

# Breeding systems, climate, and the evolution of migration in shorebirds

Gabriel E. García-Peña,<sup>a</sup> Gavin H. Thomas,<sup>b</sup> John D. Reynolds,<sup>c</sup> and Tamás Székely<sup>a</sup>

<sup>a</sup>Department of Biology and Biochemistry, University of Bath, Claverton Down, Bath BA2 7AY, UK,

<sup>b</sup>NERC Centre for Population Biology, Division of Biology, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK, and <sup>c</sup>Department of Biological Sciences, Simon Fraser University, Burnaby BC V5A 1S6 Canada

Migratory behavior incurs energetic costs that may influence the time and energy available for reproduction including territory establishment, courtship, pair formation, incubation, and brood care. Conversely pair formation and parental care may leave less time and energy available for migration and other nonbreeding behaviors. Therefore, natural selection favoring migratory behavior may influence breeding system evolution and vice versa. We used phylogenetic comparative methods to investigate relationships between migration distance and the wide diversity of breeding systems in shorebirds (sandpipers, plovers and allies). Consistent with previous studies, we show that long-distance migration is associated with reduced male care across shorebird species. We then use directional phylogenetic analyses to test whether migration distances have tended to increase or decrease over time and whether such evolutionary changes have preceded or followed changes in parental care. We show that evolutionary transitions from short-distance migration to long-distance migration have coevolved with changes from full biparental care to reduced male care. Furthermore, our directional analyses suggest that increments in migration distance are more likely to have preceded reductions in male care than vice versa. We also show that male polygamy is associated with northern breeding latitudes when the nonbreeding latitude is controlled statistically. Although this suggests that mating systems, parental care, and migration have more complex relationships than previously thought, our results are consistent with the hypothesis that migration influences breeding system evolution. *Key words:* Charadriiformes, mating system, migration distance, parental care, seasonality, sexual selection. [*Behav Ecol* 20:1026–1033 (2009)]

Seasonal migration is a prominent feature of the life cycles of many birds, mammals, fish, and insects (Baker 1978; Gauthreaux 1980; Wikelski et al. 2006). It allows animals to exploit advantageous conditions and breed in regions where the climate is hostile for most of the year (Alerstam et al. 2003; Gunnarsson et al. 2005; Mathot et al. 2007). Migration, however, requires time and energy (Wikelski et al. 2003) that may reduce budgets available for key reproductive activities such as parental care (Ashkenazie and Safriel 1979; Urano 1992; Bearhop et al. 2005) and competition for mates (Møller 1994; Kokko 1999; Drent et al. 2003). Therefore, there may be trade-offs between migration, parental care, and mating systems, such that natural selection favoring migratory behavior may influence breeding system evolution (Helm et al. 2006). Conversely, sexual selection and parental care may reduce the time and energy available for migration and other nonbreeding behaviors. Consequently, the evolution of breeding system may either determine or respond to variation in migratory behavior (note that we define breeding system as including both mating system and parental care; see Reynolds 1996).

Despite extensive empirical studies of migratory behavior and breeding systems and logical arguments for causal links between them, remarkably little is known about how migration and breeding systems may have coevolved. To our knowledge, birds are the only group in which the coevolution of breeding systems and migratory behavior has been studied. Myers (1981) and Reynolds and Székely (1997) showed that migration dis-

tances are typically longer in shorebird species (Charadriiformes) in which the male provides little or no parental care.

If there is a trade-off between the costs of parental care and migratory distance, we can envisage 2 alternative scenarios that differ in the direction of causation. First, long periods of parental care could limit the time and energy available for migration and select for short-distance migration (Ashkenazie and Safriel 1979; Myers 1981; Reynolds and Székely 1997); hence, migration distance is determined by parental care. Alternatively, long-distance migration may limit the time and energy available for parental care and favor early desertion by one or both parents such that migration distance determines parental care. These 2 alternatives predict that reduced parental care should be associated with long-distance migration. Collectively, we term these scenarios the parental care hypothesis.

It is also possible that sexual selection, rather than parental care, is the key to the relationships between migration and breeding systems. Again, 2 alternative scenarios have been proposed. The early arrival scenario proposes that the costs of sexual selection could constrain long-distance migration and favor short-distance migration and early arrival to the breeding grounds of the sex under strong sexual selection (Kokko 1999; Oring and Lank 2004). In contrast, the asynchronous breeding scenario suggests that long-distance migration may intensify sexual selection. Migrant species may arrive asynchronously at breeding areas according to their sex and condition, promoting a bias in the adult sex ratio and high variation in the quality of the mating partners, leading to strong sexual selection (Fitzpatrick 1994; Spottiswoode and Møller 2004; Smith and Moore 2005; Albrecht et al. 2007). In terms of causation, the early arrival scenario proposes that the mating system influences the evolution of migration, whereas the asynchronous breeding scenario proposes that migration influences mating systems.

Address correspondence to G.E. García-Peña. E-mail: g.e.g.pena@bath.ac.uk.

Received 18 November 2008; revised 29 May 2009; accepted 29 May 2009.

The parental care and sexual selection hypotheses are not mutually exclusive. This is because parental care and sexual selection are tightly related, with reductions in parental care in one or the other sex are often associated with strong sexual selection (Andersson 1994; Thomas and Székely 2005; Székely et al. 2006). Consequently, if, for example, reductions in care were associated with long-distance migration, they would also be associated with increases in the strength of sexual selection. However, by examining both correlations and the order of occurrence (i.e., contingency) between breeding systems and migration, it is possible to separate all but the asynchronous breeding scenario (sexual selection) from the parental care scenario in which the evolution of long-distance migration favors reductions in the duration of care.

The fact that the sexual selection and parental care hypotheses predict that natural selection favoring migration is equally likely to be driven by, and respond to, variation in sexual selection or parental care highlights why causation has proved difficult to interpret (Myers 1981; Reynolds and Székely 1997). Previous studies have attempted to distinguish cause and effect with reference to recent glaciations. They argued that recent migratory routes are likely to have evolved after successive periods of glaciation in the Quaternary epoch (Alerstam 1990; Reynolds and Székely 1997; Bell 2000; Buehler et al. 2006; Milá et al. 2006). Hence, Reynolds and Székely (1997) proposed that migratory routes most likely evolved more recently than breeding systems, implying that the evolution of migratory behavior is more likely to be driven by breeding systems than vice versa. However, glaciation cycles are unlikely to be informative in determining cause and effect for 2 reasons: First, although many contemporary migration pathways could not have existed when current breeding grounds were covered by ice, it is still possible that species that currently migrate furthest may have always done so in different locations. For example, Williams and Webb (1996) showed that contemporary migratory pathways of North American passerines could predict their migratory routes during Quaternary glaciations. Therefore, there is no reason to assume that relative migration distance must have been determined after breeding systems (Thomas et al. 2007). Second, breeding systems may be as evolutionarily labile as migratory behavior because breeding behavior varies both within and between species in birds and particularly in shorebirds (Lank and Smith 1987; Ligon 1999; Bennett and Owens 2002; Székely et al. 2006). This implies that migration and breeding systems might have coevolved before, after, and during glaciations. Consequently, the issue of the likely mechanism that relates migration and breeding systems remains unclear.

