Phylogenetics & Evolutionary Biology

Research Article   **Open Access**

Comparative Tests of Birds Support a Link between Sex-Biased Dispersal and Body Size

Fan Qiu[1]* and Michael M Miyamoto[2]

[1]Division of Biology, Kansas State University, Manhattan, KS 66506, USA
[2]Department of Biology, Box 118525, University of Florida, Gainesville, FL 32611-8525, USA

Abstract

Background: Natal dispersal is the movement of individuals from their birthplaces to their first breeding locations. Such movements constitute one of the most important events in the life histories of birds and other species and are usually biased such that one sex moves farther and/or more frequently.

Methods: In this study, we compile published data for different dispersal and mass characters for the females and males of 92 bird species from 15 different orders. We use these published data to test the prediction, as derived from species-specific dispersal studies, that sex-biased dispersal is related to body size. Our tests rely on comparative methods and alternative dated trees that directly account for the phylogenetic non-independence of species and the uncertainties in their phylogeny inference.

Results: Our comparative tests support the prediction of a link between sex-biased dispersal and body size. Specifically, we find that larger species have more male-biased dispersal, that the dispersal distance is increasing more rapidly in males than in females, and that the female and male dispersal distances are both positively correlated with their sex-specific body masses.

Conclusions: Sex-biased dispersal is related to body size. However, it remains elusive as to what is the mechanism (i.e., social/behavioral or physiological/energetic) that underlies this link. Still, this link is important, because it highlights the related area of species-specific dispersal as a source of new characters, hypotheses, and approaches for determining the underlying forces of sex-biased dispersal.

Keywords: Natal dispersal; Body mass; Comparative biology; Life history traits

Introduction

Natal dispersal is the movement of an individual from its site of origin to a different location for the purpose of reproduction [1]. Such movements constitute one of the most important lifetime events in the life history of a species [2]. The distances and frequencies at which the individuals move from their natal sites to their first breeding locations may affect many different aspects of the ecology and evolution of a species. These aspects include the dynamics and history of the species' meta-populations, the spatial structure, migration, and gene flow of its populations and demes, and the adaptability, risk of extinction, and conservation of its lineage in the face of environmental challenges [3,4].

Among animals, natal dispersal is usually biased such that one sex moves farther and/or more frequently than the other [5,6]. In birds, female-biased dispersal is the norm, as only ~15% of known species have male-biased dispersal [7]. Greenwood [1] hypothesized that the paucity of male-biased dispersal in birds is tied to their widespread mating system of resource-defense monogamy. According to his hypothesis, males are more likely to remain in their natal area, because they must defend a nest or territory, which thereby places a premium on their familiarity with the local resources. Recently, Mabry et al. [7] tested Greenwood's hypothesis with the median and average dispersal distances for the females and males of 56 bird species. Despite their use of both distance ratio and binary sex-biased dispersal characters, these authors were unable to reach any strong conclusions about the relationship between sex-biased dispersal and mating system.

As illustrated by Mabry et al. [7], previous studies of sex-biased dispersal have focused on the potential social and behavioral (i.e., mating and breeding system) determinants of its variation [5,6,8]. Conversely, previous studies of species-specific dispersal have focused instead on the potential effects of other life history traits such as body size and territory area [9-11]. In particular, prior species-specific

investigations have found that the natal dispersal distances (hereafter, referred to as distances) of a group are positively correlated with body size [12,13]. In animals, one explanation for this positive correlation is that the mass-specific energy cost of transport (COT) decreases with body size, thereby making it relatively cheaper for larger species to move farther [14,15]. Conversely, an alternative explanation is that body size is a covariate of another life history trait that has a more direct effect on distance. For example, territory size also co-varies with body mass in birds and this factor has been implicated as a major cause of their variable distances [10].

The widespread occurrence of a positive correlation between species-specific distance and body size suggests that similar relationships may also exist between the dispersal distances for the females and males of different species and their sex-specific masses. If distance and mass for females co-vary in a manner different from males, then this discrepancy may also lead to a relationship between the sex-biased dispersal and body sizes of their species. Such interrelationships may be especially likely for birds as they exhibit a sexual size dimorphism (SSD), whereby males are usually larger than females [16]. Birds also follow Rensch's [17] rule, whereby their male-biased SSD increases with the body size of the species. Conversely, female and male distances may each co-vary to a greater degree with their sex-specific masses, because of a

*Corresponding author: Fan Qiu, Division of Biology, Kansas State University, Manhattan, KS 66506, USA, Tel: 785-532-5574; Fax: 785-532-6653; E-mail: fqiu@ksu.edu

life history trait other than their sexual size dimorphism. If so, then no simple relationship may be apparent between sex-biased dispersal and body size.

