Evolution of Sex-Biased Dispersal

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EVOLUTION OF SEX-BIASED DISPERSAL

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ABSTRACT

Dispersal is central in ecology and evolution because it influences population regulation, adaptation, and speciation. In many species, dispersal is different between genders, leading to sex-biased dispersal. Several theoretical hypotheses have been proposed to explain the evolution of this bias: the resource competition hypothesis proposed by Greenwood, the local mate competition hypothesis, and the inbreeding avoidance hypothesis. Those hypotheses argued that the mating system should be the major factor explaining the direction of such bias. Sociality and the presence of handicap in genders (exaggerated sexual characters or parental care) have recently been proposed to be linked with the direction of this bias. We tested these expected coevolutions using a database of 257 species. Based on phylogenetic approaches, our findings marginally corroborated Greenwood's hypothesis by showing relationships between the direction of sex-biased dispersal, mating systems, and territoriality. More importantly, our results highlighted that the evolution of this bias was more linked to parental care and sexual dimorphism. These traits were also found to be associated with mating systems, suggesting that sexual asymmetry in morphology and parental care might be the main determinant of the evolution of sex-biased dispersal across species and not mating systems per se, as proposed in Greenwood's hypothesis.

INTRODUCTION

DISPERSAL is a key component of the life history of a species, by influencing population genetic structure, population dynamics, and persistence (Bohonak 1999; Clobert et al. 2001; Ronce 2007; Guerrini et al. 2014). Understanding the evolutionary mechanisms underlying variation in dispersal has therefore been a fundamental research question for over 30 years (Clobert et al. 2001; Bowler and Benton 2005). Measuring and predicting dispersal in space and time still remains challenging since the interaction between the individual phenotype and the particular social and environmental context all influence why, when, and where individuals disperse (Koenig et al. 1996; Clobert et al. 2009, 2012; Bonte et al. 2012; Duputié and Massol 2013). However, the investigation of phenotype-dependent dispersal has revealed a strong general pattern: there are recurrent dispersal differences between genders, individuals of one sex often dispersing more or further than individuals of the opposite sex. Such sex-biased dispersal (SBD) is also related to differential reproductive success of dispersers and residents (Schweizer et al. 2007), which could promote the establishment of fine-scale genetic structure and adaptation to local environments (Greenwood 1980; Goudet et al. 2002; Rousset 2004). Hence, SBD might have important impacts on population genetic structure and metapopulation functioning (Greenwood 1980; Goudet et al. 2002; Guerrini et al. 2014).

Most of our current understanding of SBD comes from birds and mammals: mammals usually show a tendency toward male-biased dispersal (Dobson 1982) whereas females are generally more dispersive in birds (Greenwood 1980; Clarke et al. 1997). It is now widely accepted that dispersal becomes sex-biased when the evolutionary forces acting on dispersal are unbalanced between genders (Perrin and Goudet 2001). From the contrasting pattern of SBD in birds and mammals, three hypotheses have been proposed to explain how SBD evolved: the "*resource competition hypothesis*" (Greenwood 1980); the "*local mate competition hypothesis*" (Dobson 1982; Perrin and Mazalov 2000), and the "*inbreeding avoidance hypothesis*" (Pusey 1987; Perrin and Mazalov 2000). The most dominant theory on how SBD evolved refers to the *resource competition hypothesis* (Greenwood 1980), which proposes that the interaction between local resource defense and local mate competition drives the evolution of SBD. Accordingly, the mating system type and defensibility of resources should promote the evolution of dispersal differences between genders. Greenwood suggests that in monogamous species with territory defense, the defense of resources by the territorial gender should increase philopatry in that gender. From this expectation, Greenwood anticipates that in birds (typically monogamous and exhibiting male defense of resources), local resources should be very important for territorial males, leading to female-biased dispersal (FBD). By contrast, in polygynous species (usually mammals), male-biased dispersal (MBD) is expected for two reasons: local resources are important for females because they rear young and male-male competition for mates is strong. Territorial males may defend resources that females require (resource defense polygyny; e.g., nesting sites) or defend females themselves (female defense polygyny; Emlen and Oring 1977), but it is unclear if such a distinction will influence SBD and the relevant data on resource distribution is often lacking. On the contrary, in polyandrous species, high female-female competition for mates could lead to FBD. The *resource competition hypothesis* was extended by Dobson (1982) who proposed that the expected relationship between mating systems and SBD could be expanded to other taxonomic groups with MBD occurring in polygynous species and FBD in monogamous species. He also suggested correlating the level of intrasexual competition, instead of mating systems, with the direction of SBD such that the sex that suffers from more intense intrasexual competition should disperse more (*local mate competition hypothesis*; Dobson 1982). Under the local mate competition hypothesis, female choice and intense male-male competition (which is likely to happen when the operational sex ratio is skewed) would be expected to cause male dispersal (Dobson 1982).

According to Dobson (1982), in polygynous mammals males often compete strongly for mates, but not for resources, which could lead to MBD within those species. In most monogamous species, however, both sexes are expected to disperse (Dobson 1982). Consequently, FBD is expected under conditions of low male mating competition (Pérez-González and Carranza 2009). Finally, because dispersal should be a mechanism of inbreeding avoidance (Waser et al. 1986), the *inbreeding avoidance hypothesis* (Pusey 1987; Perrin and Mazalov 2000) has been proposed to explain evolution of SBD (Johnson and Gaines 1990). For instance, in polygynous species, the effect of inbreeding on lifetime fitness might be stronger for females than for males, since males may reproduce with several partners (Thornhill 1993). Analyses to date, though, suggest that inbreeding avoidance seems to have a weak effect on the direction of SBD (Moore and Ali 1984; Perrin and Mazalov 2000; Lehmann and Perrin 2003; Guillaume and Perrin 2009). Indeed, inbreeding can effectively be avoided by kin recognition coupled with mate choice, without incurring dispersal costs (Potts et al. 1991; Brown and Eklund 1994).

Altogether, these three not mutually exclusive hypotheses suggest that mating systems should play a major role in determining the costs and benefits of dispersal to each sex and hence influence the direction of SBD (e.g., Mabry et al. 2013). However, the role of mating systems in structuring SBD within and among species is still controversial (Moore and Ali 1984; Künkele and von Holst 1996; Wang et al. 2012). Indeed, other studies have proposed that the evolution of SBD could be linked to other factors, such as social behavior (Perrin and Goudet 2001) or traits more related to competitive interactions between males and females (Sutherland et al. 2000; Lawson Handley and Perrin 2007; Gauffre et al. 2009; Lane and Shine 2011). For instance, Perrin and Goudet (2001) proposed that different levels of sociality between genders could influence dispersal, both for sex-specific dispersal rates and for the magnitude of SBD. This effect of sociality on SBD might depend on interactions between sex-specific benefits of kin cooperation and inbreeding costs (Perrin and Goudet 2001). Under this scenario, only relatives living in the same area should benefit from kin cooperation. Hence, dispersers would not benefit from kin cooperation since they left their patch and joined nonrelated individuals. Therefore, benefits of kin cooperation (i.e., sociality) should be linked to benefits of philopatry. For instance, in polygynous species where males defend females, MBD might be expected because the value of philopatry is lower than for females. Males might be more affected by local mate competition and inbreeding avoidance, while females might benefit from sharing local resources to care for their young with their sisters (Clutton-Brock 1991). Consequently, females should benefit more than males from kin cooperation and, hence, from philopatry. Moreover, behavioral traits or lifestyle might have also coevolved with SBD rendering cause and effect difficult to determine (Gardner 2010; Johnstone and Cant 2008).