Here we extend the analyses of Myers (1981) and Reynolds and Székely (1997) on the relationships between migration and breeding systems in shorebirds (Charadriiformes). In particular, we focus on sandpipers, plovers, and allies (Burhinidae, Charadriidae, Chionidae, Glareolidae, Jacanidae, Pedionomidae, Pluvianellidae, Rostratulidae, Scolopacidae, and Thinocoridae). We did not include alcids, gulls, terns, and skuas (Alcidae and Laridae) in the current study because they exhibit little variation in their breeding systems. Sandpipers, plovers, and allies breed from the Arctic to Antarctica across a wide range of latitudes and climates, and they include both long-distance migrants and resident species (Hötter et al. 1998; Piersma and Lindström 2004; van de Kam et al. 2004). They also have unusually diverse breeding systems including social monogamy, sex-role reversed polyandry with male-only care, social polygyny with female-biased care, and lekking with female-only care (Pitelka et al. 1974; Hildén 1975; Erckmann 1983; Oring and Lank 1986; Székely et al. 2006; Thomas et al. 2007). We exploited this natural diversity to evaluate the parental care and sexual selection hypotheses by testing: 1) the rela-

tionships between migration distance and parental care with mating systems used as a proxy for the strength of sexual selection, controlling for climatic effects that predict migration distance; 2) which of the causal conditions is more likely—whether increases in migration distance precede changes in the breeding systems or vice versa; and 3) an alternative scenario in which the relationships between migration distance and breeding systems could be associated with changes in latitude of the breeding or the nonbreeding grounds (Pitelka et al. 1974; Myers 1981).

## MATERIALS AND METHODS

### Breeding and wintering latitudes and migration distance

We estimated the migration distance and the breeding and nonbreeding latitudes of 138 shorebird species based on geographical distribution maps (del Hoyo et al. 1996; Riede 2004). Latitudes were estimated on a continuous scale of decimal degrees from the southernmost latitude ( $-90^\circ$ ) to the equator ( $0^\circ$ ) and to the northernmost latitude ( $90^\circ$ ). Migration distance was estimated as the latitudinal distance (kilometers) between centroids of the breeding and nonbreeding areas for each species, measured on an earth model WGS84 (Vicenty 1975; Kleder 2004). For 30 species classified as resident (nonmigrant), by del Hoyo et al. (1996), migration distance was taken as 0 km. Our estimates of migration distances are highly correlated with an independent set of migratory distance data used by Myers (1981) ( $n = 24$ , Spearman's test:  $r = 0.848$ ,  $P < 0.001$ ). The full data set and the sources of data are available in Appendix 1 of the electronic Supplementary Material.

### Breeding systems

Following Reynolds and Székely (1997) and Thomas et al. (2007), we scored the duration of parental care for each sex separately on an ordinal scale: no care, if the parent deserts the offspring immediately after egg laying; 0 = desertion before hatching of the eggs, 1 = desertion during 1st third of incubation, 2 = desertion during 2nd third of incubation, 3 = desertion at 3rd third of incubation, 4 = desertion during 1st third of fledging period, 5 = desertion during 2nd third of fledging period, 6 = desertion during 3rd third of fledging period, and 7 = care provided by the parent until (or beyond) fledging of the chicks.

The extents of male and female polygamy were used as proxies for the intensity of sexual selection on each sex, consistent with previous phylogenetic comparative analyses (Liker and Székely 2005; Olson et al. 2008). Multiple paternity is uncommon in socially monogamous shorebirds and high in polygamous species (Table 1 in Thomas et al. 2007); therefore, we are confident that the extent of polygamy provides a reasonable index of the intensity of sexual selection. Polygamy was scored independently for each sex on an ordinal scale following Thomas et al. (2006): 0 if no polygamy is reported in the species, 1 if the extent of polygamy is anecdotal ( $<1\%$ ), 2 if polygamy is 1–5%, 3 if of polygamy is 6–20%, or 4 if polygamy occurs in more than 20% of cases.

### Confounding effects

Offspring developmental mode correlates with various traits in shorebirds, including parental care and social mating system (Thomas and Székely 2005; Thomas et al. 2006). Thus, we took into account information on offspring development scored as semiprecocial (0) or precocial (1). This reflects the feeding requirements of the young; precocial chicks feed themselves within hours of hatching, whereas semiprecocial

Table 1

**Phylogenetic linear models for relationships between migration distance (response variable, in kilometers) and parental care after controlling for confounding effects such as ambient temperature (degrees celsius), length of the egg-laying season (days), and offspring development mode (precocial or semiprecocial)**

	Full model: $\beta$ (SE)	$t$ ( $P$ )	MAM: $\beta$ (SE)	$t$ ( $P$ )
Provision of parental care				
Male care	-223.927 (130.627)	-1.714 (0.089)	-275.722 (114.125)	-2.416 (0.017)
Female care	-3.084 (108.705)	-0.028 (0.977)	NS	
Confounding effects				
Offspring development	589.996 (758.951)	0.777 (0.439)	NS	
Ambient temperature ( $T$ )	-330.127 (63.904)	-5.166 (<0.001)	-328.288 (57.249)	-5.734 (<0.001)
Length of the egg-laying season ( $B$ )	-38.651 (8.673)	-4.456 (<0.001)	-40.989 (8.03)	-5.105 (<0.001)
$T \times B$	1.521 (0.484)	3.14 (0.002)	1.576 (0.45)	3.506 (0.001)

All predictors were included in the full model ( $R^2 = 0.517$ ,  $F_{7,111} = 18.583$ ,  $P < 0.001$ ), whereas nonsignificant predictors (NS) were not included in the minimum adequate model (MAM) ( $R^2 = 0.522$ ,  $F_{5,124} = 34.556$ ,  $P < 0.001$ ). Differences in sample sizes are due to missing data for some variables. Shapiro–Wilk test on the normality of residuals from MAM:  $W = 0.989$ ,  $P = 0.449$ . SE, standard error.

chicks rely on the parents for food (Lack 1968; Starck and Ricklefs 1998).

