Rapid courtship evolution in grouse (Tetraonidae): contrasting patterns of acceleration between the Eurasian and North American polygynous clades

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Sexual selection is thought to be a powerful diversifying force, based on large ornamental differences between sexually dimorphic species. This assumes that unornamented phenotypes represent evolution without sexual selection. If sexual selection is more powerful than other forms of selection, then two effects would be: rapid divergence of sexually selected traits and a correlation between these divergence rates and variance in mating success in the ornamented sex. I tested for these effects in grouse (Tetraonidae). For three species pairs, within and among polygynous clades, male courtship characters had significantly greater divergence than other characters. This was most pronounced for two species in *Tympanuchus*. In the Eurasian polygynous clade, relative courtship divergence gradually increased with nucleotide divergence, suggesting a less dramatic acceleration. Increase in relative courtship divergence was associated with mating systems having higher variance in male mating success. These results suggest that sexual selection has accelerated courtship evolution among grouse, although the microevolutionary details appear to vary among clades.

Keywords: sexual selection; lekking; mating system; rapid evolution; courtship behaviour; plumage ornaments

1. INTRODUCTION

Although it is well accepted that sexual selection has played a role in the evolution of courtship ornaments and behaviours (Andersson 1994), in most cases it is not known how rapidly these traits have evolved relative to those diversifying under other processes (i.e. genetic drift or diversifying natural selection). Because the rapid evolution of sexually selected traits may lead to reproductive isolation (Fisher 1930; West-Eberhard 1983; Coyne & Orr 2004; Mead & Arnold 2004), we can begin to explore the role of sexual selection in speciation by first assessing its effect on evolutionary rate.

To begin this assessment, it would be helpful to have some idea of which traits are being targeted by sexual selection. This may be complicated for multiply ornamented species. Several observations of mating preferences in birds suggest that individual traits in a courtship repertoire evolve by sexual selection on the repertoire itself. For example, females of zebra finch (*Poephila guttata*) and rock ptarmigan (*Lagopus mutus*) may have a preference for males wearing red leg bands owing to a more general preference for red markings (Burley 1981; Brodsky 1988). Another complication to identifying targets of sexual selection may come from trait interactions. Traits may evolve in a concerted fashion (Shutler & Weatherhead 1990; Omland & Lanyon 2000) due to adaptive, developmental or genetic correlations among traits. Also, as noted by Darwin (1871), some traits may serve to emphasize other traits (e.g. rattling or

repeated fanning of the tail may draw attention to tail ornaments, or vice versa). For studies above the species level, an additional complication to identifying targets of selection is that there may be different targets of sexual selection among species (Hoglund 1989; Shutler & Weatherhead 1990).

Despite these potential complications, it is possible to test the hypothesis that sexual selection causes rapid evolution of courtship repertoires by simply comparing the rates of divergence among two classes of traits: courtship and non-courtship. Traits that are potential courtship signals may have diversified among lineages by a combination of stabilizing and diversifying natural selection, sexual selection and random genetic drift. Some traits (e.g. average clutch size) are not potential courtship signals, therefore sexual selection is absent from the list of forces acting on their diversification. If we assume that genetic drift and natural selection will affect the courtship and non-courtship trait classes equally, then we can attribute different divergence rates between the trait classes to sexual selection. A higher rate of divergence among courtship characters may manifest in two ways: (i) if multiple courtship traits have accumulated via sexual selection (Pomiankowski & Iwasa 1993, 1998), divergence among courtship traits should be greater than divergence among non-courtship traits and (ii) the divergence among courtship characters relative to non-courtship characters should be larger for older divergences.

The ideal scenario for testing these hypotheses is a set of species in a phylogenetic framework that differ in the strength of sexual selection they have historically experienced. A clade with variable mating systems is likely to be suitable. Mating systems causing higher variance in male

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breeding success should have higher evolutionary rates for sexually selected traits (Lande 1981; Shuster & Wade 2003). Monogamous species are expected to be associated with the lowest sexually selected rates, though this may still be rapid when compared with the rates under natural selection (Kirkpatrick *et al*. 1990). Depending on the sex ratio in the population, polygamy should introduce variance in breeding success of the competing sex (Darwin 1871; Fisher 1930; Lande 1981); therefore rates due to sexual selection should tend to be higher for polygynous species when compared with monogamous species. Polygyny with lekking (hereinafter, 'lekking') is expected to be associated with the highest evolutionary rates. With lekking, many potential mates are available at a predictable place and time which increases the number of males each female can assess. Lekking also allows females to assess both long-distance signals (e.g. vocalizations) and traits that can only be inspected at close range, and this may facilitate the evolution of multiple, rapidly evolving traits (Pomiankowski & Iwasa 1993).

