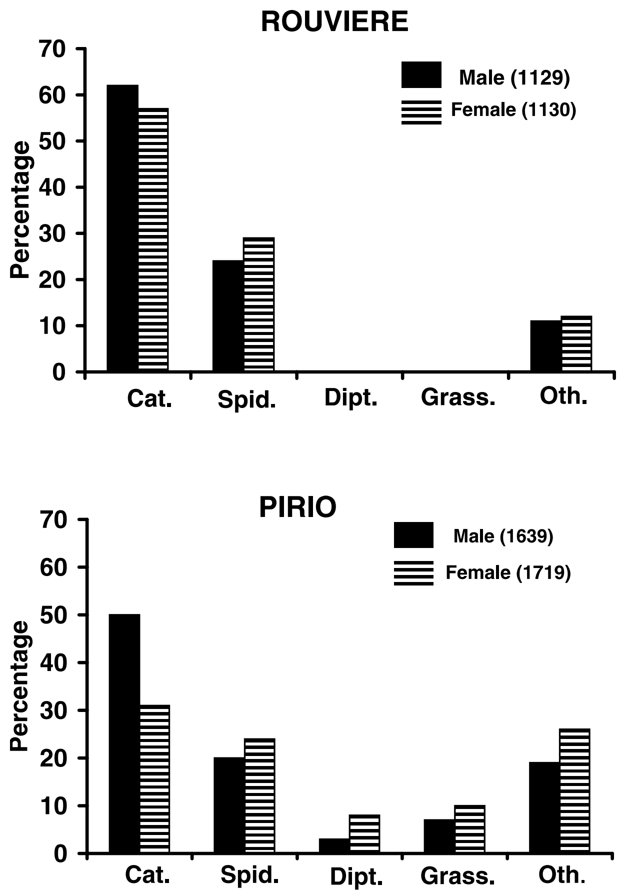

Fig. 4 Composition of the diet brought to nestlings by male and female blue tits at Rouvière and Pirio. Number of prey items in parentheses. Cat. = caterpillars, Spid. = spiders, Dipt. = dipterans, Grass. = grasshoppers, Oth. = others.

Food and feeding habits

Because caterpillar abundance is low in the evergreen Corsican habitat of Pirio (Blondel *et al.*, 1991; Banbura *et al.*, 1994), adults brought much less caterpillars to their nestlings at Pirio than at Rouvière (47 and 31% vs. 62 and 57% for males and females at Pirio and Rouvière, respectively, Fig. 4). This relatively low number of caterpillars was compensated by a large number of other prey such as grasshoppers and other arthropods (mostly dipterans, beetles, spider cocoons, ants, etc.). Interestingly males brought many more caterpillars than females at Pirio, which resulted in strong intersexual dietary differences between the two regions (males: $\chi^2 = 134.3$, $n = 2768$, $P < 0.0001$, females: $\chi^2 = 271.4$, $n = 2849$, $P < 0.0001$, Fig. 4). On average prey were larger at Rouvière than at Pirio ($F_{1,2664} = 30.79$, $P < 0.0001$), except caterpillars taken by males (Table 4), and sex differences in caterpillar volume were larger at Pirio than at Rouvière (log volume = 4.37 vs. 3.99, $P < 0.001$) at Pirio ($n = 776$ and 702) as compared with 4.49 vs. 4.33, $P < 0.0001$ at Rouvière ($n = 542$ and 646) for males and females, respectively. Thus, in both regions females took significantly smaller caterpillars than males in spite of them having a longer bill, this resulting in a significantly

Table 4 Sexual differences in volume (mm^3) of prey (caterpillars and spiders) at Pirio and Rouvière. Standard deviation in parentheses. The 'difference' line gives the probability of the two samples *t*-test for difference between males and females. In the Pirio/Rouvière columns we give the ratios of prey size and then the probability of a difference between populations (two samples *t*-test).

	Caterpillars			Spiders		
Sex	Pirio	Rouvière	Pirio/Rouv.	Pirio	Rouvière	Pirio/Rouv.
Males	132.6	125.4	1.06	23.1	45.1	0.51
	(128.49)	(100.1)	$P = 0.193$	(22.6)	(34.4)	$P < 10^{-4}$
Difference	$P < 0.001$	$P = 0.002$		$P = 0.410$	$P = 0.485$	
Females	94.6	108.5	0.87	24.5	43.2	0.57
	(106.9)	(95.1)	$P = 0.029$	(30.1)	(32.4)	$P < 10^{-4}$
Male/female	1.426	1.151		0.938	1.044	

larger intersexual difference in prey diversity and prey size at Pirio than at Rouvière.