Previous comparative studies used latitude as a proxy for ambient temperature, seasonal heterogeneity, and the length of the breeding season (Myers 1981; Reynolds and Székely 1997). Here, we separate the climatic effects associated with breeding latitude into the ambient temperature in the breeding season and the length of the egg-laying season. First, we used the number of days between the start and finish of egg laying reported for the species as an estimate for the length of the breeding season. Second, we took the ambient temperature in the breeding season as the mean of the monthly average temperatures in the breeding range during the egg-laying season. Ambient temperatures within the breeding range of each species were calculated from a grid data set of 0.5 decimal degree resolution (Lemans and Cramer 1991; Hearn et al. 2003).

### Phylogenetic comparative analyses

We used the only complete phylogenetic hypothesis available for shorebirds (a supertree phylogeny; Thomas et al. 2004) and phylogenetic general linear models (PGLMs) to test for relationships between migration distance, breeding latitude, and breeding systems. PGLMs control for the nonindependence of interspecific data ascribed to phylogenetic inertia (Felsenstein 1985; Grafen 1989; Harvey and Pagel 1991). In all models, we estimated and fitted the maximum likelihood value of  $\lambda$ : a scalar that provides the best fit of the phylogeny to the data and ensures that the appropriate degree of phylogenetic autocorrelation is accounted for (Pagel 1997, 1999; Freckleton et al. 2002). To test our hypotheses, we built a full model that included all potential predictors (specified for each analysis below). We then reduced the full model to a minimum adequate model (MAM, Crawley 2002) by starting from the full model and progressively eliminating the predictor with the highest  $P$  value in the model to produce a MAM containing only significant predictors ( $P$  value  $\leq 0.05$ ). We tested alternative models and corroborated the influence of each eliminated predictor by adding it back into the MAM. All PGLMs were performed in R software (R Development Core Team 2005), using a script kindly provided by R. P. Freckleton.

The response variables (migration distance and breeding and nonbreeding latitudes) were nonnormally distributed regardless of various transformations ( $\log [x + 1]$  or square root). Therefore, to ensure that the assumption of normal distribution of errors was not violated, we verified that the residual variation of the PGLMs was normally distributed. Shapiro–Wilk tests on the normality of residuals of each model are presented.

### Migration distance and breeding systems

We tested the relationship between migration distance (response) and breeding systems using PGLMs. Previous studies in shorebirds have shown that the extent of polygamy is associated with the provision of parental care (Thomas and Székely 2005; Székely et al. 2006). Because there is a potential risk of error if variables with redundant information are included in the same model, we performed separate analyses for parental care and for the extent of polygamy (see Appendix 2 of the electronic Supplementary Material for tests of the correlation among all pairs of predictor variables). In one analysis, we included male care, female care, offspring developmental mode, length of the breeding season, and ambient temperature as predictors; whereas in the other analysis, we included male polygamy, female polygamy, offspring developmental mode, length of the breeding season, and ambient temperature. From these full models, we eliminated nonsignificant predictors to find the MAM.

### Breeding and nonbreeding latitudes and breeding systems

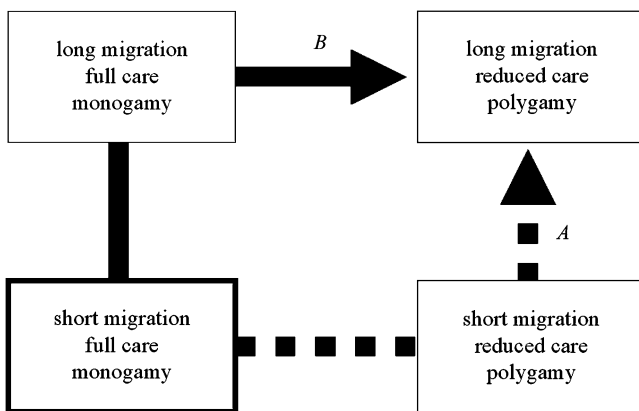
Interspecific variation in migration distance may be due to variation in the breeding latitude, nonbreeding latitude, or both. Consequently, correlations between migration and breeding systems may be driven by changes in species' distributions, rather than by migration distance per se. We tested these alternatives using PGLMs. First, we modeled the breeding latitude (response) using the nonbreeding latitude and the breeding system as predictors and produced MAMs using the procedure described previously. We expected a quadratic relationship between breeding latitude and nonbreeding latitude because resident species are likely to breed at southern and tropical latitudes and stay near the breeding areas during the nonbreeding season. In contrast, species that breed at northern latitudes are likely to be long-distance migrants that migrate to southernmost latitudes in the nonbreeding season (Steadman 2004). Second, we modeled the nonbreeding latitude (response) using the breeding latitude and its quadratic relationship as predictors and tested the relationships between breeding systems and breeding latitude following the same procedure as above.

### Contingency tests on the directions of transitions

We used the discrete method (Pagel 1994) implemented in BayesTraits (Pagel and Meade 2006, <http://www.evolution.rdg.ac.uk/>) to test whether evolutionary changes toward long-distance migration were contingent on the type of

breeding system or whether evolutionary changes in the breeding system were contingent on the type of migration (long or short distances). Contingency tests require estimates of the state of each trait at the root of the phylogeny. Thus, we reconstructed root states using maximum likelihood and parsimony methods in MESQUITE 2.01 (Maddison WP and Maddison DR 2006, <http://mesquiteproject.org/>). Parsimony methods corroborated the root states reconstructed by maximum likelihood methods, and these are consistent with previous studies: the root state of the breeding system in shorebirds is inferred to be social monogamy with male and female care (Székely and Reynolds 1995; Borowik and McLennan 1999; Reynolds et al. 2002; Thomas and Székely 2005). The root state for migration was short-distance migration using the mean of all species' migration distances (3773 km) as a cutoff point (i.e., below and equal to the mean = short-distance migrants or above the mean = long-distance migrants).