Because species of grouse and ptarmigan (Tetraonidae; hereinafter 'grouse') vary widely with respect to mating system, they provide an opportunity to test the above hypotheses using the evolutionary rates of complex courtship repertoires. Grouse are galliform birds known for their complex courtship rituals and great diversity in courtship plumage (Darwin 1871; Johnsgard 1983; Pomiankowski & Iwasa 1993). Grouse species inhabit forests and tundra of Eurasia, and in North America they inhabit forests, tundra, grasslands and desert scrub. Grouse courtship repertoires include many elements (Johnsgard 1983), such as the inflation of coloured throat sacs that act as resonating chambers for low-frequency vocalizations (e.g. *Tympanuchus* spp.), long flight displays of ptarmigan (*Lagopus* spp.), elongate rectrices in sage grouse (*Centrocercus* spp.), beard displays (*Tetrix* spp.), throat plumage resembling a white necklace (*Falcipennis* spp.) and rotational head-shaking (*Bonasia* spp.). These and other morphological and behavioural elements are combined into complex courtship repertoires which vary widely among species.

In the present study, I test the following hypotheses. First, the rate of courtship divergence has been greater than non-courtship divergence in some grouse. Second, the rate of courtship divergence is increased in mating systems that have greater variance in male mating success. These hypotheses were tested by measuring the relative divergence of discretely coded courtship and non-courtship characters.

2. MATERIAL AND METHODS

I scored 25 characters of male courtship plumage, 19 characters of male courtship behaviour and 15 non-courtship characters in grouse (see electronic supplementary material A), for a total of 59 characters from various natural history accounts (Johnsgard 1983; Boag & Schroeder 1992; Braun *et al*. 1993; Holder & Montgomerie 1993; Connelly *et al*. 1998; Hannon *et al*. 1998; Schroeder *et al*. 1999; Rusch *et al*. 2000; Zwickel & Bendell 2005). Characters were selected based on whether there was sufficient natural history information to assess their presence or absence among species, and whether they appeared to vary independently among species. All aspects of male courtship plumage were considered as potential courtship signals. Several behaviours that appear to be homologous

function in courtship for some species, but are used in agonistic interactions between males in other species (Johnsgard 1983); because these are potential targets of sexual selection, these behaviours were classified as characters of courtship. Non-courtship characters included external aspects of natal down and eggs, habitat preference, clutch size and incubation time. *Centrocercus minimus* (Young *et al*. 2000) was not considered separately from the greater sage grouse (*Centrocercus urophasianus*) in this analysis due to a lack of comparable natural history information for that species.

For both courtship and non-courtship characters, the proportion of characters that were polymorphic, the proportion of characters having missing data and the average consistency index (CI) were calculated using PAUP* 4.0b10 (Swofford 1998) and the phylogeny of Tetraonidae (Drovetski 2002). Only phylogenetically informative characters were considered in the CI calculations (Sanderson & Donoghue 1989). For the courtship characters, these statistics were also calculated for plumage and behavioural characters separately.

Genetic distances were calculated from nucleotide sequence data for Domain I of the mitochondrial control region (CR-I), and corrected for unobserved substitutions using a model of nucleotide substitution and maximum likelihood (ML) estimation. The likelihood ratio criterion was used to select a model of nucleotide substitution in MODELTEST v. 3.7 (Posada & Crandall 1998). The CR-I alignment of Drovetski (2002) was downloaded directly from GenBank (included sequence accession nos.: AF532415, AF532418, AF532421, AF532423, AF532426, AF532430, AF532432, AF532433, AF532435, AF532437, AF532440, AF532445, AF532450, AF532455, AF532457, AF532460, AF532462, AF532465). Because mitochondrial haplotypes have not sorted among the recently derived species of prairie grouse (Ellsworth *et al*. 1994; Spaulding *et al*. 2006), genetic distances between pairs of these species were recalculated as the average CR-I distance (Nei & Li 1979) using the sequence alignment of Spaulding *et al*. (2006). Nucleotide substitution models were chosen separately for each alignment. ML estimation of substitution model parameters and CR-I distances were done using PAUP* v. 4.0b10 (Swofford 1998).

Pairwise species divergences for courtship and non-courtship characters were calculated as the minimum number of state transformations required to explain the differences between two taxa. For binary and unordered characters, this is simply the proportion of characters differing between the taxa; for ordered characters (Wilkinson 1992), a transformation through an intermediate state means an additional difference is added to the proportion calculation. Some data (6.1%) were 'missing' due to lack of information. When character data was missing for a pair of taxa, that character was excluded from the distance calculation for that pair. Distance calculations were done using the SAVEDIST command in PAUP* v. 4.0b10 (Swofford 1998).

I used two tests of the hypothesis that courtship divergence has been more rapid than non-courtship divergence in some grouse. The first test was used to find instances in which pairs of species have accumulated greater courtship divergence relative to non-courtship divergence. For each pair of species, the measure of increased courtship divergence, D_{court}, was the difference between the divergence in courtship characters and the divergence in non-courtship characters. I tested for significantly large D_{court} values with a simple permutation scheme. I randomly assigned characters among the courtship

Table 1. Statistics for the phenotypic characters classes.

	number of characters	proportion polymorphic	proportion missing	number of steps in tree	CI
courtship	44	0.013	0.066	125	0.552
courtship plumage	25	0.014	0.035	70	0.688
courtship behaviour	19	0.012	0.105	55	0.346
non-courtship	15	0.086	0.051	66	0.439

and non-courtship classes, and recalculated D_{court} for the randomized data to obtain D_{court}^*; 1000 randomizations of the data were used to generate a distribution for D_{court}^*. For each species pair, the *p*-value was estimated as the proportion of the 1000 D_{court}^* values that were greater than the observed D_{court} value. I report results from the permutation analyses where character class size was allowed to vary, though results were similar when character class size was held constant.

