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A classification of the grouse (Aves: Tetraoninae) based on mitochondrial DNA sequences

R.J. Gutiérrez, George F. Barrowclough & Jeffrey G. Groth

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We propose a new classification of the grouse that brings their taxonomy into agreement with our molecular phylogenetic studies. Our analyses provide, for the first time, a robust estimate of the evolutionary history of these birds. These analyses are based on aligned sequences of 3,809 basepairs of five complete mitochondrial genes. Our classification does not require novel genera and generally results in the maintenance of accepted generic names. Only two monotypic genera are required. We recognize the grouse as a subfamily, Tetraoninae, within the family Phasianidae. We recognize three tribes; these include a tribe (Bonasini, a new taxon) for the ruffed grouse *Bonasa umbellus*, a tribe (Tetrastini, a new rank) for hazel hens in the genus *Tetrastes*, and a tribe (Tetraonini, a new rank) for all the remaining species. We divide this last, derived tribe into five subtribes that correspond to 1) Falcipennina (a new taxon) for the sharp-winged grouse *Falcipennis falcipennis*, 2) Canachitina (a new taxon) for the New World spruce grouse in the genus *Canachites*, 3) Tetraonina (a new rank) for the capercaillies and black grouse in the genera *Tetrao* and *Lyrurus*, respectively, 4) Centrocercina (a new taxon) for the New World prairie and forest grouse in the genera *Tympanuchus, Centrocercus* and *Dendragapus*, and 5) Lagopodina (a new taxon) for the ptarmigans in the genus *Lagopus*. All the taxa in our classification, at all ranks, are monophyletic with bootstrap support of 95% or more.

Key words: classification, Galliformes, grouse, mitochondrial DNA, phylogeny, Tetraoninae

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The grouse have been of special interest to wildlife biologists because of their recreational and commercial importance. In addition, aspects of their biology, such as population cycles and mating systems, have made them a favourite exemplar for population and evolutionary studies (Johnsgard 1983).

The classification of the grouse, at the specific, generic and suprageneric levels, has long been controversial (e.g. Peters 1934, Short 1967, Johnsgard 1983, Sibley & Monroe 1990, Dickerman & Gustafson 1996, Ellsworth, Honeycutt & Silvy 1996). Short (1967) noted that much of this controversy stems from the fact that male grouse possess highly exaggerated and visual secondary sexual characteristics that corresponded to the 'generic characters' of an earlier taxonomic worldview. Following the broadening of the species category in the 1930s and 1940s (e.g. Mayr 1942), many divergent forms were lumped into single species that resulted in monotypic genera. This led to a greatly increased ratio of the number of genera to species,

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a situation deplored at the time by Amadon (1943), but never successfully corrected. For example, in Peters' (1934) classification, 19 species were placed in 11 genera, five of which were monotypic. Although some authors tried to rectify the situation by lumping species into fewer genera, it was clear that the relationships among the species were poorly known and generic allocations remained controversial (Boag & Schroeder 1992). Fortunately, major technological advances within the past five years have made it possible to address questions of differentiation and relationship among these birds.

However, the problem of basing a classification on less than well-supported molecular results can be seen in the study of grouse conducted by Ellsworth et al. (1996). Ellsworth et al. (1996) sequenced a portion (609 basepairs) of the cytochrome-*b* gene for some of the species of grouse. In the abstract of their paper, they advocated basing a classification on such genetic data, but it is fortunate that they did not do so. For example, their minimum length trees failed to recover a monophyletic clade of ptarmigans and most of their minimum length trees even failed to result in a monophyletic clade for grouse. Nevertheless, others have used their results as a basis for taxonomic decisions (e.g. AOU 1998; see also below).

In this paper, we classify the grouse based on analyses of large amounts of DNA sequence data. These data allow adoption of rigorous standards for making nomenclatural decisions that previously were not possible. In addition, in our classification we recognize that species-level taxonomic opinion in birds is in a period of transition (Zink & McKitrick 1995), and that some currently recognized subspecies will warrant species-level status in future revisions (e.g. Sibley & Monroe 1990, AOU 1998). Herein, we follow the taxonomy and vernacular names used by Sibley & Monroe (1990), except when we propose changes to the classification.