As SBD could evolve according to differences in fitness costs and benefits of dispersal between the sexes, any traits implicated in sex differentiation might play a role in the evolution of SBD. For instance, if sexual selection promotes the evolution of sex-specific potential, then handicaps such as bright coloration, large antlers, or other exaggerated traits may impose additional costs during dispersal and would lead to SBD favoring dispersal in the sex without such handicaps. Similarly, parental care by one or both sexes could also be considered a handicap for the sex that is performing it. If for some reason sex-biased parental care evolved (e.g., anisogamy or certainty of paternity), then the caring sex might have less energy and time to allocate to dispersal, and dispersal might be counterselected in that sex. The evolutionary causes behind the evolution of SBD require clarification (Lawson Handley and Perrin 2007) and examination of correlated life-history traits. Mating systems can induce intrasexual competition for access to breeding and, consequently, sexual dimorphism (Darwin 1871; Avise et al. 2002). In polygynous species, for instance, males compete for access to females, which often leads to males gaining an advantage by being larger than females (Reiss 1989). Mating systems can also promote different levels of parental care (Clutton-Brock 1991; Kokko and Jennions 2008) and levels of sociality (Stacey 1982; Perrin and Goudet 2001; Devillard et al. 2004; Cornwallis et al. 2010). Indeed, because parental care, sexual dimorphism,

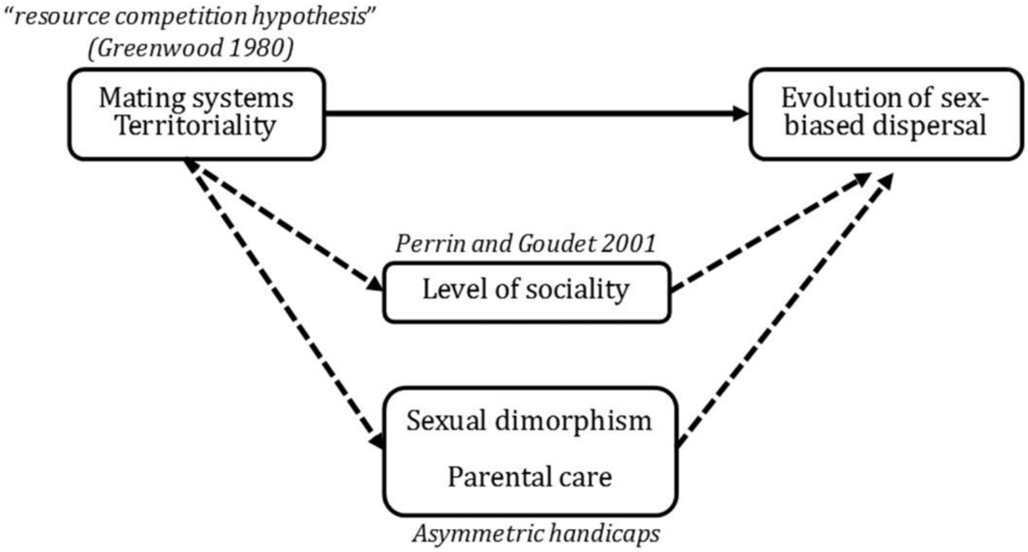

Figure 1. Potential Influence of Traits that Could Explain the Evolution of SBD
Direct correlations (solid arrows) are expected between mating systems, territoriality, and SBD under Greenwood's hypothesis, but indirect correlations (dotted arrows) could also be revealed by traits related to sociality and asymmetric handicaps.

and sociality could coevolve with the mating system, it might be that the underlying mechanisms acting on SBD are actually other traits related to mating systems (sociality and asymmetric handicaps; Figure 1), rather than mating system per se (Greenwood's hypothesis).

Although several recent studies used modern phylogenetic methods to study coevolution between behaviors in vertebrates (García-Peña et al. 2009; Shultz et al. 2011), only one examined coevolution between SBD and mating system (Mabry et al. 2013). Mabry and colleagues (2013) tested Greenwood's hypothesis on 101 species and demonstrated significant coevolution between mating systems and SBD in mammals but not in birds. However, this study only examined patterns separately within mammals and birds, but not together, and they did not account for any of the alternative hypotheses detailed above that could explain the evolution of SBD.

We used phylogenetic methods to study the relationships and the coevolution between SBD and several life-history traits including mating system. We conducted an extensive literature review yielding information on SBD for 257 species (contrast with 101 species in Mabry et al. 2013), including birds, mammals, lepidosaurs, crocodilians, turtles, amphibians, actinopterygian fishes, and arthropods. We then used this database to: test whether mating systems coevolved with the direction of SBD among all taxonomic groups together; analyze how the direction of SBD and the magnitude of the sex-bias evolved in parallel to a number of life-history traits other than mating system that could contribute to the evolution of SBD; and assess if other life-history traits linked to mating system and sociality could explain SBD across taxonomic groups.

Data Selection

how to identify sbd?

Two kinds of methods allowed identification of SBD: direct methods and indirect methods. Among direct methods, SBD was identified with either tracking or mark-release-recapture surveys consisting of marking numerous individuals and recapturing them after given time intervals (Stanley and Burnham 1998). Mark-release-recapture provides the proportion of males and females recaptured and/or the distance traveled by individuals between two captures. When the ratio of males to females recaptured at the site of first capture was significantly different from the ratio marked there (after controlling for sex-specific survival rates), SBD was assumed. SBD was also identified directly when individuals of one sex moved further away from their site of origin than individuals of the other sex.

SBD was also identified by indirect genetic methods. The principal idea behind the use of genetic methods is the difference in the genetic differentiation in female and male subpopulations using measures such as the fixation index (F_{ST}; Wright 1949; Möller and Beheregaray 2004; Palo et al. 2004). Dispersal is assumed to be biased toward the gender with the lower genetic differentiation among its subpopulations (Hapke et al. 2001; Winney et al. 2004). Another way to measure SBD with genetic data is to compare the structure obtained from nuclear markers (inherited from both parents) to the structure obtained with mtDNA (inherited from the maternal lineage only). For example, when the differentiation in mtDNA is higher than that of the nuclear markers, then MBD was assumed. Additionally, some publications combined the direct and indirect approaches, which usually lead to the same assignment when both measures were conducted in the same population at the same time.

DISPERSAL DATA

We identified 371 publications reporting SBD by screening the Web of Science (1900–present) with the following search strings: (sex-biased OR male-biased OR female-biased) AND (dispersal OR movement OR migration) AND (distances OR mark-release-recapture OR genetics OR F_{ST}). Because dispersal and migration definitions are often confused and interwoven, we chose to search SBD papers employing both terms. MBD was identified in 202 publications (N = 166 species) and FBD in 166 publications (N = 136 species).

Some publications (N = 67) either used other methods than the ones explained above (i.e., direct behavioral observations of males and females) or did not allow us to determine the method used for SBD identification despite reporting a difference in dispersal between the sexes. For statistical reasons and to compare across studies, those latter publications were not retained in our analysis.

The sex-bias of dispersal was evaluated using two parameters: *direction of sex-bias* (D_{SBD}), a binary trait that indicates the direction of the bias, and *magnitude of sex-bias in dispersal* (M_{SBD}), a continuous trait that indicates the magnitude of the bias (see below). We assigned the D_{SBD} for all species with observed sex-bias in dispersal: it was either 0 (female bias) or 1 (male bias), according to the direction of the observed bias. Both the dispersal distance and the dispersal frequency are unlikely to be exactly identical between sexes, raising the question about the biological significance of small between-sexes differences considered to determine the value of SBD. Considering small sex differences (that can be biologically meaningless, but whose statistical significance is often untested) could obviously decrease the statistical power of our analysis. However, there is no reason to believe that this sampling artifact would not be randomly distributed across the species and sexes, and it is therefore unlikely that it introduced a systematic bias in our analyses.

Dispersal can be contingent on demography (population density: Baguette and Schtickzelle 2006; Hovestadt and Nieminen 2009; sex-ratio: Trochet et al. 2013) and on environmental context (Clobert et al. 2009; Stevens et al. 2014), such that different populations within species could exhibit different types of dispersal. Indeed, in a few species, both types of sex-biased dispersal were reported. For example, in the deer *Cervus elaphus*, FBD was recorded by Pérez-Gonzalez and Carranza (2009) whereas MBD was identified by Pérez-Espona et al. (2010). In such cases, we selected a single study (and associated D_{SBD}) using objective criteria, such as, for instance, the measurement of dispersal in a natural rather than a highly artificial context (e.g., hunting season). When no such objective criteria allowed us to select a single study, or when publications with both methods revealed directions of SBD, we removed those species from the analysis for which both FBD and MBD were reported (N = 5 species).