If courtship divergence has been more rapid than non-courtship divergence, D_{court} should be greater for older divergences. Furthermore, the above test for significantly large D_{court} values may depend on divergence time. For these reasons, I also tested for a correlation between D_{court} and genetic distance. A potentially confounding factor in this test is sympatry, which may affect the rate at which prezygotic isolation evolves (Coyne & Orr 1989, 1997), and this is likely to involve courtship traits. Therefore, I used a partial Mantel test (Smouse *et al.* 1986) on pairwise species matrices for D_{court}, genetic distance and sympatry. The sympatry matrix was constructed so that cells for allopatric species pairs contained a '0', while cells for sympatric species pairs contained a '1'. Sympatry and allopatry were determined using 'historical' species ranges from Johnsgard (1983). The Mantel tests were conducted in ARLEQUIN 2.0 (Schneider *et al.* 2000) using 1000 data randomizations to generate null distributions for estimating *p*-values.

To test the hypothesis that courtship divergence rate is greater in mating systems having greater variance in male mating success, I assigned mating system scores to each species, based on descriptions of Johnsgard (1983). The mating system scores, ordered by increasing potential for variance in male breeding success, were as follows: '1' for monogamy; '2' for polygyny; and '3' for lekking. Although *L. mutus* and *L. lagopus* are primarily monogamous, they are known to exhibit polygyny in some populations (Holder & Montgomerie 1993; Hannon *et al.* 1998); therefore, I assigned a score of '1.5' to each of these species. Mating system scores in the pairwise matrix were simply average scores for the pairs. D_{court} was not used in this test because it is expected to vary with time since the most recent, common ancestor of each pair. Instead, a ratio, R_{court}, of courtship divergence to non-courtship divergence was used. I tested for a correlation between R_{court}, mating system and sympatry using a partial Mantel test, and a null distribution generated from 1000 data randomizations. *Bonasia sewerzowi* and *Falcipennis falcipennis* were omitted from this test due to lack of mating system information.

Finally, I tested the hypothesis of rapid divergence for courtship behaviour and courtship plumage separately for the mostly Eurasian polygynous clade. The partial Mantel test was used, as above, to test for a correlation between D_{court} and genetic distance; however, for these tests, D_{court} was calculated using either plumage or behavioural characters in the courtship class.

3. RESULTS

The CI of the courtship characters was higher than for non-courtship characters, largely due to higher consistency among the courtship plumage characters (table 1). The CI for courtship plumage characters was comparable to CI for morphological data used in other species-level systematic studies (Sanderson & Donoghue 1989), whereas the CI for courtship behaviour was nearly half the average value found in other studies (de Queiroz & Wimberger 1993). Although CI can be inflated in datasets with polymorphic or missing data, this does not appear to have affected the CI estimates in table 1. The three data types with similarly low levels of polymorphism are also those that had the highest and the lowest CI, while the non-courtship characters had a much higher level of polymorphism, but only a moderate CI.

For use in the ML estimates of CR-I distances, a transversional model of nucleotide substitution, with among-site rate parameters (TVMef+I+G, see Posada & Crandall 1998), was selected by the likelihood ratio criterion. This time-reversible model allows different rates for all transversion substitutions, but a single rate for transitions. The model also allows for unequal equilibrium base frequencies, and accounts for among-site rate variation by assuming a proportion of invariant sites and discrete classes of rates along a gamma distribution of rates for the remaining sites (Yang 1994).

Courtship divergence was significantly greater than non-courtship divergence for three species pairs within and between the two polygynous lekking clades of grouse (figure 1). None of the species pairs with significant D_{court} values was in either of the clades where the monogamy is prevalent (*Bonasia* and *Lagopus*). Although the pair *L. lagopus*/*L. mutus* had $D_{court} > 0$, both are known to exhibit polygyny in some populations. Among species pairings between *Falcipennis* and the dark Eurasian species of *Tetrix* and *Lyrurus*, only *Lyrurus tetrix*/*F. falcipennis* had a significantly large D_{court} value. This pair also had the largest ML divergence, so it is possible that the other species pairs may have diverged rapidly, but for a shorter time. Among the three species pairs that had significantly large D_{court} values, the species of more distantly related pairs differed in more courtship characters. For example, the recently diverged pair, *Tympanuchus pallidicinctus*/*Tympanuchus phasianellus*, differed by only seven courtship characters, whereas the more genetically divergent pair, *Ly. tetrix*/*F. falcipennis*, differed by 22 courtship characters (electronic supplementary material B).