In this study, we use birds as a model system to test the prediction that sex-biased dispersal is related to body size. Specifically, we score different dispersal and body mass characters for females and males and compare these traits to each other using alternative dated trees to account for the phylogenetic non-independence of species and the uncertainties in their phylogeny inference. Our relationships are discussed in terms of their potential ties to different life history factors and their heuristic value to future sex-biased dispersal studies.

Methods

Sex-biased dispersal and body size data

The sex-biased dispersal of birds was first scored as two binary characters that were derived from the carefully considered list of species dispersal patterns by Clarke et al. [5]. The sex-biased dispersal of birds was then scored as three continuous characters that were obtained from the separate female and male median or average distances of Sutherland et al. [9], Garrard et al. [12], and Mabry et al. [7]. These two sets of binary and continuous characters were chosen as complementary and were therefore analyzed separately throughout our study.

Clarke et al. [5] used their expert review to assign a score of either female- or male-biased dispersal to each species. In cases of uncertain interpretations or data, these authors qualified their designations with a "?" or assigned a score of "none" (for no detectable bias) to the species. Our study treated the Clarke et al. designations in two different ways (Supplemental Table 1). In the first (63 species from 12 orders), a "1" was assigned to species with unambiguous male-biased dispersal, whereas a "0" was given to all others. In the second (43 species from 12 orders), "0" was limited to species with unambiguous female-biased dispersal. Thus, our two binary dispersal characters (hereafter, "male/non-male" and "male/female", respectively) differed in whether species with ambiguous "?" and "none" designations were included among those with unambiguous "female-biased" scores. Conversely, the reciprocal treatment, whereby the ambiguous species were scored as "1," was not done given that male-biased dispersal is rare among birds [5,7].

Female and male median distances (in meters) were obtained from Sutherland et al. [9], Garrard et al. [12], and Mabry et al. [7] for 44 species from 10 orders (Supplemental Table 1). Following Mabry et al., these sex-specific median distances for 44 species were supplemented with the female and male average distances (in meters) for another 18 species that represented an additional three orders. These median and average distances were expressed as three continuous characters for female distance, male distance, and female-to-male distance ratio (hereafter, distance ratio).

Female and male estimates of average body mass (in grams and hereafter, mass) were obtained from Dunning [18,19]. These sex-specific masses were available for 78 species and for all 15 orders of the final 92 species with a binary dispersal score, a distance measure, or data for both character types (Supplemental Table 1). These estimates were expressed as three continuous characters for female mass, male mass, and female-to-male mass ratio (hereafter, mass ratio). The separate values for conspecific females and males were also averaged together to calculate a fourth continuous character for their species (i.e., species mass).

In many cases, multiple distance or mass estimates were available for one or both sexes of a species. In these cases, the median of the multiple estimates was taken as the final value for that sex. All distance and mass characters, including their ratios, were log transformed.

Dated reference trees

Three different sets of 20 dated trees each were obtained from the pseudo-posterior samples of Jetz et al. [20] (Supplemental Figure 1). These three sets were chosen to represent the alternative compilations of sampled species available for the various comparative tests. Specifically, all three were taken from the pseudo-posterior samples with the Hackett et al. [21] phylogeny as the backbone constraint. Furthermore, since three of our species were missing genetic data in the Jetz et al. study, all three sets were derived from the pseudo-posterior samples for species both with and without sequence information. The placement of the three species without genetic data in these trees was constrained by the positions of their known relatives with sequence information and was done under a pure birth model of diversification (see [20] for further details).

We used the approach of Garland et al. [22] to test whether the original branch lengths of the reference trees (in millions of years) or their log-transformed values offered an appropriate standardization for the log-transformed distance, mass, and ratio characters. Specifically, we used PDAP v1.16 of MESQUITE [23] to verify that the absolute contrast values of each continuous character were uncorrelated with their standard deviations. Prior to their log transformations, branch lengths were converted into years to avoid negative values due to original time spans of <1 million years. These diagnostic tests confirmed that the log-transformed branch lengths were appropriate for the log-transformed characters and these transformations were therefore used in all comparative tests.