We also considered the *magnitude of sex-bias in dispersal*, M_{SBD}, calculated from either the dispersal distances performed by males and females (from direct methods; N = 260) or from the genetic differentiation (F_{ST}) for each sex (from indirect methods; N = 42). The M_{SBD} should be highly informative to understand the evolutionary causes of dispersal (Murrell et al. 2002; Rousset and Gandon 2002) because the reasons for long-distance and short-distance dispersal are likely to be very different (Ronce et al. 2001; Clobert et al. 2004; Duputié and Massol 2013). In order to scale the values obtained from both methods, we calculated for each species and study a value of M_{SBD} following one of the two equations above:

For data from direct methods:

$$M_{SBD} = \ln \frac{\textit{dispersal distance males}}{\textit{dispersal distance females}}$$

For data from indirect methods:

$$M_{SBD} = \ln \frac{1 - FST\ \textit{males}}{1 - FST\ \textit{females}}.$$

A negative value of M_{SBD} indicates a female-biased dispersal pattern, and a positive one indicates a male bias. M_{SBD} was calculated for 172 species (data from 297 publications). When several studies (from mark-release-recapture/tracking and/or from genetic methods) identified SBD in the same species, we averaged the values of M_{SBD} attributed to this species.

OTHER LIFE-HISTORY TRAITS

We recorded the information on several traits pertaining to male-female interactions as binary variables: individual polygamy, sexual dimorphism (color handicap and size handicap), sociality, cooperative breeding, territoriality, and parental care (see Supporting Information 1 and 2 for definitions, available at http://www.journals.uchicago.edu/loi/qrb). For all species, we attributed to each sex a value informing the presence of the trait: 0 or 1. For instance, for polygynous species, where one male can mate with several females while females have a single mate, "male polygamy" was 1 and "female polygamy" was 0. By contrast, for species with promiscuity, both traits would have the value 1 (Supporting Information 1 and Figure 2).

For some species, a trait state varied among individuals within a population (e.g., 5% of males are polygynous and 95% are monogamous). In these cases, we attributed to the species the state of the life-history trait adopted by the majority of individuals. In 45 of 302 species, life-history data were incomplete and we removed these species from further data analysis linked to life-history traits. Our complete dataset then contained 257 species (Tables 1 and 2, Figure 2, and Supporting Information 1) for which D_{SBD} and life-history traits were reported.

PHYLOGENY

A time-calibrated, composite phylogenetic tree (Supporting Information 3 for the phylogeny of species used, available at http://www.journals.uchicago.edu/loi/qrb) was built based on time-calibrated trees with divergence times and branch lengths estimated using both fossil and molecular evidence. The general structure of this time-calibrated tree came from the time-calibrated tree of animals available from Wiens (2015a) based on the constraints from Dunn et al. (2014) that indicated the phylogenetic place of vertebrate and hexapod species used here. We first incorporated to this super-tree the time-calibrated tree of vertebrates (Wiens 2015b; adapted from Alfaro et al. 2009) and hexapods (Rainford et al. 2014). We then included in the vertebrate tree the time-calibrated trees for each clade used in our study (mammals: Rolland et al. 2014; birds: Jetz et al. 2012; actinopterygian fishes: Santini et al. 2009; lepidosaurs: Zheng and Wiens 2016; amphibians: Pyron and Wiens 2013; turtles: Jaffe et al. 2011; and crocodilians: Oaks 2011). The avian time-calibrated tree was directly computed using

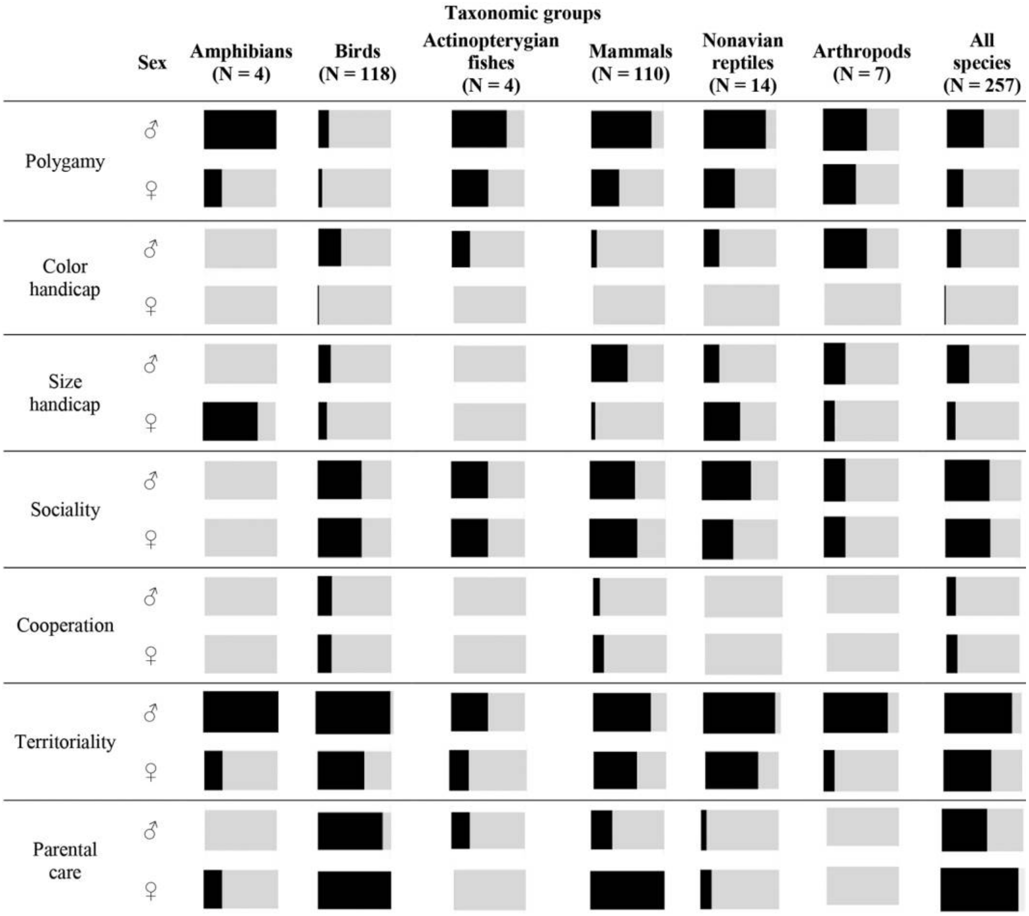

FIGURE 2. PERCENTAGE OF SPECIES USED IN OUR DATABASE FOR EACH LIFE-HISTORY TRAIT DEPENDING ON SEX AND TAXONOMIC GROUPS

N = number of species by taxonomic group. The proportion of species with different trait states are represented in bar graphs as follows: black shows species with a "Yes" state and grey shows species with a "No" state (see Table 2 for details).

the BirdTree website, by including only the species for which we had dispersal data (http://birdtree.org; Jetz et al 2012). Trees of turtles and crocodilians were available from Jaffe et al. (2011) and Oaks (2011) included in the *PhyloOrchard* R package (O'Meara et al. 2013). The composite time-calibrated tree was pruned to keep only the 257 species for which dispersal information was available (*ape* R package; Paradis et al. 2004).