When considering all grouse species, there was no evidence that the difference between courtship and non-courtship divergence (D_{court}) was greater for more genetically distant pairs ($r_{Y1} = -0.051$, $p = 0.684$), even when accounting for sympatry ($r_{Y1\_2} = -0.060$, $p = 0.721$), and
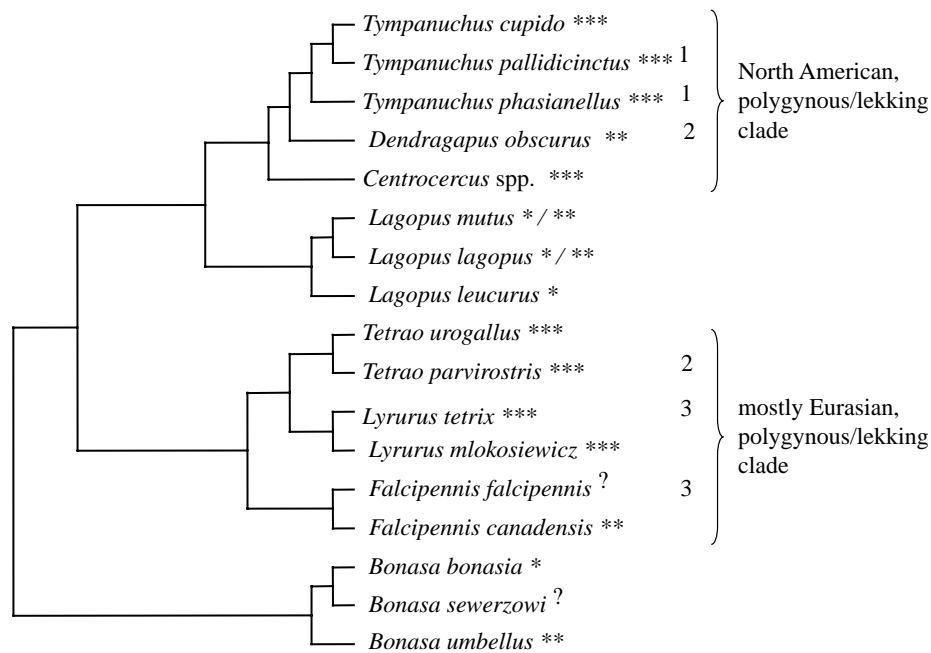
Figure 1. Phylogeny of Drovetski (2002). Numbers to the right of the taxon names identify the species pairs that had significantly large D_{court} values ($p=0.042$ for pair number '1', $p=0.045$ for '2' and $p=0.025$ for '3'). Mating systems of the species are indicated as follows: asterisks, monogamous; double asterisks, polygynous; triple asterisks, polygynous/lekking; and question mark, unknown.

neither genetic distance nor sympatry explained more than 1% of the variation in D_{court}.

The partial Mantel test indicated a marginally significant correlation between mating system and the ratio (R_{court}) of courtship to non-courtship divergence (figure 2a), but the relationship between mating system and courtship divergence appeared a little more complex when considering divergence over time. If the correlation between R_{court} and mating system is due to a rapid rate in courtship divergence, then there should be a trend of increasing D_{court} values over time for lekking species. However, this trend was absent figure 2b. Among polygynous and lekking species, the trend differed between the North American and Eurasian clades: there was a positive correlation between D_{court} and time for the polygynous Eurasian clade, but the trend was absent for the North American polygynous/lekking clade (figure 2c,d). When considering plumage and behaviour separately for the Eurasian polygynous/lekking clade, D_{court} was positively correlated with genetic distance only for the plumage characters; the trend was positive, but non-significant for the behavioural data (figure 2e,f).

The effect of including sympatry in the analyses was variable. In two of the Mantel tests, sympatry explained a greater portion of the variation in D_{court} than did genetic distance (figure 2b,d). The test with lekking species was the only one in which sympatry was found to be correlated with D_{court} ($r_{Y2}=0.400$, $p=0.010$). In three other Mantel tests, holding sympatry constant slightly increased an already significant correlation between D_{court} and genetic distance (figure 2a,c,e).

4. DISCUSSION

Darwin (1871) considered sexual selection to be a cause of rapid evolution and grouse to be an example of how sexual selection can be driven by variation in mating success. This study is a direct test of these ideas using

knowledge of grouse natural history, and measures of phylogenetic relationships and genetic divergence based on molecular data.