Discussion

The foregoing discussion assumes that the importance of body size in life history (Roff, 1992; Stearns, 1992) combined with the rapid response of morphological traits to selection (Falconer, 1989; Grant & Grant, 1995; Losos *et al*., 1997; Preziosi & Fairbairn, 2000) make body size of both adult males and females a likely target for selection. However, an increasing amount of evidence shows that differential growth patterns of the two sexes as nestlings can proximately result from environmental stress producing SSD in adults (e.g. Merilä *et al*., 1997, 1998, 1999; Sheldon *et al*., 1998; Badyaev *et al*., 2001). One possible environmental factor differentially affecting growth patterns in our blue tit populations is the high parasite load in Corsica. However, this environmental stress does not result in differential growth between male and female nestlings as demonstrated by our experiment with deparasitized broods. Although we cannot completely rule out the possibility that some part of the observed morphological variation results from environmental conditions during growth we focus in this paper on contemporary selection on body size and shape, pointing out the consequences of morphological variation on fitness components. Our rationale is that it is likely that the observed effects of body size on fitness we found in our populations contribute to evolutionary changes in morphology. Hence, differences in sex-specific selection pressures found among populations, as in another study (Badyaev & Martin, 2000), suggest that interpopulation variation in sexual dimorphism has arisen from population differences in adaptive responses in males and females.

Summarizing the effects of body size and shape, large females did on average better than small ones for several components of breeding performance and offspring condition, and these effects were stronger at Rouvière than at Pirio. At Rouvière both sexes have clearly an advantage to be large. On the other hand, at Pirio male size had a negative effect on fledging success with large males producing less offspring than small ones (Fig. 1). In this Corsican population smaller females produced offspring of better condition than larger ones, pointing out the advantage of smallness in both sexes in this population. As a result, the index of sexual size dimorphism (SSDI) was significantly larger on the mainland than on the island, with sexes being more alike and traits less variable at Pirio, with the exception of body mass. This large difference between the two regions was mostly because of male size as shown by the strong interaction male size*region (Table 3, Fig. 1). These patterns explain why SSD had no effect on any breeding parameter. The question of why such an advantage for small birds, especially males, on Corsica will be addressed by examining the predictions of the hypotheses stated in Table 1.

Two of the five hypotheses listed in Table 1 predict larger males relative to females on Corsica (larger SSD, hypotheses SSH, NVH), and three predict the opposite (smaller SSD, hypotheses TDH, ECH, ESH).

Sex-related hypotheses (SSH and TDH)

The sexual selection hypothesis predicts a larger SSD in the high-density insular population of Pirio as compared with that of Rouvière. Contrary to this expectation, SSD is actually smaller at Pirio than at Rouvière. Although there was neither size assortative nor dissortative mating in our populations [*r*-values between males and females smaller than 0.07 for all traits except for wing length ($r = 0.22$) and culmen ($r = 0.25$) at Rouvière], there is a clear advantage for females to mate with small males at Pirio. In a previous study, Blondel *et al*. (2000) showed that at Pirio where divorce rates are much higher than usually reported for tits, females rather than males make the decision to divorce, and, in doing so, try to find a better territory and/or a better mate. This suggests that 'good territories' could be held by small males. Examining male body mass in relation to territory quality (classified in two categories, 'good' and 'poor', see Blondel *et al*. (2000), it has been found that this is indeed the case: the average body mass of males is 9.43 ± 0.37 g in poor territories as compared with 9.25 ± 0.28 g in good ones ($F_{1,61} = 3.79$, $P < 0.05$). Moreover, the social behaviour of Corsican blue tits is characterized by a reduced aggressiveness and a weak territorial defence (Perret & Blondel, 1993). This provides support for the Territorial Defence Hypothesis (Stamps & Buechner, 1985) which predicts a lower SSD on Corsica. Thus in the insular context of Pirio, the biggest is not the strongest as predicted by the SSH but the smallest is the most efficient as predicted by the TDH.