Variance/randomization tests of the distance, mass, and ratio characters

Prior to our comparative tests, we verified that our log-transformed distance, mass, and ratio characters have phylogenetic signal and that phylogenies are therefore warranted for their comparisons with the variance/randomization test of Blomberg et al. [24] as implemented in PICANTE v1.6 [25]. In this test, character contrasts are calculated with a phylogeny in the usual way [26] and their variance is then compared to the variances for some large number of datasets with randomly permuted tip data. If phylogenetic signal exists within the character, then related species will share similar state values. This similarity will lead in turn to a variance for the contrasts, which is less than those for the randomized datasets from which the phylogenetic signal has been lost.

The significance of the variances for the original tip data of the seven continuous distance, mass, and ratio characters was tested with 10,000 permutations each (Supplemental Table 2). These variance/randomization tests were significant for all seven continuous characters, except for distance ratio. Thus, all continuous characters, except for one, have phylogenetic signal, which thereby supported the use of phylogenies in their comparative tests [13].

Comparative Threshold Tests of the binary dispersal and mass/mass ratio characters

The associations between the two binary dispersal and four continuous mass/mass ratio characters were tested with the Comparative Threshold Test (CTT) of THRESHML [27]. The CTT models the binary trait (i.e., male/non-male or male/female dispersal) as a continuous character known as the liability. This liability is related

Comparison	Pearson's r	R^2	Probability
Male/non-male dispersal and species mass (63)	0.644 [0.640, 0.648]	0.415 [0.410, 0.420]	<0.001, <0.001 {20}
Male/non-male dispersal and female mass (63)	0.640 [0.634, 0.643]	0.410 [0.402, 0.413]	<0.001, <0.001 {20}
Male/non-male dispersal and male mass (63)	0.638 [0.632, 0.641]	0.407 [0.399, 0.411]	<0.001, <0.001 {20}
Male/female dispersal and species mass (43)	0.745 [0.739, 0.749]	0.555 [0.546, 0.561]	<0.001, <0.001 {20}
Male/female dispersal and female mass (43)	0.749 [0.744, 0.751]	0.561 [0.554, 0.564]	<0.001, <0.001 {20}
Male/female dispersal and male mass (43)	0.736 [0.729, 0.740]	0.542 [0.531, 0.548]	<0.001, <0.001 {20}
Male/non-male dispersal and mass ratio (63)	-0.272 [-0.283, -0.264]	0.074 [0.070, 0.080]	0.025, 0.037 {20}
Male/female dispersal and mass ratio (43)	-0.295 [-0.313, -0.268]	0.087 [0.072, 0.098]	0.041, 0.082 {11}

Table 1: Comparative Threshold Tests of the binary dispersal and mass/mass ratio characters. Pearson's r and the coefficient of determination (R^2) are summarized as their means and ranges (in square brackets) for the 20 reference trees of each comparison (Supplemental Figure 1). Probability is summarized as its range across these trees with the number of individual significant tests at α=0.05 presented in curly brackets. The number of species per comparison is given in parentheses.

Comparison	Pearson's r	R^2	Probability
Female-on-male distances (60)	0.740 [0.733, 0.747]	0.548 [0.537, 0.558]	<0.001, <0.001 {20}
Female-on-male masses (78)	0.981 [0.980, 0.982]	0.962 [0.960, 0.964]	<0.001, <0.001 {20}
Mass ratio on species mass (78)*	-0.275 [-0.304, -0.200]	0.076 [0.040, 0.092]	0.007, 0.079 {17}
Female distance on mass (48)	0.313 [0.300, 0.328]	0.098 [0.090, 0.108]	0.023, 0.038 {20}
Male distance on mass (47)	0.329 [0.321, 0.342]	0.108 [0.103, 0.117]	0.019, 0.028 {20}
Female distance on mass ratio (48)	0.190 [0.185, 0.207]	0.036 [0.034, 0.043]	0.158, 0.208 {0}
Male distance on mass ratio (47)	0.176 [0.160, 0.192]	0.031 [0.026, 0.037]	0.196, 0.283 {0}
Distance ratio on female mass (47)	-0.102 [-0.111, -0.095]	0.010 [0.009, 0.012]	0.525, 0.458 {0}
Distance ratio on male mass (47)	-0.100 [-0.108, -0.090]	0.010 [0.008, 0.012]	0.547, 0.470 {0}
Distance ratio on mass ratio (47)	-0.100 [-0.108, -0.090]	0.000 [0.000, 0.000]	0.931, 0.995 {0}