Because Discrete requires a fully bifurcating phylogeny, we resolved all polytomies by randomly placing branches of 0.00001 million years in length using TreeEdit v1.0a10 (Rambaut and Charleston 2002), and the same phylogeny was used in the PGLMs (above). Discrete requires binary traits, but the cutoff point when coding a continuous variable as a discrete variable can influence the results, particularly if the cutoff is essentially arbitrary with respect to biology (Pérez-Barbería et al. 2002). We therefore scored each species as a short-distance migrant (0) or as a long-distance migrant (1) using 4 alternative cutoff points: migration distance was scored as 1 if its value was above or equal to: 1) the first quantile (249.1 km), 2) the third quantile (6784.0 km), 3) the median (2927 km), and 4) the mean (3773.4 km) migration distance across species. In this way, we were able to test the robustness of our results to different cutoff points. We transformed parental care into a binary scale using hatching as a biologically meaningful cutoff point in offspring development. Specifically, male and female parental care were scored as: reduced care (0), if parental care is only provided by the focal sex before the young hatch, or full care (1), if parental care is provided by the focal parent both before and after the young hatch. We only performed contingency tests for relationships that were statistically significant in the PGLMs; thus, we did not test the relationships between migration distance and the extent of polygamy (see Results).



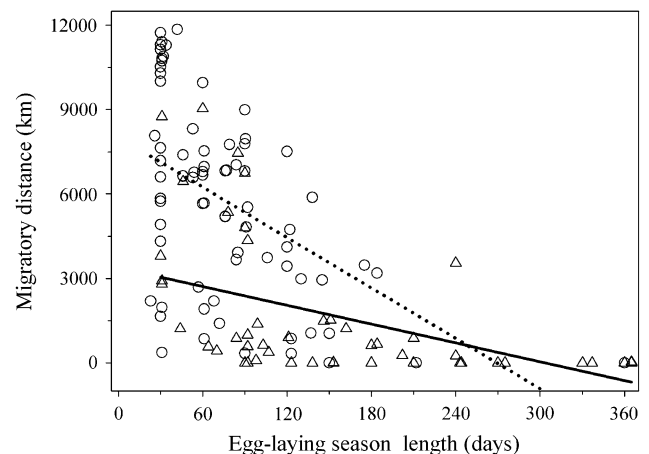
**Figure 1**  
Two evolutionary pathways (A, dashed lines and B, solid lines) compared in the contingency tests to determine the direction of transitions. The reconstructed state at the root of the phylogeny (bold box) was full care by males and females, social monogamy, and short or no migration (<3773 km).

We first tested correlated evolution between migration and breeding systems. Then, we used contingency tests to compare the likelihoods of 2 hypothesized evolutionary pathways: (A) changes in the breeding system preceded changes in migration distance or (B) changes in migration distance preceded changes in the breeding system (Figure 1). Statistical significance of the most likely pathway was tested by comparing the maximum likelihoods (Lhs) of 2 models: the precedence model that estimated a separate parameter of the likelihood for each evolutionary pathway ( $A \neq B$ ) against a null model that assumed the evolutionary pathways were equally likely ( $A = B$ ). The maximum likelihood of the precedence model and the null model were compared using the likelihood ratio statistic ( $LR = 2[Lh_{\text{precedence}} - Lh_{\text{null}}]$ ), and statistical significance of the difference between the 2 models was tested with a  $\chi^2$  test of 1 degree of freedom (df), by assuming that LR has an asymptotic  $\chi^2$  distribution of df equal to the difference of the number of parameters estimated between 2 nested models (Pagel 1994, 1997). This assumption is consistent with previous studies (Pagel 1994, 1997; Pérez-Barbería et al. 2002). Note that the precedence model and the null model are nested models that differ by one parameter.

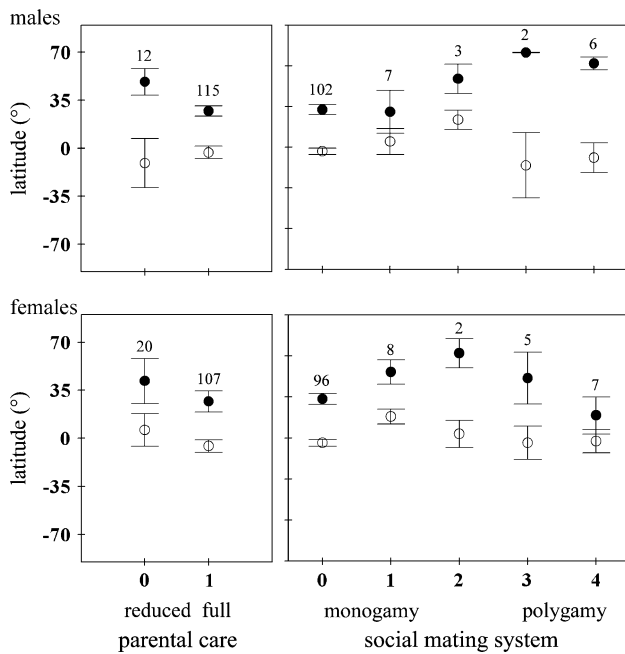
## RESULTS

### Migration distance and breeding systems

Migration distance was correlated with the length of the egg-laying season and ambient temperature. Thus, not surprisingly, shorebirds that breed in cold environments and have short breeding seasons migrate over larger distances than species that breed in warm environments and have long breeding seasons (Table 1). There was also a significant interaction between length of the egg-laying season and ambient temperature such that in cold environments migration distance decreases more rapidly with increases in the egg-laying season than in warm environments (Figure 2). By controlling for these climatic effects, we confirmed that reduced care was correlated with long-distance migration and that this relationship is only significant in males but not in females (Table 1). There were no significant relationships between migration distance and male polygamy ( $t = 0.511$ ,  $P = 0.610$ ) or female



**Figure 2**  
Migration distance of shorebird species decreases as the length of the egg-laying season (number of days) and ambient temperature (mean degree celsius) on the breeding grounds increase. Triangles and solid lines represent taxa in warm environments (ambient temperature equal to or above the mean temperature of 11.9 °C), and circles and dotted lines represent taxa in cold environments in which ambient temperature is lower than the mean temperature.



**Figure 3**  
Breeding latitudes (closed circles) and nonbreeding latitudes (open circles) of shorebird species in relation to parental care and mating system of males (top panel) and females (bottom panel). Means (circles) and standard errors and sample sizes (numbers) are presented.

polygamy ( $t = 0.358$ ,  $P = 0.722$ ) after controlling for phylogeny and climatic effects ( $R^2 = 0.516$ ,  $F_{7,101} = 16.731$ ,  $P < 0.001$ ).