Material and methods

Taxa examined

In order to maximize the utility of our classification to both avian systematists and wildlife biologists, we included all of the generally recognized species of extant grouse (e.g. Sibley & Monroe 1990). Subsequent to the beginnings of our study, a new species was discovered (but not yet described) in the genus *Centrocercus* (Kahn, Braun, Young, Wood, Mata & Quinn 1999); unfortunately tissue samples of this taxon were not available to us.

The biological species concept (Mayr 1963) has generally been used to recognize species taxa of grouse (e.g. Short 1967). However, in several cases, we included well-differentiated forms that would probably be recognized as phylogenetic species in a modern revision of the grouse (Zink & McKitrick 1995). Consequently, we included both major taxa of the North American spruce grouse complex (spruce grouse *Canachites canadensis* and Franklin's grouse *C. franklinii*), both forms of the blue grouse complex (dusky grouse *Dendragapus obscurus* and sooty grouse *D. fuliginosus*), and both the red grouse *Lagopus scoticus* and willow ptarmigan *L. lagopus*. All these taxa are as diagnosable as are the two capercaillies *Tetrao urogallus* and *T. parvirostris*, the two black grouse *Lyrurus tetrix* and *L. mlokosiewiczi*, and the two hazel hens *Tetrastes bonasia* and *T. sewerzowi*. The North American species pairs have been recognized recently as subspecies because they hybridize locally. However, we treat all these taxa as species-level taxa in this paper. Finally, we sequenced Old and New World forms of two species of ptarmigan (willow ptarmigan and rock ptarmigan *Lagopus mutus*) that occur in both the nearctic and palearctic because they might represent divergent genetic populations that simply appear similar in plumage (i.e. they might represent cryptic species). The remaining taxa in our study were the ruffed grouse *Bonasa umbellus*, white-tailed ptarmigan *Lagopus leucurus*, sage grouse *Centrocercus urophasianus*, greater and lesser prairie chicken *Tympanuchus pinnatus* and *T. pallidicinctus*, respectively, and sharp-tailed grouse *T. phasianellus*.

Grouse are phylogenetically placed in the family Phasianidae, and within that assemblage most closely related to the pheasants and turkeys (e.g. Sibley & Ahlquist 1990). Consequently, we included several Phasianids as outgroups to enable us to reliably root the network of grouse relationships. Jungle fowl *Gallus gallus*, grey partridge *Perdix perdix*, Lady Amherst's pheasant *Chrysolophus amherstiae*, wild turkey *Meleagris gallopavo*, and ocellated turkey *Agriocharis ocellata* were used for that purpose.

Genes sequenced

In order to obtain a sufficient amount of sequence to ensure robust estimates of relationships, we completely sequenced five mitochondrial genes for all taxa. The genes were cytochrome-*b*, cytochrome oxidase-3, adenosine triphosphatase-8, adenosine triphosphatase-6, and NADH dehydrogenase-2. These loci were amplified using oligonucleotide primers and PCR followed by sequencing in an ABI377 automated sequencer

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using standard mitochondrial DNA protocols (e.g. Hillis, Moritz & Mable 1996). The primers and techniques used to obtain these mtDNA sequences will be described in details in a future paper (J.G. Groth, G.F. Barrowclough & R.J. Gutiérrez, unpubl. manuscript).

Data analysis

DNA sequences were visually aligned. All three codon positions and transitions and transversions were given equal weight in phylogenetic analysis. Relationships among the taxa were determined using the program PAUP* (Swofford 1998); we searched for minimum length trees using parsimony with 500 heuristic searches with random addition of sequences. In order to estimate which relationships were strongly supported by the data, 500 bootstrap replicate analyses were performed with two random additions of taxa nested within each replicate. In the bootstrap analyses, the data matrix was resampled with replacement over DNA base positions. A consensus of the 500 resampled trees was found using PAUP* and the percentage of the bootstrap samples in which a node occurred was taken as a measure of the support in the data for that node in the consensus tree of relationships (Sanderson 1995, Efron, Halloran & Holmes 1996).