To confirm that results were robust to phylogenetic reconstruction methods, our analyses were also run with a second uncalibrated phylogenetic tree. This uncalibrated phylogeny was based on a super-tree including both Arthropoda and Deuterostomia, available from the Tree of Life Project (2002), to which clade trees were branched (after the required addition and polytomy resolutions). Arbitrary branch lengths were then computed using Grafen's (1989) method implemented in the *compute.brlen* function (*ape* R package), and the tree was pruned to retain only the 257 species with reported SBD. The results of the analyses with this uncalibrated tree are in the Supporting Infor-

TABLE 1

Number of species retained in our study by taxonomic group, for which sex-biased dispersal has been identified, either from direct methods (mark-release-recapture and radio-tracking), indirect methods (genetics from nuclear or mitochondrial DNA), or both

	Methods of sex-biased dispersal identification						
	Direct methods		**Indirect methods**				
Taxonomic groups	**Mark-release-recapture**	**Radio-tracking**	**Nuclear DNA**	**Mitochondrial DNA**	**Both**	**Proportion of male- and female-biased dispersal**	**Total (species)**
Amphibians	1	0	3	0	0		*4*
Arthropods	6	0	1	0	0		*7*
Birds	109	2	5	1	1		*118*
Actinopterygian fishes	0	0	2	0	2		*4*
Mammals	56	11	21	6	16		*110*
Nonavian reptiles	5	0	6	1	2		*14*
Total	*177*	*13*	*38*	*8*	*21*		**257**

The proportion of sex-biased dispersal is shown where the black part represents male-biased dispersal and the grey part refers to female-biased dispersal.

mation 4 (available at http://www.journals.uchicago.edu/loi/qrb).

PHYLOGENETIC SIGNAL ON SBD AND OTHER TRAITS

We tested if the D_{SBD} and the values of life-history traits showed a significant phylogenetic signal by computing the D value (Fritz and Purvis 2010), as a measure of the phylogenetic signal in binary traits based on the sum of differences between sister clades in a phylogenetic tree, as implemented in the *caper* R package (Orme et al. 2012). D was tested against a random distribution of traits throughout the phylogenetic tree (in which case D would be close to 1) and against a distribution of trait values resulting from a Brownian motion model of evolution (in which case D would be close to 0; Fritz and Purvis 2010).

In order to test whether the M_{SBD} shows a significant phylogenetic signal, we computed the K statistic (Blomberg et al. 2003; *picante* R package), a test used with continuous variables. For this index, a value close to 0 indicates phylogenetic independence and a value close to 1 indicates that traits are distributed among species as expected under a Brownian model of evolution. The upper limit of Blomberg's K can take values higher than one, indicating stronger trait similarity between related species than expected under Brownian evolution.

MODEL BUILDING TO TEST EFFECTS OF LIFE-HISTORY TRAITS ON SBD

We explored the correlation between SBD (D_{SBD} and M_{SBD}) and life-history traits. In particular, we tested whether the variation in the D_{SBD} and the variation of M_{SBD} were correlated with life-history traits that form the basis of specific hypotheses on the evolution of SBD.

To test the relationships between the D_{SBD} and life-history traits, we controlled for the phylogenetic dependence of the data us-

TABLE 2

Life-history traits and their categories, definitions, and abbreviations used in the text

Life-history traits	**Category abbreviation**	**N**	**Definition**
Direction in sex-bias of dispersal	MBD	129	Male-biased dispersal: males disperse more often/ farther than females
	FBD	128	Female-biased dispersal: females disperse more often/ farther than males
Method of sex-bias identification	Direct method	194	Mark-release-recapture and tracking showing ecological dispersal
	Indirect method	42	Genetic methods showing effective dispersal (gene flow)
	Both	21	Use of both direct and indirect methods
♂ Polygamy[1]	No	126	Males are monogamous
	Yes	131	Males are polygamous
♀ Polygamy[1]	No	197	Females are monogamous
	Yes	60	Females are polygamous
♂ Color handicap	No	204	Males are not more colored than females
	Yes	53	Males are more colored than females
♀ Color handicap	No	256	Females are not more colored than males
	Yes	1	Females are more colored than males
♂ Size handicap	No	177	Males are not bigger than females
	Yes	80	Males are bigger than females
♀ Size handicap	No	226	Females are not bigger than males
	Yes	31	Females are bigger than males
♂ Sociality[2]	No	108	No sociality in males
	Yes	149	Sociality in males
♀ Sociality[2]	No	105	No sociality in females
	Yes	152	Sociality in females
♂ Cooperation	No	224	No cooperative breeding in males
	Yes	33	Cooperative breeding present in males
♀ Cooperation	No	219	No cooperative breeding in females
	Yes	38	Cooperative breeding present in females
♂ Territoriality	No	33	No territory defense by males during the breeding season
	Yes	224	Territory defense by males during the breeding season
♀ Territoriality	No	104	No territory defense by females during the breeding season
	Yes	153	Territory defense by females during the breeding season
♂ Parental care	No	119	Males do not provide parental care
	Yes	138	Males provide parental care
♀ Parental care	No	27	Females do not provide parental care
	Yes	230	Females provide parental care

N = number of species in a variable's category.

[1] In "Polygamy" categories, an association between ♂ Polygamy = 1 and ♀ Polygamy = 1 means a promiscuous mating system; ♂ Polygamy = 0 and ♀ Polygamy = 1 means a polyandrous mating system; ♂ Polygamy = 1 and ♀ Polygamy = 0 means a polygynous mating system; and ♂ Polygamy = 0 and ♀ Polygamy = 0 means a monogamous mating system.

[2] In "Sociality" categories, an association between ♂ Sociality = 1 and ♀ Sociality = 1 means a gregarious species; and between ♂ Sociality = 0 and ♀ Sociality = 0 means a solitary species.

ing phylogenetic logistic regressions for binary dependent variables (Ives and Garland 2010), implemented in the *phyloglm* function (*phylolm* R package; Ho and Ané 2014). We then report the alpha values (the phylogenetic correlation parameter) for each model as an estimate of the phylogenetic correlation. To directly compare our results with those reported by Mabry et al. (2013), we performed a separate analysis for mammals and birds following the same method.

To control for the nonindependence of data attributed to phylogenetic inertia (Felsenstein 1985; Grafen 1989; Harvey and Pagel 1991), we modeled associations between continuous traits (M_{SBD}) with phylogenetic generalized least squares (PGLS; Martins and Hansen 1997; Székely et al. 2004). Compared to coevolution analyses (see below), application of PGLS here was used to examine the relationship between two or more continuous variables. In order to take into account the strength of a potential phylogenetic signal, we used a value of λ optimized from the data. In PGLS, λ is a measure of phylogenetic correlation and varies between 0 and 1. When $\lambda = 1$, a Brownian model of evolution is assumed whereas a phylogenetically independent model is assumed when $\lambda = 0$ (no relationship between traits and phylogeny). λ can be optimized by performing a null PGLS model with the trait (in this case the M_{SBD}) as a response variable using the maximum-likelihood method implemented in the *pgls* function (*caper* R library; Orme et al. 2012). To avoid under- or overestimation of a potential phylogenetic effect on life-history traits in our three models (see below), we compared the log-likelihood of the PGLS model using the optimized λ with the log-likelihood of PGLS models where $\lambda = 1$ (M_{SBD} evolves under a Brownian model) or where $\lambda = 0$ (M_{SBD} is independent of the phylogeny) using likelihood ratio tests (LRT; see Freckleton et al. 2002). If the PGLS models using the optimized λ was significantly different from the phylogenetically nonindependent model ($\lambda = 1$) and from the phylogenetically independent model ($\lambda = 0$), we used PGLS models with the optimized λ for model selection analysis. If the PGLS models using the optimized λ was not significantly different from the phylogenetically independent model ($\lambda = 0$), we used generalized linear models (GLM) without phylogeny for model selection (Stevens et al. 2014).

For M_{SBD}, the maximum-likelihood score of the null PGLS model with optimized λ (0.254) was not statistically different from the maximum likelihood score of the GLM (LRT: $\chi^2 = -113.6761$, $P = 1$). Controlling for phylogeny was therefore not needed for studying the correlation between the M_{SBD} and other life-history traits and we therefore used GLM to model M_{SBD} in subsequent analyses.

We constructed a different model to investigate each of the three tests on the evolution of SBD (see below) using the D_{SBD} as a binary trait (0 for FBD and 1 for MBD) and M_{SBD} as a continuous trait, and where life-history traits were selected depending on the tests described in the literature. Model selection was then performed for PGLS models (M_{SBD}) using backward elimination of nonsignificant terms. Interaction terms were removed first and the least significant variable was then removed step by step. At each step, successive models were compared using LRT to determine the significance of the variable removed as recommended by Burnham and Anderson (2002). If the effect of this variable was not significant, the simpler model was kept and the backward elimination continued. The procedure was stopped when all explanatory variables had a significant effect on the response variable. Analyses were done using R version 2.12 (R Development Core Team 2011).