### Breeding latitude, nonbreeding latitude, and breeding systems

The relationship between migration distance and breeding system appeared more likely to have been driven by changes in both breeding latitude and nonbreeding latitude than either of these alone. In species that breed in the north, males but not females were more likely to provide reduced care to the offspring and to be more polygamous than species that breed in the south (Figure 3, Tables 2 and 3). In addition, we found that species that spend the nonbreeding season in the south relative to their breeding latitude were likely to have reduced care by males but not by females, although the relationship was weaker than with breeding latitude (Figure 3, Table 4).

**Table 2**

**Full phylogenetic linear model (PGLM) between breeding latitude (response variable degrees) and parental care ( $R^2 = 0.426$ ,  $F_{6,114} = 16.007$ ,  $P < 0.001$ ) after controlling for the nonbreeding latitude (degrees) and offspring development (precocial or semiprecocial)**

	$\beta$ (SE)	$t$ ( $P$ )
Provision of parental care		
Male care	-3.89 (1.574)	-2.471 (0.015)
Female care	-2.228 (1.294)	-1.721 (0.088)
Confounding effects		
Offspring development	17.83 (8.998)	1.982 (0.05)
Nonbreeding latitude	0.797 (0.124)	6.451 (<0.001)
Square of nonbreeding latitude	-0.01 (0.004)	-2.383 (0.019)

The MAM contained only the predictors that were significant in the full PGLM presented (see Materials and methods). Shapiro–Wilk test on the normality of residuals from MAM:  $W = 0.978$ ,  $P = 0.056$ . SE, standard error.

**Table 3**

**Full phylogenetic linear model (PGLM) between breeding latitude (response variable degrees) and the social mating systems ( $R^2 = 0.361$ ,  $F_{6,104} = 11.095$ ,  $P < 0.001$ ) after controlling for the nonbreeding latitude (degrees) and offspring development (precocial or semiprecocial)**

	$\beta$ (SE)	$t$ ( $P$ )
Social mating system		
Male polygamy	7.397 (3.336)	2.218 (0.029)
Female polygamy	-3.443 (2.771)	-1.242 (0.217)
Confounding effects		
Offspring development	24.543 (9.511)	2.58 (0.011)
Nonbreeding latitude	0.744 (0.136)	5.483 (<0.001)
Square of nonbreeding latitude	-0.009 (0.004)	-1.95 (0.054)

The MAM contained only the predictors that were significant in the full PGLM presented (see Materials and methods). Shapiro–Wilk test on the normality of residuals from MAM:  $W = 0.988$ ,  $P = 0.473$ . SE, standard error.

Neither male polygamy ( $t = -0.329$ ,  $P = 0.743$ ) nor female polygamy ( $t = 0.210$ ,  $P = 0.834$ ) were associated with nonbreeding latitudes after controlling for breeding latitude ( $R^2 = 0.396$ ,  $F_{6,104} = 14.514$ ,  $P < 0.001$ ).

### Directions of transitions

We followed up the previous regression analyses of migration distance and male care by testing whether there was a tendency for changes in one trait to precede the other. First, we corroborated that changes in migration distance evolve in association with transitions in male care (correlated models in Table 5). We found that the null model, that is, that the alternative pathways *A* and *B* in Figure 1 are equally likely, was rejected in favor of the precedence model in which the likelihoods of pathways *A* and *B* differ (LR = 8.554,  $P = 0.003$ ,  $df = 1$ , Table 5). In the precedence model, using the mean as cutoff point of long-distance migration, the likelihood of *B* (0.0118) was significantly higher than the likelihood of *A* (0), suggesting that transitions toward reduced care are contingent on increases in migration distance. This result remained significant when using the mean, the median, or the third quartile, but not the first quartile, as the cutoff point for migration distance (Table 5).

### DISCUSSION

This study provides the first evidence concerning the directions of the evolutionary transitions that have led to contemporary associations between breeding systems and migration distances in shorebirds. Our results corroborate previous studies, which indicated that long-distance migration in shorebirds is correlated with reduced care (Myers 1981) and that this reduction is true for care provided by males but not by females (Reynolds and Székely 1997). We have now extended these analyses to include relationships with climatic variables on the breeding grounds (i.e., ambient temperature and the length of the egg-laying season) as well as considering explicitly the latitudes where the birds breed or spend the winter. We showed that the association between migratory behavior and breeding systems is independent of climatic factors that favor the evolution of migration (Cotton 2003; Outlaw and Voelker 2006; Boyle and Conway 2007; Dawson 2007).

A key discovery is that increases in migration distance are more likely to have preceded reductions in male parental care than vice versa during the evolutionary history of shorebirds. This result does not support the hypothesis that changes in

**Table 4**

**Phylogenetic linear models between the nonbreeding latitude (response variable degrees) and parental care full model ( $R^2 = 0.478$ ,  $F_{6,114} = 19.772$ ,  $P < 0.001$ ) and MAM  $R^2 = 0.436$ ,  $F_{4,127} = 31.704$ ,  $P < 0.001$ )**

	Full model: $\beta$ (SE)	$t$ ( $P$ )	MAM: $\beta$ (SE)	$t$ ( $P$ )
Provision of parental care				
Male care	1.27 (0.935)	1.359 (0.177)	1.79 (0.839)	2.133 (0.035)
Female care	-1.06 (0.776)	-1.366 (0.175)	NS	
Confounding effects				
Offspring development	-2.411 (5.466)	-0.441 (0.66)	NS	
Breeding latitude	0.622 (0.071)	8.731 (<0.001)	0.609 (0.066)	9.276 (<0.001)
Square of breeding latitude	-0.008 (0.002)	-5.404 (<0.001)	-0.008 (0.001)	-5.386 (<0.001)

Differences in sample sizes are due to missing data for some variables. NS = a nonsignificant predictor ( $P < 0.05$ ). Shapiro–Wilk test on the normality of residuals from MAM:  $W = 0.980$ ,  $P = 0.059$ . SE, standard error.

parental care may have preceded changes in migration distance (Reynolds and Székely 1997). Instead, if the relationships between the distance of migration and breeding system are ascribed to causality, it is possible that long-distance migration may impose a cost to males providing parental care. Our sensitivity analyses (Table 5) support the hypothesis that migration distance, rather than migration per se, influences breeding systems because the relationship remained significant when migration was classified as long-distance migration above the median (2927 km) but not when it was classified below the first quartile (249.1 km). We note that the first quartile essentially separates resident or vagrant species from migrants, whereas the mean, median, and third quartile separate short-distance migrants from long-distance migrants. This evidence supports the idea that natural selection favoring long-distance migration has influenced breeding system evolution (Ashkenazie and Safriel 1979; Myers 1981). In regard to the effects of sexual selection on migration, we do not support the hypothesis that intense sexual selection constrains long-distance migration (i.e., the early arrival scenario) because we found no relationship between the extent of polygamy and migration distance. In fact, the tests on the direction of transitions suggest that increases in migration distance were more likely to influence the breeding system than vice versa, providing opposite evidence to the early arrival scenario. However, we cannot reject the asynchronous arrival hypothesis because long-distance migration may intensify sexual selection (Fitzpatrick 1994; Spottiswoode and Møller 2004) and consequently favor reductions in parental care. Therefore, the observed relationship between male care and migration distance may arise if the duration of parental care is influenced by the intensity of sexual selection (Thomas and Székely 2005).