Table 2: Phylogenetic Independent Contrasts of the distance, mass, and ratio characters. See Table 1 for a description about the presentation of these results.

to a threshold that determines whether its current value corresponds to state "0" or "1". The CTT relies on Markov Chain Monte Carlo integration to infer the covariance between the liability and a second character (i.e., species mass, female mass, male mass or mass ratio). This covariance is then used to estimate Pearson's r for the association of the binary and second traits.

Separate CTTs were performed for each pair of binary dispersal and mass/mass ratio characters. Each CTT relied on 30 consecutive chains of one million steps apiece, a burn-in of 1000 initial liabilities, and a proposal size of 7 for the Metropolis updates of the tip liabilities. These longer runs and larger proposal size were necessary to keep the acceptance rate of the newly proposed tip liabilities at ~0.50 and to reduce the transformation errors to <2%.

Phylogenetic Independent Contrasts of the distance, mass, and ratio characters

The correlations between the seven continuous characters (two distances, three masses, and two ratios) were tested with Phylogenetic Independent Contrasts (PICs) that were conducted with CONTRAST of PHYLIP v3.695 [26,28]. These PICs were done in a pairwise fashion (i.e., two log-transformed characters at a time) to maximize the sample size of each comparison. Correspondingly, species that were missing data for one or both characters of a comparison were pruned from their reference trees prior to testing with PAUP* v4.0b [29]. The significance of each correlation was tested with Pearson's r. These correlation analyses were complemented with ordinary least squares regressions whose y intercept was set to 0 [22]. Characters of mass are routinely taken in regression analyses as the independent variables [9-13], because body size imposes physical constraints on the variation of many biological traits [14]. Thus, the mass and mass ratio characters were treated as the independent variables in their regressions with distance and distance ratio. Conversely, male distance, male mass, and species mass were arbitrarily selected as the independent variables in

their regressions with female distance, female mass, and mass ratio, respectively.

Results

Associations between the binary dispersal and mass/mass ratio characters

Positive associations are found in all six CTTs between the binary dispersal and mass characters (Table 1). This significance applies to both binary dispersal characters (i.e., to whether or not only species with unambiguous scores are counted), to all three mass characters (species, female, and male), and to all reference trees. The three mass characters each explain between 40.7-56.1% of the total variation in the liabilities for male/non-male and male/female dispersals. These positive associations indicate that larger species have more male-biased dispersal.

In turn, negative associations are found in the two CTTs between the binary dispersal and mass ratio characters (Table 1). This significance applies to all reference trees for the male/non-male comparison, but to only 11 of the 20 phylogenies for the male/female test. The log-transformed mass ratio character is a measure of a species' female-to-male SSD with values of <0, >0, and 0 corresponding to male-biased SSD, female-biased SSD, and sexual size monomorphism, respectively (cf. [16]). Thus, these negative associations indicate that species with greater male-biased SSD are more likely to have male-biased dispersal. However, although often significant, these negative associations are consistently weak as mass ratio explains only 7.4-8.7% of the total variation in the liabilities for male/non-male and male/female dispersals.