The results presented here support the hypothesis of rapid courtship divergence in grouse. First, the difference between divergence in courtship and non-courtship characters (D_{court}) was found to be significantly large for one species pair within each of the two polygynous/lekking clades, and also for one pair between these clades. Although D_{court} values were not significantly large for many other polygynous/lekking species pairs, courtship divergence may still have been rapid in these cases, but not for long enough to be detected by this test. This can be visualized by thinking of the time required in a sprinting race before it is clear who is travelling at the greater speed. The second result supporting rapid courtship evolution is that, in the mostly Eurasian polygynous/lekking clade, D_{court} was positively correlated with genetic distance. This suggests that as character divergence proceeded in time, courtship divergence was overtaking or pulling away from non-courtship divergence. It might seem counter-intuitive that courtship divergence would have to overtake non-courtship divergence, if courtship traits are to be implicated in initiating the divergence process. However, reproductive isolation by sexual selection may entail quantitative differences in traits that are not detectable by the methods used here. Also, these data are only a sample of grouse characters, and courtship traits other than those sampled may have initiated reproductive isolation among some species. Finally, it should be noted that, since non-courtship characters were fewer (15 out of the 59 characters), each difference in a non-courtship character increases non-courtship divergence by 7% versus 2% courtship divergence for each courtship difference. Thus, four courtship differences are required before courtship divergence is greater than a single non-courtship difference.
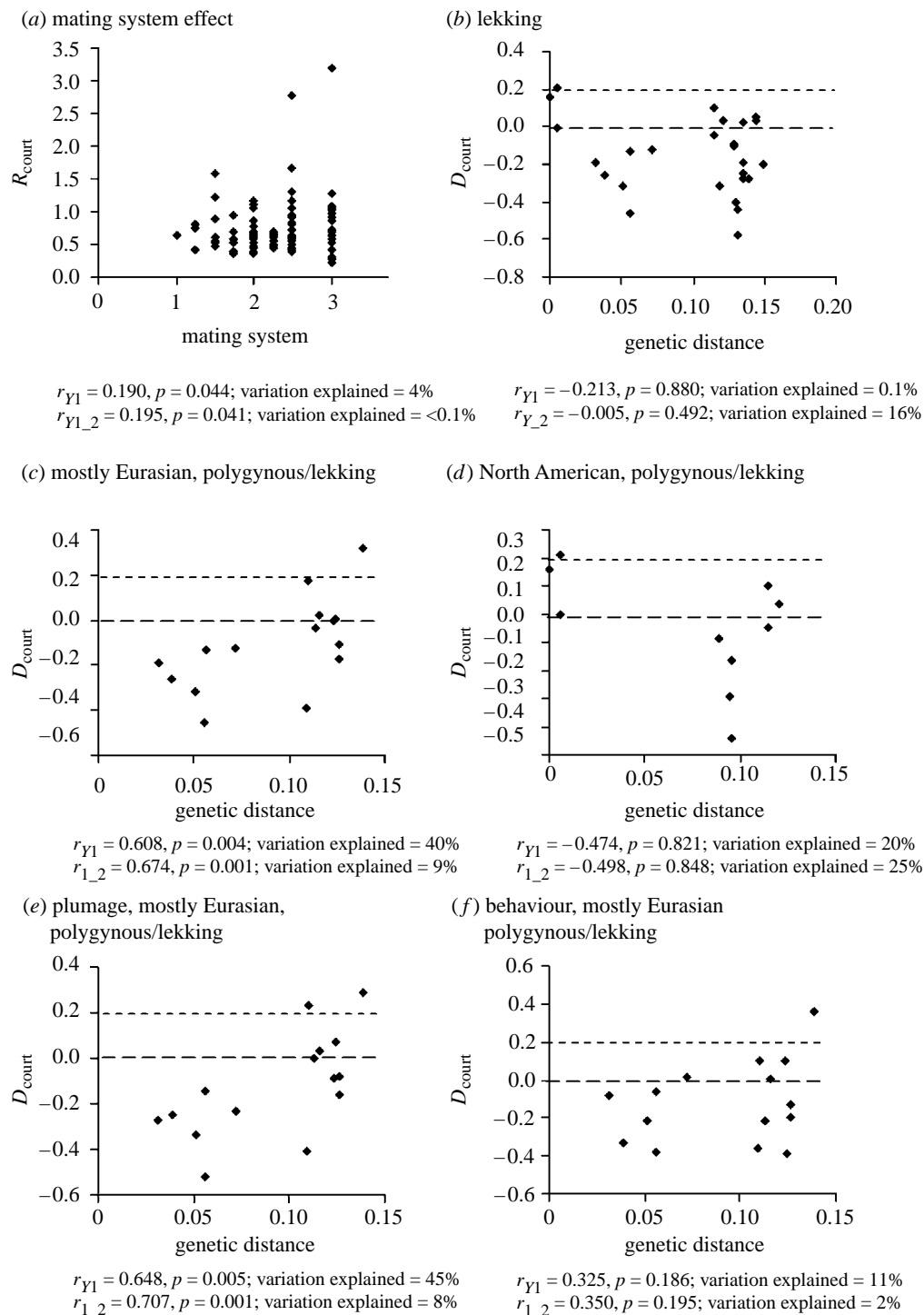
Figure 2. Plots of relative courtship divergence with mating system and genetic distance for species pairs. Statistics from the partial Mantel tests are shown below each plot: the correlation coefficient, p-value and the per cent explained variation are shown on the first line; on the second line, the effect of holding sympatry constant is shown by the partial correlation coefficient, p-value, and the increase in variation explained. R_{court} plot (a) showing how the ratio of courtship to non-courtship divergence changes with mating system. Mating system scores for each species were as follows: 1, monogamy; 2, polygyny; 3, lekking. Mating systems scores were averaged for each species pair. D_{court} plots show how the difference between courtship and non-courtship divergence changes with genetic distance for species pairs that are lekking (b), of the mostly Eurasian polygynous/lekking clade (c) or of the North American polygynous/lekking clade (d). D_{court} plots for the mostly Eurasian polygynous/lekking clade are also shown where courtship divergence was measured only for plumage (e) or behaviour (f). Positive values of D_{court}, above long-dashed line, indicate courtship divergence exceeding non-courtship divergence. D_{court} values above the short-dashed line are cases where the greater divergence of courtship characters were significant.