Classification

In order to obtain a classification for the grouse based on the sequence data, we followed taxonomic procedures designed to produce maximally predictive classifications (Farris 1979, Wiley 1981) while adhering to the guidelines of the International Code of Zoological Nomenclature (ICZN 1985) with respect to priority of names. Our use of suprageneric ranks and other conventions follows that of Wiley (1981) and Livezey (1998).

Results and discussion

Molecular results

We obtained aligned sequences of 3,809 basepairs of protein-coding genes. The data will be described completely, including Genbank accession numbers, in a future paper by J.G. Groth, G.F. Barrowclough & R.J. Gutiérrez. Although there was a single shortest tree (Fig. 1E), some of the apparent relationships may not be strongly supported by the data. Therefore, we based our proposed classification on the consensus of 500 bootstrap trees (Fig. 1F, see Table 1) because we believe it is most useful to derive classifications from results that are robust. No nodes are shown within the grouse with support of ≤90%. Bootstrap proportions of ≥90% are strongly supported (i.e. they have only a 10% chance of not being supported given further data of the same type). For our classification, we base hierarchical levels, and thus names, only on nodes that have bootstrap support of ≥95%; this corresponds to standard statistical levels of error.

The results strongly (100% bootstrap) support the monophyly of a clade consisting of all grouse. In addition, members of the genus *Lagopus* were recovered as monophyletic (98%). Further, some suprageneric relationships that had been widely suspected were recovered, including the existence of a clade consisting of capercaillies plus black grouse (100%). Finally, a clade consisting of the two prairie chickens plus the sharp-tailed grouse is sister to a clade of the dusky grouse plus sooty grouse (99%); this in turn is a sister to the sage grouse (98%). This latter clade of North American grouse has not been recognized traditionally. In fact, some authors suggest that blue and spruce grouse are close relatives (e.g. Short 1967, AOU 1983). However, our finding is not particularly surprising as others failed to find evidence for relationships between blue and spruce grouse (e.g. Boag & Schroeder 1992, Dickerman & Gustafson 1996, Ellsworth et al. 1996). Additionally, the *Centrocercus, Dendragapus* and *Tympanuchus* clade is consistent with biogeography.

We did not find strong support for a close relationship between the New World ruffed grouse and the two Old World hazel hens. This may seem surprising, but their recognition as congenerics was recent (Short 1967). The DNA data (Ellsworth et al. 1996, J.G. Groth, G.F. Barrowclough & R.J. Gutiérrez, unpubl. manuscript) strongly indicated that these two lineages represent an old divergence that may actually predate the origin of the remainder of the extant grouse. Nevertheless, the non-*Bonasa* grouse (*sensu* Short 1967) did form a single, well-supported clade (100%).

Classification

We believe that a useful classification should be predictive of additional characters besides those used to create the classification. That is, the classification should indicate how the states of additional characters will be distributed among grouse, perhaps including new behavioural or physiological ones currently not recognized or of interest. A cladistic classification based on a phylogeny has such properties (Farris 1979). However, in converting our phylogeny into such a classification, we choose to recognize only those groups that are thoroughly supported by the data (bootstrap values > 95%). We also continue the use of widely recognized