Test 1: Coevolution of SBD and Mating Systems (Greenwood 1980)

We expected to find a significant effect of the interaction between mating system and territoriality on the D_{SBD}. Hence, for monogamous species with territory defense, dispersal should be biased in favor of the least territorial sex. We modeled the relationships between the D_{SBD} and mating system and territoriality using a phylogenetic logistic regression for binary dependent variables as follows: D_{SBD} ~ *mating systems* + *error* where mating system was either ♂ polygamy or ♀ polygamy (N = 257 species). We then modeled two other relationships between the D_{SBD} and the two traits related to territoriality separately as follows: D_{SBD} ~ *parental care trait* + *error* (N = 257 species) where parental care trait was either ♂ territoriality or ♀ territoriality. We also performed this analysis separately for mammals and birds.

Test 2: Coevolution of SBD and Sociality/Cooperation (Perrin and Goudet 2001)

We expected M_{SBD} to increase with increasing levels of social complexity. We modeled relationships between absolute values of the M_{SBD} (using a Poisson distribution and a log link) and sociality and cooperation. As sociality can be related to mating systems, a relationship between the M_{SBD} and sociality can be confounded by an existing correlation between the level of polygamy and the level of social complexity. Hence, we added polygamy in the models. The test was performed using GLM (no significant evidence of phylogenetic constraint) thus: absolute values of M_{SBD} ~ ♂ polygamy + ♀ polygamy + ♂ sociality + ♀ sociality + ♂ cooperation + ♀ cooperation + *first order interactions* + *error* (N = 172 species).

Test 3: Coevolution of SBD and Handicaps

We expected dispersal to be biased in favor of the sex having a lower handicap due to exaggerated secondary sexual characters or parental care. To test this, we first modeled four different relationships between the D_{SBD} and the four traits related to handicaps separately using phylogenetic logistic regression for binary dependent variables: D_{SBD} ~ *handicap* + *error* where handicap was either ♂ color handicap, ♀ color handicap, ♂ size handicap, or ♀ size handicap (N = 257 species). We then modeled two other relationships between the D_{SBD} and the two traits related to parental care separately as following: D_{SBD} ~ *parental care trait* + *error* (N = 257 species) where parental care trait was either ♂ parental care or ♀ parental care.

CONTROL FOR THE COEVOLUTION OF SBD AND TRAITS

Covariation between two discrete binary traits may result from coevolution over time that can be observed in the phylogeny. We tested the correlated evolution of D_{SBD} with life-history traits using the BayesDiscrete module implemented in BayesTraits V2.0 software (available at http://www.evolution.rdg.ac.uk/BayesTraits.html; Pagel et al. 2004; Barker and Pagel 2005; Pagel and Meade 2006) where hard polytomies are now supported. BayesDiscrete allows estimation of the ancestral state of each life-history trait by attributing a trait state at each node of the tree. BayesDiscrete then optimizes transition rates (transition 0 → 1 and 1 → 0; see Pagel 1994) based on maximum log-likelihoods (ML). Coevolution between only two binary traits (here D_{SBD} and each life-history trait as binary variables) was then tested by comparing the log-likelihood of two continuous-time Markov models: one model with no correlation between the traits (the traits evolved independently on the phylogeny) and a second model where the state of one trait was dependent of the state of the other trait (coevolution between the two traits; Pagel 1994; Pagel and Meade 2006). Statistical significance of ML differences were estimated by likelihood ratio tests calculated as follows: $LRT = 2 \times (\ln_{ML2} - \ln_{ML1})$, where $\ln_{ML1}$ is the log-likelihood of the phylogenetically independent model and $\ln_{ML2}$ is the log-likelihood of the phylogenetically dependent model. Significance of these tests were assessed relative to a chi-squared distribution with four degrees of freedom and allowed us to determine the probability that the two traits coevolved through the phylogenetic tree. When the log-likelihood of the dependent model ($\ln_{ML2}$) was significantly higher than the log-likelihood of the independent model ($\ln_{ML1}$), the hypothesis of coevolution between the traits cannot be rejected.

To test the robustness and the significance of coevolution when found, we used Bayesian Markov Chain Monte Carlo (MCMC) statistics (Pagel and Meade 2006) to compare the fit of both models (independent evolution and coevolution of traits). As the reconstruction of ancestral characters can be subject to errors, MCMC statistics also accounted for phylogenetic uncertainty (see Pagel and Meade 2006). Bayesian MCMC statistics calculate the total harmonic mean of the maximum likelihoods as an approximation of the marginal likelihood for the phylogenetically independent and the phylogenetically dependent models. As recommended by the authors of BayesTraits (Pagel and Meade 2006), we performed a burn-in of $5{*}10^4$ iterations and sampled every

TABLE 3

Phylogenetic signal of each life history-trait used in our analysis: D *statistic (Fritz and Purvis 2010) and associated probabilities*

Life-history traits	***D***	**p_{rand}**	**p_{brown}**
Sex-biased dispersal	0.526	0	0.001
♂ Polygamy	0.096	0	0.422
♀ Polygamy	0.552	0	0.001
♂ Color handicap	0.528	0	0.004
♀ Color handicap	0.494	0.420	0.390
♂ Size handicap	0.561	0	0
♀ Size handicap	0.207	0	0.172
♂ Territoriality	0.743	0.004	0
♀ Territoriality	0.705	0	0
♂ Parental care	0.183	0	0.252
♀ Parental care	−0.745	0	1
♂ Sociality	0.575	0	0
♀ Sociality	0.586	0	0
♂ Cooperation	0.352	0	0.060
♀ Cooperation	0.427	0	0.011

p_{rand} is the probability that the trait distribution follows a random distribution ($p_{rand} > 0.05$ indicate that the trait distribution is not different from a random shuffle of tips on the phylogeny) and p_{brown} is the probability that the trait distribution follows a Brownian model of evolution ($p_{brown} > 0.05$ indicate that the distribution is not different from that obtained with the Brownian model of evolution).

100th step from a total of $5*10^6$ iterations. We then calculated the difference between the harmonic means of log-likelihoods of both models. This difference, called the "Bayes-Factor," was interpreted as follows: when < 0, we considered no evidence for trait coevolution (traits evolved independently); > 2, we considered that there was positive evidence for the coevolution of the traits; > 5 was strong evidence for coevolution; and > 10 was very strong evidence for coevolution (Pagel and Meade 2006).

Transition rates estimated by the model where used to investigate the relative stability of evolutionary states in the phylogenetic tree. In the phylogenetically dependent model with two binary traits, four combinations of states are possible: 1 [1-1], 2 [1-0], 3 [0-1], and 4 [0-0]. Overall, 12 transitions were possible. Between two combinations a q value was estimated, corresponding to the relative frequency of the transition rate between both. For example, q_{12} indicates an estimated transition rate from state 1 to state 2. If two traits have evolved independently, transitions rates should be equiprobably distributed between the four combinations. To test for this independence, we verified if the four transition rates estimated by the model were significantly different from a random distribution using chi-square tests. Transition rates between states were then represented in flow diagrams.

Relationships and Coevolution Between Sex-Biased Dispersal and Traits

phylogenetic signal on sex-biased dispersal and other life-history traits

For most traits investigated (including D_{SBD}) the phylogenetic pattern was non-random and significantly different from a Brownian motion model (Table 3). Only female color handicap had a phylogenetic distribution not statistically different from the random distribution (Table 3: $p_{rand} = 0.420$; others: $p_{rand} < 0.05$) and also from a Brownian motion model (Table 3: $p_{brown} = 0.390$). Our results indicated that both male and female parental care had a phylogenetic pattern not significantly different from that resulting from a Brownian motion model ($p_{brown} = 0.252$ and $p_{brown} = 1$ respectively) but different from the random distribution ($p_{rand} < 0.05$). Male polygamy and female size handicap also showed the same pattern ($p_{brown} = 0.422$ and $p_{brown} = 0.172$ respectively; with $p_{rand} < 0.05$). We also found that the M_{SBD} showed a significant phylogenetic signal (K = 0.063, P = 0.027). Generally, bird dispersal was female-biased whereas mammals generally displayed male-biased dispersal (chi-square tests: $\chi^2 = 57.534$, P < 0.001, d.f. = 5 and Tukey's tests: between mammals and birds: P < 0.001; between nonavian reptiles and birds: P < 0.001).