The results of this study are also consistent with the theoretical expectation that mating systems that increase variance in male breeding success also increase the rate of courtship evolution. First, none of the three species pairs having significantly large D_{court} values included the species in which monogamy is prevalent. Second, mating system score was positively correlated with the ratio of courtship to non-courtship divergence (R_{court}).

Sympatry appears to have had some effect on the rate of courtship evolution in grouse, because a significant

correlation with sympatry was found in the test for lekking species. Among the two polygynous/lekking clades, there appeared to be a relatively stronger effect of sympatry in the North American clade when compared with the Eurasian clade (figure 2c,d), possibly due to the large D_{court} values observed between *T. phasianellus* and the other lekking species in this clade with which it was historically sympatric (*Tympanuchus cupido*, *T. pallidicinctus* and *C. urophasianus*). Although D_{court} is not meant to be a measure of prezygotic isolation, a correlation of D_{court} with sympatry suggests reinforcement of speciation by sexual selection (Coyne & Orr 2004). While it is possible that reinforcement has played a role in diversification in the North American polygynous/lekking clade, these results show less support for reinforcement in the Eurasian polygynous/lekking clade.

Character divergences among the North American prairie grouse (*Tympanuchus* spp.) showed a high D_{court} value at low genetic distances, suggesting extremely rapid divergence reminiscent of Fisher's 'runaway' traits appearing instantaneously in geologic time. This was remarked upon by Ellsworth *et al.* (1994) when their mitochondrial haplotype and allozyme data did not allow them to distinguish between these morphologically and behaviourally distinct species. Spaulding *et al.* (2006) questioned the rapidity of evolutionary change in these sexually selected traits when they found that *T. phasianellus* was readily distinguished from *T. cupido* with hypervariable nuclear markers, and that the lack of lineage sorting for the mitochondrial haplotypes may have been partly due to a recent range expansion for all *Tympanuchus*. The present study supports the conclusion of Ellsworth *et al.* (1994) that sexual selection has caused rapid evolution in these species, and the comparison with evolutionary rates in other grouse species shows the rate courtship evolution in *Tympanuchus* to be particularly rapid.

The contrasting pattern for the mostly Eurasian, polygynous clade, in which the acceleration of courtship evolution was less extreme, does not necessarily indicate an absence of Fisherian sexual selection. Individual traits within the courtship repertoires of these species may have undergone rapid quantitative change, but may have also alternated from periods of increase to periods of decrease (Mead & Arnold 2004). Such a process need not cause 'runaway' divergence of courtship repertoires, though it may accelerate repertoire divergence to some degree. In any case, the contrasting patterns of rapid courtship evolution suggest different microevolutionary processes.

The courtship repertoires studied here include characters of both behaviour and morphology. This may be a matter of concern since the inheritance of behavioural characters may have a cultural component (e.g. song learning and imprinting in oscine passerine birds; Grant & Grant 1996), and it is not clear whether such traits can evolve by the Fisherian process. The correlation between D_{court} and genetic distance in the mostly Eurasian polygynous/lekking clade was due to traits of plumage rather than behaviour (figure 2e,f). However, this may not be due to a slower rate of evolution of courtship behaviour. Characters of courtship behaviour appear to be quite homoplastic in grouse, particularly among polygynous and lekking species; in other studies, behavioural characters generally are not more homoplastic than are characters of morphology (de Queiroz & Wimberger 1993). This suggests that the lack of correlation between D_{court} and courtship behaviour

for this clade may be due to convergence, limiting the rate of behavioural divergence. In fact, 10 out of the 19 behavioural characters (53%) were found to be convergent within the Eurasian polygynous/lekking clade, when compared with only 7 out of the 25 plumage characters (28%). One possible explanation is that there may be some limitation on the range of courtship behaviours grouse can evolve. Most cases of convergence in courtship behaviour were between, rather than within, the two polygynous/lekking clades, so it may be that convergence tended to occur between species for which reproductive isolation was better established. Another possibility is that the order in which display behaviours are performed may be an important component of the courtship repertoire, and not including this in the analysis could have reduced the measure of divergence in courtship behaviour.

Many mechanisms have been described in which traits of courtship may evolve rapidly (see reviews by Andersson 1994 and Mead & Arnold 2004). Congruence in the dynamics of several Fisherian-based models suggests that they may describe processes that occur in nature (Mead & Arnold 2004). Rapid courtship evolution in grouse may be due to one or more of these processes or perhaps some mechanism yet to be described. The purpose of this study was to test hypotheses relevant to the role of sexual selection in speciation without reference to any specific model of sexual selection. In future studies, comparisons of quantitative traits in courtship and non-courtship classes would be helpful for better understanding of the evolution of courtship repertoires. A method that may be useful, and analogous to the one used in this study, would measure trait variances within and among populations, and compare the strength of population structure for courtship, non-courtship and neutral traits. Other authors have begun finding evidence for greater strength of sexual selection, relative to natural selection, using measures from components of fitness (Hoekstra *et al.* 2001; Svensson *et al.* 2004, 2006). Studies of realized population divergence in heritable variation would complement such analyses. Recent studies suggest that variation in acoustic and behavioural courtship traits is greater among than within species of *Centrocercus* (Young *et al.* 1994; Taylor & Young 2006), and, as in *Tympanuchus*, the relatively small genetic divergence among species suggests these differences have arisen rapidly (Young *et al.* 2000). Although sexual selection is clearly important in the evolution of highly ornamented species, it would be interesting to investigate the relative importance of sexual selection, natural selection and random genetic drift in speciation for groups with high and low levels of ornamentation. Studies of both population divergence and additional macroevolutionary studies, like the one presented here, can be used to study the variation in sexual selection's influence in the origins of sexual species.