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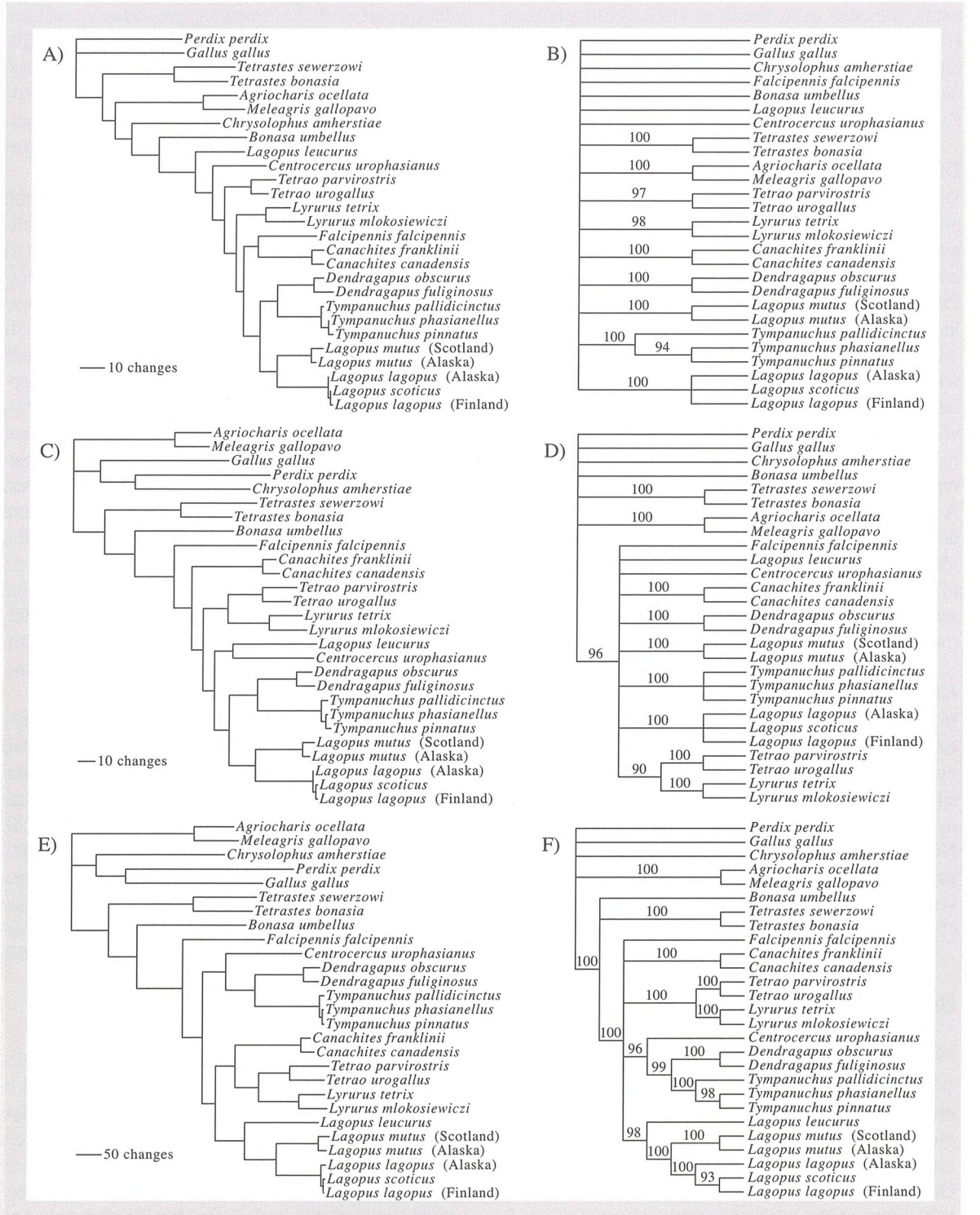


Figure 1. Relationships of grouse based on mitochondrial DNA sequences. A) One of four minimum length trees based on a 609 basepair fragment of the mitochondrial cytochrome-*b* gene; B) consensus tree based on 500 bootstrap samples from the 609 basepair fragment; C) one of two minimum length trees based on the complete 1,143 basepair cytochrome-*b* gene; D) consensus tree based on 500 bootstrap samples from the complete cytochrome-*b* gene; E) single minimum length tree from 3,809 basepairs representing five complete mitochondrial protein-coding genes; F) consensus tree based on 500 bootstrap samples from the five complete mitochondrial genes. Numbers above branches on right panel indicate percentage of bootstrap replicates in which clades occurred.

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generic names when they are not in conflict with our results. It is possible within a cladistic classification to attach a name to every node, but we do not do so. Rather, we recognize major clades where possible, and avoid the problem of a name for every node by adopting the sequencing convention described by Wiley (1981), where feasible, in which successive names at the same rank correspond to successively more derived clades. We present our complete classification in Table 1.

The grouse have sometimes been recognized as a family-level taxon (Peters 1934), but this cannot be justified given their position within Phasianids. A family-level treatment for grouse would require many additional family-level taxa in order to avoid a paraphyletic Phasianidae. More recently, the grouse have been treated as a subfamily (AOU 1998). We continue that treatment here, but recognize that this may cause problems when a cladistic classification of the entire Galliformes is prepared; recognition of a subfamily for grouse may eventually require the recognition of a large number of subfamilies in the Phasianidae.