Environment-related hypotheses (NVH, ECH, ESH)

The Niche Variation Hypothesis (or food niche differentiation hypothesis) also predicts a larger SSD and a larger intrapopulation variation of traits at Pirio than at Rouvière. This hypothesis would be supported if bill morphology showed a greater dimorphism than expected from differentiation of overall body size, and in a direction consistent with the niche differentiation hypothesis but inconsistent with SSH. Although bill SSD is slightly larger at Pirio than at Rouvière (Table 2) variation of bill size is not higher at Pirio than at Rouvière and bill dimorphism does not correlate with dietary divergence between the sexes because the short-billed (males) actually takes larger prey than the long-billed (females). Finally variation in bill dimensions is not higher in the habitat where the preferred food is scarcer (Pirio) as predicted by NVH (Rothstein, 1973; Gosler, 1987). All these points run counter to the niche variation hypothesis. Finally the fact that SSD had no effect on any reproductive trait and is not larger in characters related to foraging (e.g. bill size) is an indication that the most probable cause of the dimorphism is not selection for ecological displacement between the sexes to reduce competition (Ebenman, 1986). These results are quite similar to those of Przybylo (1995) and Przybylo & Merilä (2000) which also do not support the intersexual food niche differentiation hypothesis in populations of great and blue tits. These authors point out that in fact evidence for intraspecific niche differentiation in passerines is weak.

The second environment-related hypothesis, the ECH, assumes that the two sexes are exposed to different selection pressures because of their differing reproductive roles that translate into different relationships between body size and fitness (Shine, 1989). At Pirio the combination of food shortage and heavy loads of parasites (see Introduction) is expected to influence the sex-specific allocation of time and energy in offspring care. Selection may shape parental investment depending on how parasites affect the relationship between reproductive effort and current reproductive success (Forbes, 1993; Perrin *et al*., 1996). At Pirio, parasites increase the energetic requirements of the birds because parents have to compensate for the considerable draining of the chicks' blood (up to 50% daily). As a consequence, males considerably accelerate their feeding frequencies, although no such effect was found in females (Hurtrez-Boussès *et al*., 1998; see also Christe *et al*., 1996; Tripet & Richner, 1997). This means that males must play a crucial role in providing much of the food to nestlings both in quality and quantity because they take more and larger caterpillars than females (Table 4). In this context selection should favour a smaller size because foraging efficiency is higher in smaller individuals as a result of reduced energetic costs of maintenance, increased manoeuvrability and less expensive foraging as predicted by the 'Small male hypothesis' (Andersson & Norberg, 1981; Norberg, 1981; Merilä & Wiggins, 1997). This hypothesis is consistent with the expectation that in populations living in more severe environments there is an enforcement of the share in time and care activities between sexes (Wittenberg & Tilson, 1980) so that SSD is not the target of selection but a by-product of mechanisms that operate at the level of individual sexes.

Population differences in SSD are in agreement with differences in sex-specific responses to habitat-specific environmental factors and constraints. The sex-specific roles, especially the male's function as forager for the family and the female's function in parental care and nest sanitation determine to a large extent the direction and degree of SSD at Pirio, a pattern very similar to that explaining the reversed SSD in raptors (Andersson, 1994).

In conclusion, processes underlying SSD presumably involve an interplay between adaptive, exaptive and nonadaptive genetic influences on the one hand, and environmental variables on the other (Shine, 1990). The conceptual distinction between the roles of sexual selection and natural selection is difficult because the two processes are closely linked so that sex-related and environment-related theories are not mutually exclusive. It is therefore unlikely that SSD might be explained by a single clear-cut hypothesis, which incidentally explains the large scatter of points on Figs 1 and 3, but rather from a combination of factors which vary from population to population. Hence, explanations of SSD cannot be generalized from a particular empirical case study. Many aspects of SSD are still poorly understood but one conclusion of this study is that population differences in body size and SSD may result from a balance between several habitat-specific selection pressures. Several selective factors can influence sex differences in body size and the multifarious population-specific combinations of these factors make any generalization and hypothesis testing difficult (Selander, 1966; Slatkin, 1984; Shine, 1989). More experimental studies and selection analyses performed across populations should help clarify the causes and consequences of sex differences in parental role and foraging, and assess the relative importance of natural and sexual selection (e.g. Saether *et al*., 1986).

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