REFERENCES

Andersson, M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.

Boag, D. A. & Schroeder, M. A. 1992 Spruce grouse (*Dendragapus canadensis*). In *Birds of North America*,

vol. 5 (eds A. Pool & F. Gill). Philadelphia, PA: Birds of North America, Inc. (doi:10.2173/bna.5)

Braun, C. E., Martin, K. & Robb, L. A. 1993 White-tailed ptarmigan (*Lagopus leucurus*). In *Birds of North America*, vol. 68 (eds A. Pool & F. Gill). Philadelphia, PA: Birds of North America, Inc. (doi:10.2173/bna.68)

Brodsky, L. M. 1988 Ornament size influences mating success in male rock ptarmigan. *Anim. Behav.* **36**, 662–667. (doi:10.1016/S0003-3472(88)80148-9)

Burley, N. 1981 Sex ratio manipulation and selection for attractiveness. *Science* **211**, 721–722. (doi:10.1126/science.211.4483.721)

Connelly, J. W., Gratson, M. W. & Reese, K. P. 1998 Sharp-tailed grouse (*Tympanuchus phasianellus*). In *Birds of North America*, vol. 354 (eds A. Pool & F. Gill). Washington, DC: American Ornithologists' Union. (doi:10.2173/bna.354)

Coyne, J. A. & Orr, H. A. 1989 Patterns of speciation in *Drosophila*. *Evolution* **43**, 362–381. (doi:10.2307/2409213)

Coyne, J. A. & Orr, H. A. 1997 "Patterns of speciation in *Drosophila*" revisited. *Evolution* **51**, 295–303. (doi:10.2307/2410984)

Coyne, J. A. & Orr, H. A. 2004 *Speciation*. Sunderland, MA: Sinauer Associates.

Darwin, C. 1871 (1874) The descent of man and selection in relation to sex. Akron, OH: The Werner Company.

de Queiroz, A. & Wimberger, P. H. 1993 The usefulness of behavior for phylogeny estimation: levels of homoplasy in behavioral and morphological characters. *Evolution* **47**, 46–60. (doi:10.2307/2410117)

Drovetski, S. 2002 Molecular phylogeny of grouse: individual and combined performance of W-linked, autosomal, and mitochondrial loci. *Syst. Biol.* **51**, 930–945. (doi:10.1080/10635150290102500)

Ellsworth, D. L., Honeycutt, R. L., Silvy, N. J., Rittenhouse, K. D. & Smith, M. H. 1994 Mitochondrial-DNA and nuclear-gene differentiation in North-American prairie grouse (Genus *Tympanuchus*). *Auk* **111**, 661–671.

Fisher, R. A. 1930 *The genetical theory of natural selection*. New York, NY: Dover Publications.

Grant, B. R. & Grant, P. R. 1996 Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution* **50**, 2471–2487. (doi:10.2307/2410714)

Hannon, S. J., Eason, P. K. & Martin, K. 1998 Willow ptarmigan (*Lagopus lagopus*). In *Birds of North America*, vol. 369 (eds A. Pool & F. Gill). Philadelphia, PA: Birds of North America, Inc. (doi:10.2173/bna.369)

Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hoang, A., Hill, C. E., Beerli, P. & Kingsolver, J. G. 2001 Strength and tempo of directional selection in the wild. *Proc. Natl Acad. Sci. USA* **98**, 9157–9160. (doi:10.1073/pnas.161281098)

Hoglund, J. 1989 Size and plumage dimorphism in lek-breeding birds: a comparative analysis. *Am. Nat.* **134**, 72–87. (doi:10.1086/284966)

Holder, K. & Montgomerie, R. 1993 Rock Ptarmigan (*Lagopus mutus*). In *Birds of North America*, vol. 51 (eds A. Pool & F. Gill). Philadelphia, PA: Birds of North America, Inc. (doi:10.2173/bna.51)

Johnsgard, P. A. 1983 *The grouse of the world*. Lincoln, NE: University of Nebraska Press.