TESTING CLASSICAL HYPOTHESES OF SEX-BIASED DISPERSAL EVOLUTION

Test 1: Coevolution of SBD and Mating Systems (Greenwood 1980)

Our results showed that the D_{SBD} was negatively linked to the territoriality of males, with FBD associated with male territoriality (alpha = 0.023, P = 0.009) and was also correlated with male polygamy (alpha = 0.024, P = 0.001), with MBD when males are polygamous. D_{SBD} was not significantly correlated with either female territoriality or polygamy (alpha = 0.021, P = 0.124 and alpha = 0.023, P = 0.069 respectively). Our analysis supported coevolution between D_{SBD} and polygamy (Table 4; BayesFactor = 33.568 for male polygamy and 6.881 for female polygamy) and with male territoriality only (Table 4; BayesFactor = 7.792). Based on both parsimony and likelihood reconstruction, the ancestral condition of D_{SBD} seemed to be male bias (state 1 of D_{SBD}; Supporting Information 5, available at http://www.journals.uchicago.edu/loi/qrb). Flow diagrams (Figure 3A) showed that the most probable evolutionary route from the ancestral state (MBD and polygamy in males) to the double derived state (FBD and monogamous males) was a change in mating system followed by a change in dispersal bias (Figure 3A). The most stable state (positive value associated) was the state [0,0] with FBD and monogamy in males.

We also found that male territoriality was related to the D_{SBD} in mammals, with a female bias when males were territorial (alpha = 0.038, P = 0.020). No relationships between D_{SBD} and either male or female polygamy were found in mammals. In birds, D_{SBD} was not correlated to polygamy and territoriality of both sexes.

Test 2: Coevolution of SBD and Sociality/Cooperation (Perrin and Goudet 2001)

We did not find a significant effect of cooperation, sociality, or the traits related to mating systems (male polygamy and female polygamy) on M_{SBD} (LRT: $\chi^2 = -3.750$, P = 0.710). We did not detect any significant coevolution between SBD and sociality or cooperation (Table 4).

Test 3: Coevolution of SBD and Handicaps

The color handicap in males showed an effect on the D_{SBD} (alpha = 0.018, P = 0.049), with males with coloration more often associated with MBD. The color handicap in females did not show relationship with the D_{SBD} (alpha = 0.027, P = 0.581). We found evidence for positive coevolution between D_{SBD} and male color handicap (Bayes Factor = 14.537; Table 4). MBD was associated with the presence of color handicap in males while FBD was linked to the absence of such sexual dichromatism (Table 4). The most likely ancestral state of color handicap in males was when males were more colored than females (state 1 of male color handicap; Supporting Information 6, available at http://www.journals.uchicago.edu/loi/qrb). Flow diagrams (Figure 3B) showed that the most probable evolutionary route from the ancestral state (MBD and males more colored than females) to the double derived state (FBD and males not more colored than females) was a change in handicap followed by a change in dispersal bias (Figure 3B). The most stable state (positive value associated) was the state [1,0] with MBD and absence of color handicap in males.

Our results also showed no direct impact of the degree of the sexual size handicap on the D_{SBD} (male size handicap: alpha =

TABLE 4

Results of maximum likelihood and Bayesian Markov Chain Monte Carlo (MCMC) statistics of coevolution between the direction of SBD and life-history traits

Trait for which a coevolution with the direction of sex-biased dispersal is tested	**Likelihood ratio**	**P-value**[1]	**Model favored**	**BayesFactor**[2]	**Direction of the coevolution**
♂ Polygamy	4.015	0.404	NS	33.568	+
♀ **Polygamy**	31.689	**< 0.001**	Dependent	6.881	+
♂ Color handicap	2.567	0.633	NS	14.537	+
♀ Color handicap	2.737	0.603	NS	1.291	NS
♂ **Size handicap**	9.737	**0.045**	Dependent	8.558	+
♀ Size handicap	0.698	0.952	NS	−28.170	NS
♂ Territoriality	14.172	**0.007**	Dependent	7.792	–
♀ Territoriality	1.310	0.860	NS	−0.249	NS
♂ **Parental care**	15.436	**0.004**	Dependent	21.890	–
♀ **Parental care**	52.043	**< 0.001**	Dependent	27.483	–
♂ Sociality	2.596	0.627	NS	−0.080	NS
♀ Sociality	2.679	0.613	NS	−0.366	NS
♂ Cooperation	1.133	0.889	NS	−11.848	NS
♀ Cooperation	4.997	0.288	NS	−3.505	NS

Significant coevolutions with negative likelihood ratio values (when the likelihood of the phylogenetic dependent model was better than the likelihood of the independent model) are in bold. Directions of the coevolution were given for significant coevolution only (NS when the coevolution was not significant).

[1] Significance based on a chi-squared test with four degrees of freedom (Pagel 1994).

[2] BayesFactor values supported a model of coevolution as following: > 2 = positive evidence for coevolution; > 5 = strong evidence for coevolution; and > 10 = very strong evidence for coevolution. See also Table 1.

0.026, P = 0.543; female size handicap: alpha = 0.023, P = 0.215). The most likely ancestral state of size handicap degree in males was when males were not bigger than females (state 0 of male size handicap; Supporting Information 6). Analyses of coevolution between SBD and male size handicap had a Bayes Factor of 8.558, considered as strong positive evidence for coevolution between those traits (Table 4). FBD was associated with the absence of size handicap in males.

Our analysis supports that biased parental care had an influence on the D_{SBD} (male parental care: alpha = 0.024, P = 0.006; female parental care: alpha = 0.023; P = 0.016), as the sex that performs parental care tends to be more philopatric than the other. Analyses of coevolution between SBD and both male and female parental care demonstrated a very strong negative coevolution between them (Bayes Factor of 21.890 and 27.483 respectively; Table 4). The most likely ancestral condition of both male and female parental care was the absence of parental care in males and tended to be the presence of parental care in females (Supporting Information 6). Regarding the coevolution between SBD and male parental care, estimated transition rates suggested that the state [1,0] (MBD and absence of parental care in males) and the doubly derived state (FBD and presence of parental care in males) were the most stable states (Figure 3C). The most probable evolutionary route from the ancestral state (MBD and absence of parental care in males) to the doubly derived state was a change in handicap followed by a change in dispersal bias (Figure 3C). In females, the most probable evolutionary route from the state [0,0] (FBD and absence of parental care in females) to the double derived state (MBD and presence of female parental care) was a change in handicap followed by a change in dispersal bias (Figure 3D). The most stable state (positive value associated) was the state [1,1] with MBD and presence of parental care in females.

The least stable life-history traits were D_{SBD}, male size handicap, female territorial-

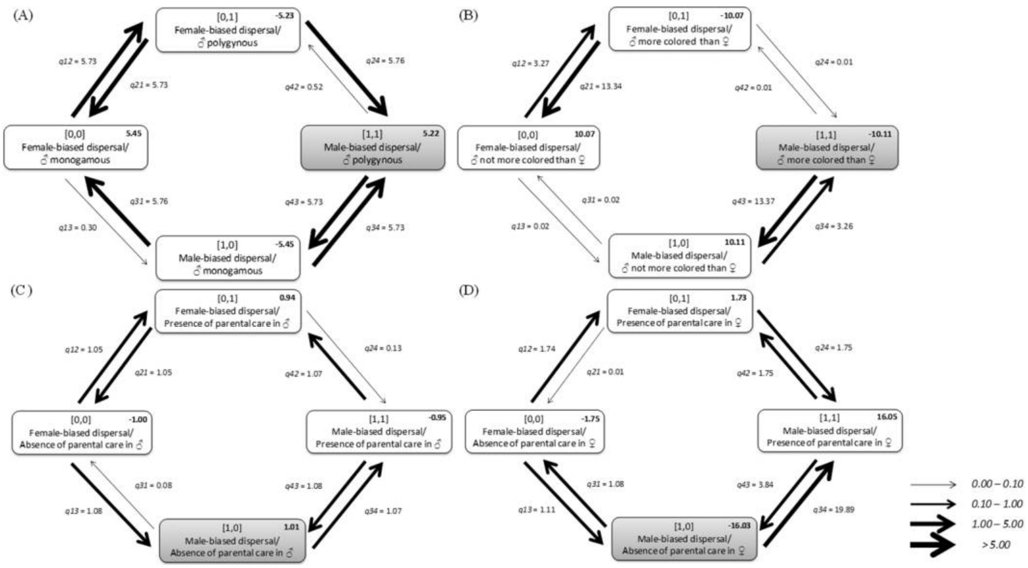

Figure 3. Path Diagrams Showing the Frequency of Transitions between the Four Evolutionary States in the Direction of SBD (Male or Female Bias) and a Life-History Trait