It remains difficult to explain why only males and not females reduce their contribution of parental care in relation to migration distance. One possibility is that our proxy of migration may not incorporate all the complexities of the migration phenology such as sex-specific migration distances or

arrival dates. This could be relevant as sex-specific and age-specific migrations have been documented in other studies of some passerines and shorebirds (Reynolds et al. 1986; Belthoff and Gauthreaux 1991; Komar et al. 2005; Nebel 2005; O'Hara et al. 2005). Another possibility is that the energetic costs of long-distance migration, relative to the benefits of having energy reserves on arrival, may be higher for males than for females because sexual selection to arrive early in the breeding season is usually stronger in males (Møller 1994; Morbey and Ydenberg 2001; Kokko et al. 2006; Spottiswoode et al. 2006). Previous studies have found that long-distance migrant species have larger testes and higher rates of extrapair paternity than resident species (Møller 1994; Spottiswoode and Møller 2004; Stutchbury et al. 2004; Albrecht et al. 2007). Furthermore, the majority of shorebird species in which sexual selection is stronger in females than males breed in the tropics or subtropics, are not migratory, and come from a single monophyletic clade (jacanas, Jacanidae and painted-snipes, Rostratulidae; Thomas et al. 2004; Baker et al. 2007). Thus, a signal of sexual selection in long-distance migrant shorebirds that exhibit polyandry may be swamped by the unusual evolutionary history of the single clade of jacanas.

One major result has been to show that polygynous species, in which parental care by the male is reduced, are more likely to breed at northern latitudes and spend the nonbreeding season at southern latitudes than socially monogamous species in which males provide full parental care. Therefore, the social breeding behavior of long-distance migrants may be influenced by the quality of the breeding and nonbreeding grounds and the costs of migration. These results corroborate Myers' (1981) study that showed that breeding systems are associated with the nonbreeding and breeding latitudes. Our advance has been to use multivariate analyses to test the association between breeding and nonbreeding latitudes as well as to provide the first phylogenetic tests that allow inference of the precedence of evolutionary transitions. We suggest that long-distance migration may influence breeding systems in

**Table 5**

**Contingency tests for correlated evolution of migration distance and male parental care**

Model	df	First quartile (249.1 km)	Median (2927 km)	Mean (3773 km)	Third quartile (6784.0 km)
Correlated	4	5.464 (0.243)	8.377 (0.079)	9.903 (0.042)	15.906 (0.003)
Precedence	1	1.691 (0.193)	6.276 (0.012)	8.554 (0.003)	7.249 (0.007)

Likelihood ratio (LR) tests are presented for 2 models: the "correlated" model tests for correlated evolution of long-distance migration and male parental care and the "precedence" model tests in which evolutionary pathway is more likely along the evolutionary history of shorebirds. Tests were performed at 4 cutoff points for migration distance (see Materials and methods). The first value in each cell is the LR and  $P$  values are in parentheses.

2 additive ways: directly by influencing male care and the intensity of sexual selection and indirectly by allowing birds to breed in northern habitats where ecological conditions allow male polygamy and reduced male care (Pitelka et al. 1974; Chalfoun and Martin 2007). Indeed, previous studies have shown that the provision of parental care in shorebirds is associated with the quality of the breeding habitat (Reynolds 1987; Ens et al. 1992; Székely and Cuthill 1999).

Taken together, our results show that climatic factors can predict migration distance in shorebirds and that the evolution of long-distance migration may have preceded reductions of parental care by the male but not by the female. This evolutionary pathway may be the outcome of 2 additive processes. First, long-distance migration may influence breeding systems directly by inflicting an energetic cost and increasing the strength of sexual selection. Second, long-distance migration may influence breeding systems indirectly by allowing species to breed at high-latitude habitats in which ecological conditions could favor polygamy and allow uniparental care.

### SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

### FUNDING

NERC Centre of Population Biology at Imperial College to G.H.T.; Canadian NSERC Discovery and Accelerator Supplement grants to J.D.R.

We would like to thank the 2 anonymous reviewers for their constructive comments on the manuscript and B. Riley for proof reading the text. The first author was supported by a PhD scholarship from the Consejo Nacional de Ciencia y Tecnología (CONACyT).