Kirkpatrick, M., Price, T. & Arnold, S. J. 1990 The Darwin–Fisher theory of sexual selection in monogamous birds. *Evolution* **44**, 180–193. (doi:10.2307/2409533)

Lande, R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**, 3721–3725. (doi:10.1073/pnas.78.6.3721)

Mead, L. S. & Arnold, S. J. 2004 Quantitative genetic models of sexual selection. *Trends Ecol. Evol.* **19**, 264–271. (doi:10.1016/j.tree.2004.03.003)

Nei, M. & Li, W. H. 1979 Mathematical model for studying genetic variation in terms of restriction nucleases. *Proc. Natl Acad. Sci. USA* **76**, 5269–5273. (doi:10.1073/pnas.76.10.5269)

Omland, K. E. & Lanyon, S. M. 2000 Reconstructing plumage evolution in orioles (Icterus): repeated convergence and reversal in patterns. *Evolution* **54**, 2119–2133. (doi:10.1554/0014-3820(2000)054[2119:RPEIOI]2.0.CO;2)

Pomiankowski, A. & Iwasa, Y. 1993 Evolution of multiple sexual preferences by Fisher's runaway process of sexual selection. *Proc. R. Soc. B* **253**, 173–181. (doi:10.1098/rspb.1993.0099)

Pomiankowski, A. & Iwasa, Y. 1998 Runaway ornament diversity caused by Fisherian sexual selection. *Proc. Natl Acad. Sci. USA* **95**, 5106–5111. (doi:10.1073/pnas.95.9.5106)

Posada, D. & Crandall, K. A. 1998 Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**, 817–818. (doi:10.1093/bioinformatics/14.9.817)

Rusch, D. H., Destefano, S., Reynolds, M. C. & Lauten, D. 2000 Ruffed grouse (*Dendragapus obscurus*). In *Birds of North America*, vol. 515 (eds A. Pool & F. Gill). Philadelphia, PA: Birds of North America, Inc. (doi:10.2173/bna.515).

Sanderson, M. J. & Donoghue, M. J. 1989 Patterns of variation in levels of homoplasy. *Evolution* **43**, 1781–1795. (doi:10.2307/2409392)

Schneider, S., Roessli, D. & Excoffier, L. 2000 *Arlequin ver. 2.000: a software for population genetics data analysis*. Geneva, Switzerland: Genetics and Biometry Laboratory.

Schroeder, M. A., Young, J. R. & Braun, C. E. 1999 Sage grouse (*Centrocercus urophasianus*). In *Birds of North America*, vol. 425 (eds A. Pool & F. Gill). Philadelphia, PA: The Birds of North America, Inc. (doi:10.2173/bna.425)

Shuster, S. M. & Wade, M. J. 2003 *Mating systems and strategies*. Princeton, NJ: Princeton University Press.

Shutler, D. & Weatherhead, P. J. 1990 Targets of sexual selection song and plumage of wood warblers. *Evolution* **44**, 1967–1977. (doi:10.2307/2409607)

Smouse, P. E., Long, J. C. & Sokal, R. R. 1986 Multiple regression and correlational extensions of the Mantel test of matrix correspondence. *Syst. Zool.* **35**, 627–632. (doi:10.2307/2413122)

Spaulding, A. W., Mock, K. E., Schroeder, M. A. & Warheit, K. I. 2006 Recency, range expansion, and unsorted lineages: implications for interpreting neutral genetic variation in the sharp-tailed grouse (*Tympanuchus phasianellus*). *Mol. Ecol.* **15**, 2317–2332. (doi:10.1111/j.1365-294X.2006.02935.x)

Svensson, E. I., Kristoffersen, L., Oskarsson, K. & Bensch, S. 2004 Molecular population divergence and sexual selection on morphology in the banded demoiselle (*Calopteryx splendens*). *Heredity* **93**, 423–433. (doi:10.1038/sj.hdy.6800519)

Svensson, E. I., Eroukhmanoff, F. & Friberg, M. 2006 Effects of natural and sexual selection on adaptive population divergence and premating isolation in a damselfly. *Evolution* 1242–1253. (doi:10.1554/06-036.1)

Swofford, D. L. 1998 *PAUP*. Phylogenetic analysis using parsimony (* and other methods)*. Sunderland, MA: Sinauer Associates.

Taylor, S. E. & Young, J. R. 2006 A comparative behavioral study of three Greater Sage-Grouse populations. *Wilson J. Ornithol.* **118**, 36–41. (doi:10.1676/1559-4491(2006)118[0036:ACBSOT]2.0.CO;2)

West-Eberhard, M. J. 1983 Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**, 155–183. (doi:10.1086/413215)

Wilkinson, M. 1992 Ordered versus unordered characters. *Cladistics* **8**, 375–385. (doi:10.1111/j.1096-0031.1992.tb00079.x)

Yang, Z. 1994 Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. *J. Mol. Evol.* **39**, 306–314. (doi:10.1007/BF00160154)

Young, J. R., Hupp, J. W., Bradbury, J. W. & Braun, C. E. 1994 Phenotypic divergence of secondary sexual traits among sage grouse, *Centrocercus urophasianus*, populations. *Anim. Behav.* **47**, 1353–1362. (doi:10.1006/anbe.1994. 1183)

Young, J. R., Braun, C. E., Oyler-McCance, S. J., Hupp, J. W. & Quinn, T. W. 2000 A new species of sage-grouse (*Phasianidae*: *Centrocercus*) from southwestern Colorado. *Wilson Bull.* **112**, 445–453. (doi:10.1676/0043-5643(2000) 112[0445:ANSOSG]2.0.CO;2)

Zwickel, F. C. & Bendell, J. F. 2005 Blue Grouse (*Dendragapus obscurus*). In *Birds of North America*, vol. 15 (ed. A. Pool). Ithaca, NY: Cornell Laboratory of Ornithology. (doi:10.2173/bna.15).