Correlations between the distance, mass, and ratio characters

The female and male distances are always positively correlated with each other and the same is true of their sex-specific masses (Table 2;
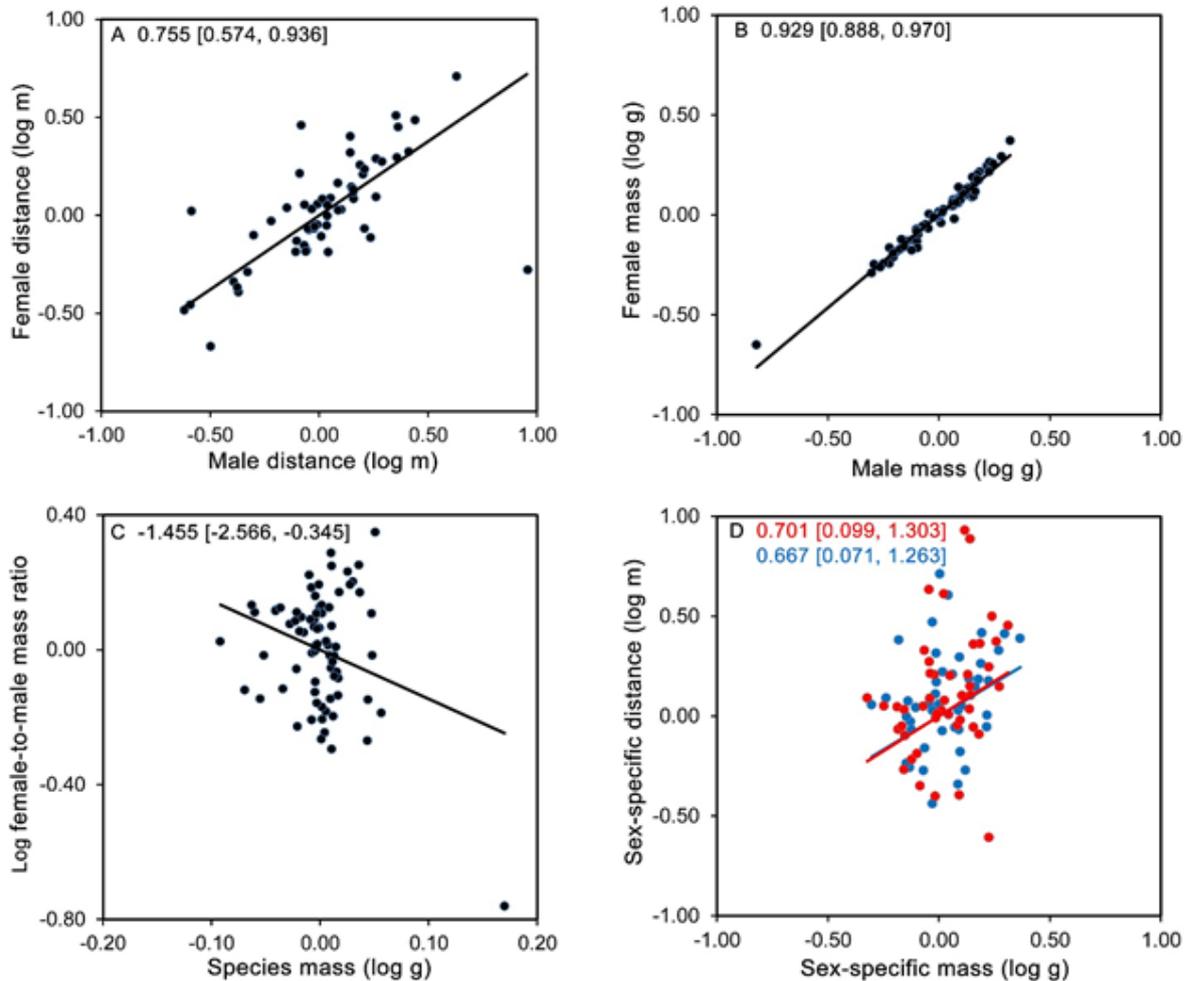
Figure 1: Plots of the contrasts for the female-on-male distance (A), female-on-male mass (B), mass ratio-on-species mass (C), and sex-specific distance-on-mass (D) PICs. These plots are based on trees 16, 20, 12, and 17, respectively (Supplemental Figure 1). The contrasts for these phylogenies are presented, because their slopes most closely approximate the medians for their 20 reference trees (Supplemental Table 3). Slopes and 95% CIs (in square brackets) are provided for each regression. Blue and red designate females and males, respectively.

Figure 1A and 1B). In particular, Pearson's r for the female-on-male mass PIC averages 0.981 and this near-perfect positive correlation is the basis of the similar CTTs for the species, female, and male masses with either the male/non-male or male/female dispersal (Table 1). The slopes for the regressions of the female-on-male distance and mass comparisons are both consistently <1 according to their non-overlapping 95% confidence intervals (CIs; Supplemental Table 3). A slope of <1 indicates that both distance and mass are increasing more rapidly in males than in females.