### REFERENCES

- Albrecht T, Schnitzer J, Kreisinger J, Exnerová A, Bryja J, Munclinger P. 2007. Extra pair paternity and the opportunity for sexual selection in long-distant migratory passerines. *Behav Ecol*. 18:477–486.
- Alerstam T. 1990. *Bird migration*. New York: Cambridge University Press.
- Alerstam T, Hedenström A, Åkesson S. 2003. Long-distance migration: evolution and determinants. *Oikos*. 103:247–260.
- Andersson M. 1994. *Sexual selection*. Princeton (NJ): Princeton University Press.
- Ashkenazie S, Safriel UN. 1979. Time-energy budgets of the semipalmated sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology*. 60:783–799.
- Baker AJ, Pereira SL, Paton TA. 2007. Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. *Biol Lett*. 3:205–209.
- Baker R. 1978. *The evolutionary ecology of animal migration*. London: Hodder and Stoughton.
- Bearhop S, Fiedler W, Furness RW, Votier SC, Waldron S, Newton J, Bowen GJ, Berthold P, Farnsworth K. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science*. 310:502–504.
- Bell CP. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. *J Avian Biol*. 31:258–265.
- Belthoff JR, Gauthreaux SAJ. 1991. Partial migration and differential winter distribution of house finches in the eastern United States. *Condor*. 93:374–382.
- Bennett PM, Owens IPF. 2002. *Evolutionary ecology of birds: life history, mating system and extinction*. Oxford: Oxford University Press.
- Borowik OA, McLennan DA. 1999. Phylogenetic patterns of parental care in calidridine sandpipers. *Auk*. 116:1107–1117.
- Boyle WA, Conway CJ. 2007. Why migrate? A tests of the evolutionary precursor hypothesis. *Am Nat*. 169:344–359.
- Buehler DM, Baker AJ, Piersma T. 2006. Reconstructing paleoflora of the late Pleistocene and early Holocene red knot *Calidris canutus*. *Ardea*. 94:485–498.
- Chalfoun AD, Martin TE. 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Anim Behav*. 73:579–585.
- Cotton PA. 2003. Avian migration phenology and global climate change. *Proc Natl Acad Sci USA*. 100:12219–12222.
- Crawley MJ. 2002. *Statistical computing: an introduction to data analysis using S-Plus*. Chichester (UK): John Wiley and Sons, Ltd.
- Dawson A. 2007. Seasonality in a temperate zone bird can be entrained by near equatorial photoperiods. *Proc R Soc Lond B Biol Sci*. 274:721–725.
- del Hoyo J, Elliott A, Sargatal J. 1996. *Handbook of the birds of the world*. Barcelona (Spain): Lynx Edicions.
- Drent R, Both C, Green M, Madsen J, Piersma T. 2003. Pay-offs and penalties of competing migratory schedules. *Oikos*. 103:274–292.
- Ens BJ, Kersten M, Brenninkmeijer A, Hulscher JB. 1992. Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *J Anim Ecol*. 61:703–715.
- Erckmann WJ. 1983. The evolution of polyandry in shorebirds: an evaluation of hypotheses. In: Wasser SK, editor. *Social behavior of female vertebrates*. New York: Academic Press. p. 113–168.
- Felsenstein J. 1985. Phylogenies and the comparative method. *Am Nat*. 125:1–15.
- Fitzpatrick S. 1994. Colourful migratory birds: evidence for a mechanism other than parasite resistance for the maintenance of 'good genes' sexual selection. *Proc R Soc Lond B Biol Sci*. 257:155–160.
- Freckleton RP, Harvey PH, Pagel MD. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am Nat*. 160:712–726.
- Gauthreaux SAJ. 1980. *Animal migration, orientation and navigation*. New York: Academic Press.
- Grafen A. 1989. The phylogenetic regression. *Philos Trans R Soc Lond B Biol Sci*. 326:119–157.
- Gunnarsson TG, Gill JA, Newton J, Potts PM, Sutherland WJ. 2005. Seasonal matching of habitat quality and fitness in a migratory bird. *Proc R Soc Lond B Biol Sci*. 272:2319–2323.
- Harvey PH, Pagel MD. 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Hearn PJ, Hare T, Schruben P, Sherrill D, LaMar C, Tsushima P. 2003. *Global GIS: global coverage DVD*. Digital data series DDS-62H. Alexandria (VA): AGI-USGS-ESRI.
- Helm B, Piersma T, Van-der-Jeugd H. 2006. Sociable schedules: interplay between avian seasonal and social behaviour. *Anim Behav*. 72:245–262.
- Hildén O. 1975. Breeding system of Temminck's stint *Calidris temminckii*. *Ornis Fenn*. 52:117–146.
- Hötter H, Lebedeva E, Tomkovich PS, Gromadzka J, Davidson NC, Evans J, Stroud DA, West RB. 1998. Migration and international conservation of waders. Research and conservation on north Asian, African and European flyways. *Int Wader Stud*. 10:1–500.
- Kleder M. 2004. Geodetic distance on WGS84 earth ellipsoid. MATLAB Central File Exchange. The Mathworks Inc. [Internet]. Natick, MA: The Mathworks, Inc. [cited 2006 March]. Available from: <http://www.mathworks.com/matlabcentral/fileexchange/loadFile.doobjectId=5379>.
- Kokko H. 1999. Competition for early arrival in migratory birds. *J Anim Ecol*. 68:940–950.
- Kokko H, Gunnarsson TG, Morrell LJ, Gill JA. 2006. Why do female migratory birds arrive later than males? *J Anim Ecol*. 75:1293–1303.
- Komar O, ÓShea BJ, Peterson AT, Navarro-Sigüenza AG. 2005. Evidence of latitudinal sexual segregation among migratory birds wintering in Mexico. *Auk*. 122:938–948.
- Lack D. 1968. *Ecological adaptations for breeding in birds*. London: Methuen and Co.
- Lank DB, Smith CM. 1987. Conditional lekking in ruff (*Philomachus pugnax*). *Behav Ecol Sociobiol*. 20:137–145.
- Lemans R, Cramer WP. 1991. The IASA database for mean monthly values of temperature, precipitation and cloudiness on a global terrestrial grid. Luxembourg (Austria): International Institute of Applied Systems Analyses. IASA Research Report RR-91-18.