The lack of monophyly for Short's (1967) enlarged *Bonasa* requires the resurrection of *Tetrastes* for the two hazel grouse. Consequently, the three early diverging lineages of grouse consist of the genera *Bonasa* and *Tetrastes*, and a clade of all other grouse. These are the major basal clades and we treat them as tribes.

Within the largest of these three clades, the relationships of the sharp-winged grouse are not clear. Thus, it cannot be merged into any other genus; consequently, the (monotypic) genus *Falcipennis* is required in any classification. Therefore, the two New World spruce grouse must have their own genus; this must be *Canachites* by priority. *Tetrao* and *Lyrurus* are traditionally used genera and there seems to be no point in lumping them; although that would be consistent with our results, it is not required. A similar line of reasoning applies to *Centrocercus*, *Dendragapus* and *Tympanuchus*; they could be lumped, but are widely used and do correspond to monophyletic taxa. However, no unique generic name can be used for the sharp-tailed grouse (e.g. *Pediocetes*); such a monotypic genus would result in a paraphyletic *Tympanuchus*; consequently it is not justified. In *Lagopus*, a new genus could be created for *L. leucurus*, but this is not required; the problem of recovering the hierarchical relationships within that genus is obviated by the use of the sequencing convention with *L. leucurus* first in the sequence.

Thus, our molecular results and the above reasoning leave us with five monophyletic clades within the largest of the three basal tribes of grouse (see Fig. 1F and Table 1). We believe it is useful to acknowledge these major divisions by naming each as a subtribe. This does not affect common usage as most authors will continue to refer to the individual species by their generic and specific appellations; however, the five subtribes will allow persons consulting the classification to realize that some evolutionary characteristics of grouse are predicted to be distributed at those subtribal levels. In our classification, the three tribes and the five subtribes are annotated *sedis mutabilis* because they result from a consensus of bootstrap trees and their relative hierarchical relationships are not known at the 95% level.

Table 1. A classification of the grouse (see section Classification for details).

Subfamily Tetraoninae (all tribes *sedis mutabilis*)
Tribe Bonasini, new taxon
Bonasa umbellus
Tribe Tetrastini, new rank
Tetrastes bonasia
Tetrastes sewerzowi
Tribe Tetraonini, new rank (all subtribes *sedis mutabilis*)
Subtribe Falcipennina, new taxon
Falcipennis falcipennis
Subtribe Canachitina, new taxon
Canachites canadensis
Canachites franklinii
Subtribe Tetraonina, new rank
Tetrao urogallus
Tetrao parvirostris
Lyrurus tetrix
Lyrurus mlokosiewiczi
Subtribe Centrocercina, new taxon
Centrocercus urophasianus
[*Centrocercus* sp. nov.]
Dendragapus obscurus
Dendragapus fuliginosus
Tympanuchus pallidicinctus
Tympanuchus phasianellus
Tympanuchus pinnatus
[†*Tympanuchus cupido*]
Subtribe Lagopodina, new taxon
Lagopus leucurus
Lagopus mutus
Lagopus lagopus
Lagopus scoticus

The heath hen *Tympanuchus cupido* is extinct and is consequently preceded by a dagger in the classification (see Table 1); it was completely allopatric from the greater prairie chicken *Tympanuchus pinnatus* and based on several diagnostic characters (Ridgway & Friedmann 1946), we judge it to be a species-level taxon. Attwater's prairie chicken *Tympanuchus pinnatus attwateri* had a range that at one time was contiguous with that of the greater prairie chicken from which it apparently does not differ by any diagnosable characters (Ridgway & Friedmann 1946). Consequently, we do not judge it to be a separate species-level taxon. Tissue samples of the heath hen and a new sage grouse were not available for sequencing as part of our study.

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Therefore, they are placed in the classification based on available descriptions of their plumage but in the absence of molecular data; these placements are indicated by square brackets (see Table 1).