For each transition, *q* corresponds to the relative frequency that a particular transition occurs on 1000 simulated evolutionary pathways. Arrow width is proportional to the magnitude of the transition rate. Number associated with each state (block) comes from the addition of the four *q* values connected to the block and signifies if the state was stable (positive value) or unstable (negative value). Grey blocks refer to ancestral states. Transitions rates of 0 were removed from diagrams. (A) Path diagram with transition rates among four states combining SBD and ♂ polygamy; (B) Path diagram with transition rates among four states combining SBD and ♂ color handicap; (C) Path diagram with transition rates among four states combining SBD and ♂ parental care; and (D) Path diagram with transition rates among four states combining SBD and ♀ parental care. See Table 2 for more details on traits. ♂ for males; ♀ for females.

ity, male sociality, and female sociality (with transition frequencies > 0.15; Table 5). Our analyses using the nontime calibrated tree (Supporting Information 4) revealed the same relationships between SBD and life-history traits under several hypotheses (Supporting Information 4; Table 4).

Discussion

Although much effort has focused on the demonstration of sex-biased dispersal in the past decades, less attention has been paid to its evolution. The major goals of this study were to test the well-known hypotheses proposed to explain the evolution of SBD and to explore more recently proposed coevolutionary models of SBD and other traits. Our results provide limited support for the *resource competition hypothesis* (Greenwood 1980) by showing a relationship between the D_{SBD} and polygamy and territoriality. However, strong correlations between D_{SBD} with parental care and sexual dimorphism contribute to support Greenwood's hypothesis in an indirect way: sexual dimorphism and parental care are related to the evolution of SBD and these traits could have coevolved with the mating system.

EVOLUTION OF SBD

In agreement with the *resource competition hypothesis* (Greenwood 1980), we found that the D_{SBD} was significantly different among taxonomic groups, with female-biased dispersal prevailing in birds, male-biased dispersal in mammals, and species displaying male territoriality more likely showing FBD. A predictable link between the D_{SBD} and territoriality was previously discussed in birds (Greenwood 1980; Clarke et al. 1997; Mabry

TABLE 5
Transition frequency between trait states across the phylogeny

Life-history trait	**Transition** "No" → "Yes"	**Transition** "Yes" → "No"	**Total**
Sex-biased dispersal	0.058	0.113	0.171
♂ Polygamy	0.051	0.070	0.121
♀ Polygamy	0.144	0.000	0.144
♂ Color handicap	0.078	0.016	0.093
♀ Color handicap	0.004	0.000	0.004
♂ Size handicap	0.128	0.027	0.156
♀ Size handicap	0.074	0.004	0.078
♂ Territoriality	0.004	0.089	0.093
♀ Territoriality	0.051	0.156	0.206
♂ Parental care	0.089	0.031	0.121
♀ Parental care	0.016	0.004	0.019
♂ Sociality	0.109	0.078	0.187
♀ Sociality	0.109	0.089	0.198
♂ Cooperation	0.078	0.004	0.082
♀ Cooperation	0.086	0.004	0.089

Life-history traits are presented in Table 2.

et al. 2013) suggesting two consequences of territoriality that could promote SBD. Territoriality may either increase philopatry of individuals of the less dispersing sex (because the territorial sex monopolizes local resources) or it may induce dispersal to find mates (*local mate competition hypothesis*; Fretwell and Lucas 1969; Dobson 1982; Johnson 1986). Our findings suggest that philopatry could be advantageous to the territorial sex (Baker 1978; Greenwood 1980).

The coevolution analysis also suggests that when males are polygynous, dispersal tends to be male-biased. In contrast to an earlier study on mammals (Mabry et al. 2013), we did not find any evidence of coevolution of SBD with traits related to the mating system in mammals. However, we found that D_{SBD} in mammals was linked to territoriality in males, with FBD present when males were territorial. In birds, and in concordance to Mabry et al. (2013), our findings did not support any relationships between D_{SBD} and mating systems or territoriality. This discrepancy could be explained by a higher number of species in the present study (mammals: N = 110; birds: N = 118; as compared to mammals: N = 45; birds: N = 56; Mabry et al. 2013). Moreover, Mabry et al. (2013) categorized mating systems in only two different states, such as monogamous and nonmonogamous species. Here, we categorized mating systems depending on sex (male monogamous, female monogamous, male polygynous, and female polygynous) to better reflect the diversity of mating systems and to more precisely test the influence of traits on sex differences in dispersal, including all mating patterns. We thereby increased the variability of mating systems between species relative to Mabry et al. (2013) and were better able to detect the influence of mating system on SBD. Overall, our findings suggest that mating systems are linked to differences in the direction of SBD at higher taxonomic levels, but not within clades. Our results also suggest that other life-history traits could be more closely associated with the evolution of SBD than just the mating system (Gauffre et al. 2009; Lane and Shine 2011). Finally, our phylogenetic reconstruction suggests that MBD is an ancestral state in mammals (Hammond et al. 2006; Clutton-Brock and Lukas 2012; Mabry et al. 2013), but we cannot confirm earlier results suggesting that FBD is the ancestral state of SBD in birds (Mabry et al. 2013).

We expected to find a strong relationship between the magnitude of sex-bias and the interaction between sociality and cooperation (i.e., level of social complexity) if philopatry improves cooperation. Contrary to this expectation, we did not find either a significant relationship or coevolution between the SBD and sociality or cooperation. Moreover, transitions between the presence or absence of sociality in both males and females were relatively equal and numerous, suggesting that social behavior is a labile trait and could switch frequently through time. This instability of sociality states could explain the fact that we did not find a relationship between this trait and SBD.

The evolution of exaggerated traits (in size or in color) due to sexual selection is thought to be associated with dispersal costs of possessing exaggerated traits. In that case, FBD would be expected when males have exaggerated secondary sexual characters, and vice versa. Second, sexual dimorphism can also be related to mating systems (Frayer and Wolpoff 1985; Owens and Hartley 1998; Dunn et al. 2001; Geary and Flinn 2001). In polygynous species, male competition for access to females is more intense than in monogamous systems, which could lead to increased phenotypic variations among males. For instance, large males could have an advantage in male-male competition for access to females. In polygynous species and if sexual dimorphism occurred, MBD should be expected due to the *local mate competition hypothesis* (Dobson 1982). We therefore expected that every trait related to sex differentiation might play a role in the evolution of SBD, but that the direction of the relationship would indicate the underlying influence that dimorphism has on SBD evolution.

Our findings revealed strong positive coevolution between the D_{SBD} and sexual dimorphism in males (which also strongly coevolved with mating systems; BayesFactor between size handicap in males and male polygamy: 70.79). Such a result highlights that the presence of sexual dimorphism leads to SBD, but contrary to expectations, dispersal should be biased toward the sex with the size handicap. Consequently, the bigger sex should disperse more as a consequence of intense sexual competition. Indeed, sexual dimorphism in body size in birds is often related to a high cost of male-male competition for access to females (Promislow et al. 1992; Andersson 1994). Consequently, the cost of mortality might lead to male dispersal because of both local inter- and intrasexual competition (Dobson 1982; Pusey 1987; Owen-Smith 1993). Our results generally suggest that the presence of sexual size dimorphism should promote SBD.