Furthermore, negative correlations are found between mass ratio and species mass (Table 2; Figure 1C). However, this relationship, which is indicative of Rensch's rule (i.e., male-biased SSD increases with species body size), is weak as its significance does not apply to three of its 20 reference trees and species mass explains only 7.6% of the total variation in mass ratio.

In turn, the female and male distances are each always positively correlated with their sex-specific masses (Table 2; Figure 1D). However, the female and male slopes in these sex-specific distance-on-mass comparisons are indistinguishable as their 95% CIs broadly overlap

(Supplemental Table 3). The five remaining PICs compare the distance and mass ratios with each other or with a sex-specific distance. All five of these PICs are consistently non-significant (Table 2).

Discussion

Our comparative tests support the prediction that sex-biased dispersal is related to body size [9,10,12]. Specifically, we find that larger species have more male-biased dispersal, that distance is increasing more rapidly in males than in females, and that female and male distances are both positively correlated with their sex-specific masses (Tables 1 and 2; Figure 1; Supplemental Table 3). These relationships are consistent (i.e., they are supported by all reference trees), as well as strong for the sex-biased dispersal and body size link (R^2=40.7-56.1%) and female-on-male distance correlation (R^2=54.8%). Conversely, they are not corroborated by the PICs of the distance and mass ratios with each other or with a sex-specific distance. However, these latter tests are constrained by their use of ratios that assume a strict isometry, rather than a broader range of allometric coefficients [30].

Of our 63 species with a binary dispersal score, only nine from

four different orders have the "1" state for male-biased dispersal (Supplemental Table 1). These nine species exhibit a wide range of mating and breeding systems, including (1) the mate-defense mating arrangement of the six duck, goose, and swan species (Anseriformes); (2) the sex role reversal of the northern goshawk (*Accipiter gentilis*, Falconiformes); (3) the exploded lekking of the great bustard (*Otis tarda*, Gruiformes); and (4) the colonial nesting of the Adélie penguin (*Pygoscelis adeliae*, Sphenisciformes) [5]. Our 54 species with the alternative "0" state also exhibit a wide range of mating and breeding systems [7,9]. This heterogeneity is the reason why previous authors (see above) have concluded that no obvious tie exists between sex-biased dispersal and reproductive sociality/behavior.

Similarly, we also find no consistent support for a tie between sex-biased dispersal and a physiological/energetic explanation. Specifically, because COT decreases with mass [14,15] and male-biased SSD is typical for birds [16], it is the bigger males of the larger species that should benefit the most from a reduction in COT. As this extra benefit would become amplified in the larger species (following Rensch's rule), it could reach a point whereby males begin to disperse longer distances than females (i.e., male-biased dispersal). A tie between sex-biased dispersal and COT/SSD/Rensch's rule is suggested by our negative relationships between the binary dispersal and mass ratio characters and between mass ratio and species mass and by the faster increase in the male distance than in the female distance (Tables 1 and 2; Figure 1A; Supplemental Table 3). However, the former negative associations are neither consistent nor strong as their significance applies to $\leq 85\%$ of the reference trees in two of their three comparisons and R^2 is always $\leq 8.7\%$ (cf. the two binary dispersal and mass ratio CTTs and the PIC for Rensch's rule). Most importantly, this tie specifies that the male distance will increase more rapidly with its sex-specific mass than will female distance. However, we find instead that the female and male slopes in their sex-specific distance-on-mass PICs are indistinguishable (Figure 1D). Given these discrepancies, we cannot support a tie between sex-biased dispersal and physiology/energetics.

Thus, it remains unclear as to what is the underlying mechanism of our sex-biased dispersal/body size link. Still, our link is important, because it documents that the related area of species-specific dispersal offers new characters, hypotheses, and approaches for future sex-biased dispersal studies. For example, since territory size has been implicated as a major factor of species-specific distance [10], this life history trait now becomes an obvious target for future studies of sex-biased dispersal in birds.

Conclusions

Our comparative tests support the prediction that sex-biased dispersal is related to body size. Specifically, we find that larger species have more male-biased dispersal, that distance is increasing more rapidly in males than in females, and that the female and male distances are each positively correlated with their sex-specific body masses. However, it remains elusive as to what is the underlying cause of this link. Nevertheless, this link is valuable, because it emphasizes that the related areas of sex-biased and species-specific dispersals are interconnected. By exploiting this connection, we expect that new insights will be achieved as to which life history traits are the primary determinants of sex-biased dispersal.