In our classification, we recognize a single species of rock ptarmigan; it is possible that future analysis of this taxon may result in the discovery of monophyletic lineages that are geographically separate. In such a case, some current subspecies-level taxa of *Lagopus mutus* would be elevated to species taxa. Likewise, it is possible that further analysis of the willow ptarmigan may result in the discovery of monophyletic New World and Old World clades of this taxon. That would require the addition of another species-level taxon. We sequenced rock ptarmigan from Alaska and Scotland; they differed by approximately 1%. Our individuals of willow ptarmigan from Alaska and Finland differed by approximately 0.5%. These levels of sequence divergence are roughly equivalent to the divergence between sharp-tailed grouse and the two prairie chickens; thus it is plausible that with further detailed sampling, the rock and willow ptarmigan might require splitting; we have no evidence either way for that at present. Both the spruce grouse/Franklin's grouse pair and the sooty grouse/dusky grouse pair differ by more than 1%; this is more than the sequence divergence between prairie chickens and sharp-tailed grouse. Our recognition of the red grouse as a species, due to its derived plumage pattern, moult, and biogeography, leaves a paraphyletic willow ptarmigan. However, paraphyletic taxa at the specific level are often required because, during the process of speciation, monophyly does not arise precisely at the same time in both daughter species.

Sequence length and robustness

We investigated the effects of the quantity of DNA sequence data on the robustness of the resulting phylogeny by reanalysing portions of our own data. First, we analysed 609 basepairs of cytochrome-*b* corresponding to the fragment used by Ellsworth et al. (1996). However, we used all grouse species and our outgroups (Ellsworth et al. (1996) used only a subset of these). The tree we obtained from the data using PAUP* showed neither the grouse, in general, nor *Lagopus*, in particular, to be monophyletic (see Fig. 1A). These problematical results were similar to those of Ellsworth et al. (1996). Thus, if a classification based on a fraction of the cytochrome-*b* gene were developed, not only would some startling changes be necessary but the classification itself would be unstable because it would not be strongly supported by the data (see below).

We used bootstrap resampling of the 609 basepair fragment of our data to determine which hierarchical relationships were present in more than 90% of 500 subsamples. Few relationships are strongly supported by this small fragment of the mitochondrial genome (Fig. 1B); the only suprageneric clade recovered is that consisting of the two turkeys. Thus, there is little robust support for higher level phylogenetic relationships in 609 basepairs of cytochrome-*b*.

We next repeated the analysis using the complete 1,143 basepair cytochrome-*b* gene (Fig. 1C shows the shortest tree). The grouse were monophyletic, but other problems remained, including polyphyly of *Lagopus*. However, the bootstrap tree (Fig. 1D) indicated that there was no bootstrap support (at the 90% level or higher) for monophyly of grouse, and many lineages stem from a large multifurcation, including for example, three separate lineages of *Lagopus*. Thus, even the entire cytochrome-*b* molecule does not support a robust classification. This is symptomatic of a general problem in molecular systematics; there is a tendency for researchers to place too much trust in results that do not meet standards that would be routine in other branches of science.

Finally, when the entire 3,809 basepairs of data were analysed, robust hierarchical structure was found in the grouse that was not well supported, and in some cases contradicted, by a 609 basepair fragment or even the entire cytochrome-*b* gene. Thus, by increasing the amount of sequence sampled from approximately 5% to over 30% of the protein-coding portion of the mitochondrial genome, we obtained dramatically improved results.

Future directions

Based on 3,809 mitochondrial basepairs, we have developed a relatively robust estimate of much of the evolutionary history of grouse. However, there are still some unknown relationships within the subfamily as evidenced by lack of resolution of the precise branching patterns among the three tribes and among the five subtribes. In particular, we remain uncertain concerning two salient issues: the possibility of a monophyletic clade of *Bonasa* plus *Tetrastes*, as reflected in classifications such as that of Short (1967), and the position of *Falcipennis*. In these two cases, mitochondrial data, when analyzed using parsimony, do not provide robust support for the relative positions of these taxa. Both of these problems concern relatively deep divisions within the phylogeny of grouse and, consequently, suggest that slower-evolving genes, such as nuclear introns or exons, might be useful future additions to the data. Alter-

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natively, more sophisticated models of DNA evolution than simple parsimony, such as parameter-rich likelihood methods (e.g. Hillis et al. 1996), may provide more precision. Such approaches might enable one to further 'fine-tune' our classification; however, because our classification only treats robust nodes as higher taxa, further data are unlikely to result in a disconcordant classification.

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