- Ligon JD. 1999. The evolution of avian breeding systems. Oxford: Oxford University Press.
- Liker A, Székely T. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution*. 59:890–897.
- Maddison WP, Maddison DR. 2006. Mesquite: a modular system for evolutionary analysis. Version 1.12 ed [Internet]. [cited 2007 July]. Available from: <http://mesquiteproject.org/>.
- Mathot KJ, Smith BD, Elner RW. 2007. Latitudinal clines in food distribution correlate with differential migration in the western sandpiper. *Ecology*. 88:781–791.
- Milá B, Smith TB, Wayne RK. 2006. Postglacial population expansion drives the evolution of long-distance migration in a songbird. *Evolution*. 60:2403–2409.
- Møller AP. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behav Ecol Sociobiol*. 35:115–122.
- Morby YE, Ydenberg RC. 2001. Protandrous arrival timing to breeding areas: a review. *Ecol Lett*. 4:663–673.
- Myers JP. 1981. Cross-seasonal interactions in the evolution of sandpiper social systems. *Behav Ecol Sociobiol*. 8:195–202.
- Nebel S. 2005. Latitudinal clines in bill length and sex ratio in a migratory shorebird: a case of resource partitioning? *Acta Oecol*. 28: 33–38.
- O'Hara PD, Fernández G, Becerril F, de-la-Cueva H, Lank DB. 2005. Life history varies with migration distance in western sandpipers *Calidris mauri*. *J Avian Biol*. 36:191–202.
- Olson VA, Liker A, Freckleton RP, Székely T. 2008. Parental conflict in birds: comparative analyses of offspring development, ecology and mating opportunities. *Proc R Soc Lond B Biol Sci*. 275:301–307.
- Oring LW, Lank DB. 1986. Polyandry in spotted sandpipers: the impact of environment and experience. In: Rubenstein DI, Wrangham RW, editors. *Ecological aspects of social evolution: birds and mammals*. Princeton (NJ): Princeton University Press. p. 21–42.
- Oring LW, Lank DB. 2004. Sexual selection, arrival times, philopatry and site fidelity in the polyandrous spotted sandpiper. *Behav Ecol Sociobiol*. 10:185–191.
- Outlaw DC, Voelker G. 2006. Phylogenetic tests of hypotheses for the evolution of avian migration: a case study using the *Motacillidae*. *Auk*. 123:455–466.
- Pagel MD. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc R Soc Lond B Biol Sci*. 255:37–45.
- Pagel MD. 1997. Inferring evolutionary processes from phylogenies. *Zool Scripta*. 26:331–348.
- Pagel MD. 1999. Inferring the historical patterns of biological evolution. *Nature*. 401:877–884.
- Pagel MD, Meade A. 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am Nat*. 167:808–825.
- Pérez-Barbería FJ, Gordon IJ, Pagel MD. 2002. The origins of sexual dimorphism in body size in ungulates. *Evolution*. 56:1276–1285.
- Piersma T, Lindström Å. 2004. Migrating shorebirds as integrative sentinels of global environmental change. *Ibis*. 146(Suppl 1):61–69.
- Pitelka FA, Holmes RT, MacLean SFJ. 1974. Ecology and evolution of social organization in Arctic sandpipers. *Am Zool*. 14:185–204.
- R Development Core Team. 2005. R: a language and environment for statistical computing. R version 2.6.2 ed. Vienna (Austria): R Foundation for Statistical Computing.
- Rambaut A, Charleston M. 2002. TreeEdit: phylogenetic tree editor. v1.0 a10 ed [Internet]. Oxford. [cited 2007 July]. Available from: <http://tree.bio.ed.ac.uk/>.
- Reynolds JD. 1987. Mating system and nesting biology of the red-necked phalarope *Phalaropus lobatus*: what constrains polyandry? *Ibis*. 129:225–242.
- Reynolds JD. 1996. Animal breeding systems. *Trends Ecol Evol*. 11: 68–72.
- Reynolds JD, Colwell MA, Cooke F. 1986. Sexual selection and spring arrival times of red-necked and Wilson's phalaropes. *Behav Ecol Sociobiol*. 18:303–310.
- Reynolds JD, Goodwin NB, Freckleton RP. 2002. Evolutionary transitions in parental care and live bearing in vertebrates. *Philos Trans R Soc Lond B Biol Sci*. 357:269–281.
- Reynolds JD, Székely T. 1997. The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. *Behav Ecol*. 8: 126–134.
- Riede K. 2004. Global register of migratory species—from global to regional scales. Bonn (Germany): Federal Agency for Nature Conservation.
- Smith RJ, Moore FR. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behav Ecol Sociobiol*. 57:231–239.
- Spottiswoode CN, Møller AP. 2004. Extrapair paternity, migration, and breeding synchrony in birds. *Behav Ecol*. 15:41–57.
- Spottiswoode CN, Tøttrup AP, Coppack T. 2006. Sexual selection predicts advancement of avian spring migration in response to climate change. *Proc R Soc Lond B Biol Sci*. 273:3023–3029.
- Starck JM, Ricklefs RE. 1998. Patterns of development: the altricial-precocial spectrum. In: Starck JM, Ricklefs RE, editors. *Avian growth and development: evolution within the altricial-precocial spectrum*. Oxford: Oxford University Press. p. 3–30.
- Steadman DW. 2004. The paleoecology and fossil history of migratory landbirds. In: Greenberg R, Marra PP, editors. *Birds of two worlds: the ecology and evolution of migration*. London: Johns Hopkins University Press. p. 5–17.
- Stutchbury BJM, Morton ES, Trevor EP. 2004. Sex roles in migrants: extra-pair mating systems and winter social systems. In: Greenberg R, Marra PP, editors. *Birds of two worlds the ecology and evolution of migration*. London: Johns Hopkins University Press. p. 307–320.
- Székely T, Cuthill IC. 1999. Brood desertion in Kentish plover: the value of parental care. *Behav Ecol*. 10:191–197.
- Székely T, Reynolds JD. 1995. Evolutionary transitions in parental care in shorebirds. *Proc R Soc Lond B Biol Sci*. 262:57–64.
- Székely T, Thomas GH, Cuthill IC. 2006. Sexual conflict, ecology and breeding systems in shorebirds. *Bioscience*. 56:801–808.
- Thomas GH, Freckleton RP, Székely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proc R Soc Lond B Biol Sci*. 273:1619–1624.
- Thomas GH, Székely T. 2005. Evolutionary pathways in shorebird breeding systems: sexual conflict, parental care, and chick development. *Evolution*. 59:2222–2230.
- Thomas GH, Székely T, Reynolds JD. 2007. Sexual conflict and the evolution of breeding systems in shorebirds. *Adv Study Behav*. 37: 279–342.
- Thomas GH, Wills MA, Székely T. 2004. A supertree approach to shorebirds phylogeny. *BMC Evol Biol*. 4:28.
- Urano E. 1992. Early settling the following spring: a long-term benefit of mate desertion by male great reed warblers *Acrocephalus arundinaceus*. *Ibis*. 134:83–86.
- van de Kam J, Ens BJ, Piersma T, Zwarts L. 2004. Shorebirds. An illustrated behavioural ecology. Utrecht (The Netherlands): KNNV Publishers.
- Vicenty T. 1975. Direct and inverse solutions of geodesics on the ellipsoid with application of nested equations. *Surv Rev*. 22: 88–93.
- Wikelski M, Moskowitz D, Adelman JS, Cochran J, Wilcove DS, May ML. 2006. Simple rules guide dragonfly migration. *Biol Lett*. 2: 325–329.
- Wikelski M, Tarlow EM, Raim A, Diehl RH, Larkin RP, Visser GH. 2003. Costs of migration in free-flying songbirds. *Nature*. 423: 703–704.
- Williams TC, Webb T 3rd. 1996. Neotropical bird migration during the ice ages: orientation and ecology. *Auk*. 113:105–118.