Another asymmetric handicap could result from parental care performed by only one sex. When sex-biased parental care evolves, the caring sex might have less energy and time to allocate to dispersal. We found strong significant coevolution between the D_{SBD} and the presence of parental care in males: the presence of paternal care leads to FBD and vice versa. One explanation could be that when a sex performs parental care, it could be more dependent on the local resources to care for their young, which should induce philopatry in that sex. Transitions from absence to presence of paternal care were more frequent than the reverse, suggesting either that presence of parental care in males might bring more advantages than its absence, or that male parental care could be an evolutionary black hole. The strong relationships found between parental care, sexual dimorphism, and the D_{SBD} could be interrelated, because parental care might be a consequence of mating systems, which could also act on sexual dimorphism.

TECHNICAL BIASES AND PERSPECTIVES

Mammals and birds are currently the only taxonomic groups for which SBD has been relatively well studied (Table 6). The lack of data in other taxa led to an unbalanced number of species among taxonomic groups in our dataset. Since species included in our tree might be a biased sample of SBD, and because in mammals and birds SBD might not be that frequent, it could introduce a bias in our analyses. Indeed, incomplete phylogenetic sampling can lead to a bias in the tree shape, and consequently in phylogenetic reconstruction methods (Heath et al. 2008). Furthermore, the exclusions of a few species due to a lack of data on life-history traits may also introduce a bias in our analysis, even if we assumed that removing these ambiguous data should limit the bias.

TABLE 6

Summary of data availability (number of species) in five reviews of sex-biased dispersal

	Greenwood 1980	Dobson 1982	Lawson Handley and Perrin 2007	Mabry et al. 2013	This study
Birds					
MBD identified	3	0	0	9	30
FBD identified	40	0	0	47	88
No SBD	2	0	0	0	0
Mammals					
MBD identified	55	40	25	32	77
FBD identified	5	2	22	13	33
No SBD	9	9	0	0	0
Other taxonomic groups	0	0	0	0	29
All species	114	51	47	101	257

The context of SBD detection in the studied publications, such as particular demographic conditions, could also have biases our analyses. For instance, relationships between dispersal pattern and population density had been demonstrated in some species (Lecomte et al. 2004; Baguette and Schtickzelle 2006; Hovestadt and Nieminen 2009). This density dependence of dispersal might reduce SBD in some populations. Moreover, if there is a sex by density effect on dispersal, density dependence alone can be responsible of observed SBD. Besides, as dispersal can be age dependent, the age structure of the sampled population might also affect the detection and/or the D_{SBD}. For example, in amphibians, dispersal is mostly ensured by juveniles (Semlitsch 2008), while most studies on amphibians survey adult dispersal. We cannot correct for such bias here, since stage or age structure is most often not reported in the publications used.

To examine the evolution of SBD, data on species with no significant SBD are also important. However, studies on species for which no SBD was detected are rarely published (we recorded only three publications reporting nonsignificant SBD) and it is difficult to determine what level of bias is biologically meaningful. Our analysis and those of other studies (Table 6) rarely included empirical examples with no SBD even though this pattern is plausible and would be evolutionarily informative. Therefore, ancestral reconstruction of SBD states reported here could be biased because this third state (no SBD) is insufficiently documented in our phylogenetic analysis due to a lack of reporting in the scientific literature. Once more data on species with no dispersal bias are made available, a new analysis may shed light on how life-history traits are related to the evolution of SBD or sex-similar dispersal.

The consideration of male and female mating strategies separately in our analysis allowed a more detailed analysis of the impact of mating systems on SBD as compared to the standard male-centered view with three mating system categories: monogamy, polygyny, or promiscuity (e.g., Greenwood 1980). This approach allowed us to use Bayesian comparative methods to infer a life-history trait's state through time for each node of the phylogeny. Our findings showed strong correlations and coevolution between traits, because parental care might be a consequence of mating systems, which could also act on sexual dimorphism. However, no methods are currently available to test for coevolution between more than two traits and future research might be needed to fully elucidate the impact of these relationships on the evolution of complex traits.

Conclusions

Our results showed that the D_{SBD} could be explained by an association between mating systems and three life-history traits: parental care, sexual dimorphism, and territoriality. Taken together, our results partly corroborate the *resource competition hypothesis* (Greenwood

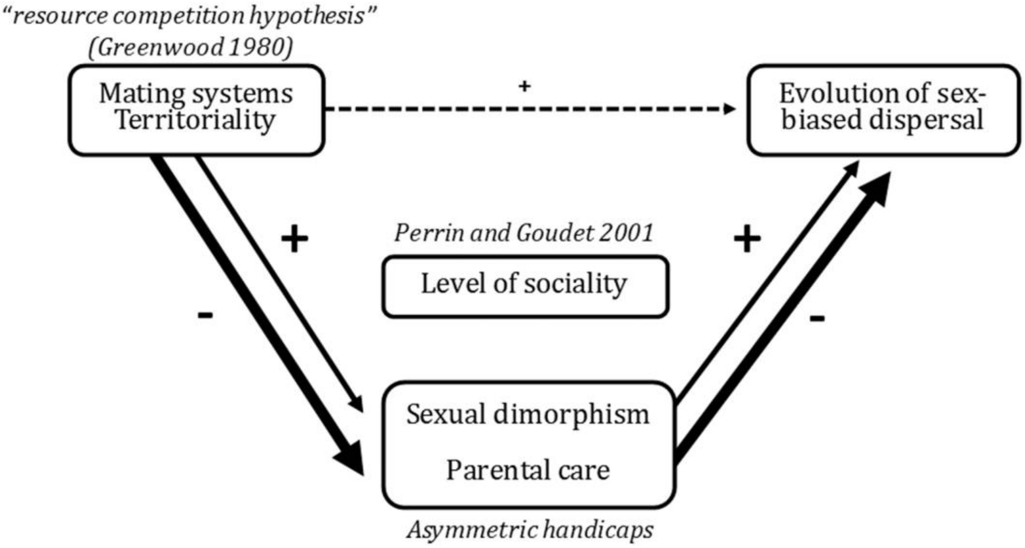

FIGURE 4. SCHEMATIC REPRESENTATION OF OUR RESULTS LINKING THE DIRECTION OF SBD TO DIFFERENT LIFE-HISTORY TRAITS

Arrow width varies with the intensity of the relationship. The dotted line between mating systems/territoriality and evolution of SBD referring to the Greenwood's hypothesis (*resource competition hypothesis*) represented an indirect way to explain the evolution of SBD, because we found significant effect of male territoriality in PGLS but no evidence of coevolution between those traits. Nevertheless, because gender handicap and parental care were strongly related to mating systems, we could not completely exclude the influence of mating systems on SBD. Coevolutions between sexual dimorphism, parental care, and SBD were stronger and were represented by black lines. The "+" represents cases where the gender with the higher level of a given life-history trait (sex with handicaps) disperses more than the other sex. The "–" represents cases where the sex with the higher level of a given life-history trait (sex performing parental care) disperses less than the other sex.

1980) by indicating a relationship between the D_{SBD} and territoriality of males. Our findings also demonstrated strong coevolution between parental care, sexual dimorphism, and the D_{SBD} (Figure 4), which are all traits that might coevolve with mating systems, but which may be more closely related to the evolution of SBD than resource competition per se. It follows that sexual asymmetry in morphology and parental care might be the main determinant of the evolution of SBD across species rather than mating systems. Hence, the relationship between mating system and the D_{SBD} seems more complex than previously thought.

Understanding the coevolutionary relationships between SBD and life-history traits could help in developing theoretical models for the impact of SBD on population dynamics, especially if environmental factors also have an impact on SBD (Wang et al. 2012; Driscoll et al. 2014). Indeed, as SBD and its magnitude could have important impacts on demographic and genetic population structure (Aars and Ims 2000; Blundell et al. 2002; Prugnolle and de Meeus 2002; Schmeller and Merilä 2007), SBD should be taken into account in evolutionary models on local adaptation. Predicting SBD based on species characteristics that are generally more readily available than actual dispersal rates might also help devise more appropriate conservation plans.

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