Acknowledgements

References

1. Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28: 1140-1162.

2. Clobert J, Baguette M, Benton TG, Bullock JM (Eds) (2012) Dispersal Ecology and Evolution. Oxford University Press, Oxford, UK.

3. Hanski I, Gaggiotti O (Eds) (2004) Ecology, Genetics and Evolution of Metapopulations. Elsevier, Burlington, MA.

4. Anderson AS, Reside AE, VanDerWal JJ, Shoo LP, Pearson RG, et al. (2012) Immigrants and refugees: the importance of dispersal in mediating biotic attrition under climate change. Glob Change Biol 18: 2126-2134.

5. Clarke AL, Sæther B-E, Røskaft E (1997) Sex biases in avian dispersal: a reappraisal. OIKOS 79: 429-438.

6. Lawson Handley LJ, Perrin N (2007) Advances in our understanding of mammalian sex-biased dispersal. Mol Ecol 16: 1559-1578.

7. Mabry KE, Shelley EL, Davis KE, Blumstein DT, Van Vuren DH (2013) Social mating system and sex-biased dispersal in mammals and birds: A phylogenetic analysis. PLOS ONE 8: e57980.

8. Clutton-Brock TH, Lukas D (2012) The evolution of social philopatry and dispersal in female mammals. Mol Ecol 21: 472-492.

9. Sutherland GD, Harestad AS, Price K, Lertzman KP (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. Conserv Ecol 4: 16.

10. Bowman J (2003) Is dispersal distance of birds proportional to territory size? Can J Zool 81: 195-202.

11. Jenkins DG, Brescacin CR, Duxbury CV, Elliott JA, Evans JA, et al. (2007) Does size matter for dispersal distance? Glob Ecol Biogeog 16: 415-425.

12. Garrard GE, McCarthy MA, Vesk PA, Radford JQ, Bennett AF (2012) A predictive model of avian natal dispersal distance provides prior information for investigating response to landscape change. J Anim Ecol 81: 14-23.

13. Whitmee S, Orme CDL (2013) Predicting dispersal distance in mammals: a trait-based approach. J Anim Ecol 82: 211-221.

14. Schmidt-Nielsen K (1972) Locomotion: energy cost of swimming, flying, and running. Science 177: 222-228.

15. Alexander RM (2005) Models and the scaling of energy costs for locomotion. J Exp Biol 208: 1645-1652.

16. Székely T, Lislevand T, Figuerola J (2007) Sexual size dimorphism in birds. In: Fairbairn DJ, Blanckenhorn WU, Székely T (Eds) Sex, Size and Gender Roles. Oxford University Press, Oxford, UK, 27-37.

17. Rensch B (1959) Evolution above the Species Level. Methuen and Company, London, UK.

18. Dunning JBJ (2008) CRC Handbook of Avian Body Masses, 2nd edn. CRC Press, Boca Raton, FL.

19. Dunning JBJ (2014) Body Masses of Birds of the World. http://www.ag.purdue.edu/fnr/Documents/BodyMassesBirds.pdf

20. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. Nature 491: 444-448.

21. Hackett SJ, Kimball RT, Reddy S, Bowie RCK, Braun EL, et al. (2008) A phylogenomic study of birds reveals their evolutionary history. Science 320: 1763-1768.

22. Garland T Jr, Harvey PH, Ives AR (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst Biol 41: 18-32.

23. Midford PE, Garland T Jr, Maddison WP (2005) PDAP Package of Mesquite version 1.07. http://mesquiteproject.org/pdap_mesquite

24. Blomberg SP, Garland T Jr, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57: 717-745.

25. Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, et al. (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26: 1463-1464.

26. Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125: 1-15.

27. Felsenstein J (2012) A comparative method for both discrete and continuous characters using the threshold model. Am Nat 179: 145-156.

28. Felsenstein J (1989) PHYLIP - Phylogeny Inference Package (version 3.2). Cladistics 5: 164-166.

29. Swofford DL (2003) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods) version 4. Sinauer Associates, Sunderland, MA.

30. Wong A (2014) Covariance between testes size and substitution rates in primates. Mol Biol Evol 31: 1432-1436.