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Evolutionary Origin and Genetic Diversity of Ring-necked Pheasants in the Upper Midwest United States

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Abstract

We compared mitochondrial cytochrome *b* sequences of ring-necked pheasants (*Phasianus colchicus*) from Midwestern United States (SD and NE, USA) to a molecular phylogeographic hypothesis of pheasants in the native Eurasian range to understand which subspecies are represented by wild and captive released birds. We found that these birds represent 2 Eurasian lineages, which we refer to generally as northern Eurasian (*Colchicus* group) and eastern China (*Torquatus* group). These mitochondrial DNA lineages occur in different frequencies in the wild, with the latter being 3 times more common. This suggests that 1) the eastern China lineage is either better suited to surviving in natural environments of the Midwestern United States outside captivity; 2) this group was more highly represented in original or ongoing releases; or 3) this group is more easily harvested. Confirmation of these possibilities could affect the type of pheasants bred for release. We also detected a low level of genetic variability in Midwestern birds relative to those from the native range, suggestive of an inbreeding effect.

Keywords evolutionary relationships, mitochondrial DNA, *Phasianus colchicus*, population genetics, ring-necked pheasant, subspecies.

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The ring-necked pheasant (*Phasianus colchicus*) is a well-established exotic species in parts of North America, ranging west to southern Alberta and Saskatchewan in Canada, with small populations in several regions of the western United States and northern Mexico (Johnsgard 1999, Giudice and Ratti 2001). This species has become an iconic game-bird in the United States following development of agricultural land, and concomitant loss of native game-bird habitats (Errington and Gewertz 2015). Thus, most state agencies are involved in population management of wild pheasants and many private and local governmental groups are involved with release of captive-reared pheasants for the purpose of improved hunting opportunity.

The native range of the species, where it is referred to as the common pheasant, includes much of Eurasia, exclusive of desert and high-latitude areas (Kayvanfar et al. 2017). Taxonomically, 5 groups of subspecies have been recognized based on morphological characteristics (Madge and McGowan 2002). Each of these groups includes from one to many subspecies: black-necked pheasant (*colchicus* group), white-winged pheasant (*principalis* group), Tarim pheasant (*tarimensis* group), Kirghiz pheasant (*mongolicus* group), and grey-rumped pheasant (*torquatus* group; Table 1). Assignment of subspecies within the groups was based on morphological features, albeit these features are more subtle than those separating the 5 main groups. The populations present in North America allegedly originated from stock imported from eastern Asia and perhaps also from captive-bred stock from England (Prince et al. 1988).

Population densities have been influenced by release of captive-raised birds, likely reaching millions of birds annually throughout the range (Burden 2013). Individuals representing all 5 subspecies groups have been introduced into various regions of the United States at various times, with varying degrees of success (Prince et al. 1988). For example, in Nebraska, USA, pheasants representing *P. c. colchicus*, and *P. c. torquatus* were released during the early stages of pheasant management (Baxter and Wolfe 1973). Birds from Mongolia were also released, but it is unclear if they were from the *P. c. mongolicus* subspecies, or other subspecies that occur in Mongolia (e.g., *P. c. hagenbackii*, *P. c. edzinen-sis*). Subspecies identities of birds introduced into South Dakota, USA, are unclear (Trautman 1982).

With the identification of subspecific genetic markers, it is possible to ascertain which taxonomic subspecies, or at least subspecies groups, are present in wild and captive populations, test historical introduction accounts, and determine whether subspecies groups survive equally well (Kayvanfar et al. 2017). However, no investigations of DNA sequence variation have addressed the evolutionary origin of ring-necked pheasants in the United States. Studies have addressed levels of *in situ* genetic variability in North American pheasants (Vohs and Carr 1969, Giesel et al. 1997, Baratti et al. 2001). Warner et al. (1988) attempted to distinguish wild and captive-reared birds within Illinois, USA. Therefore, we investigated the historical origin of pheasants from Nebraska and South Dakota by comparing mitochondrial DNA (mtDNA) sequences of birds from this area with an mtDNA phylogeny (Kayvanfar et al. 2017). In addition, we discuss levels of variability of North American and Eurasian populations, and relative proportions of different genetic clades among harvested pheasants in the Upper Midwest, United States (hereafter, Midwest).

Methods

Review of Past Molecular Studies of Subspecies of Ring-Necked Pheasants

To determine the evolutionary affinities of Midwest pheasants it is necessary to examine the most comprehensive phylogenetic hypothesis. Two recent papers addressed relationships of some subspecies from parts of the native Eurasian range (Liu et al. 2010, Zhang et al. 2014). However, these analyses only include the eastern portion of the native range and thus have limited taxonomic information. Kayvanfar et al. (2017) provide the most extensive examination of subspecies relationships, including 17 of 30 subspecies, distributed among the 5 groups as follows: *colchicus* group (3 subspecies), *principalis* group (3), *tarimensis* group (1), *mongolicus* group (1), and *torquatus* group (14; **Table 1**). Kayvanfar et al. (2017) sequenced 2 mitochondrial genes, cytochrome *b* (cyt *b*) and control region, and 2 nuclear genes. The mtDNA genes exhibited 61 parsimony-informative sites, whereas none were found in the nuclear genes; both nuclear genes exhibited a few singletons. Thus, as in

Table 1. Summary of taxonomy of common pheasant (*Phasianus colchicus*). *Phasianus colchicus elegans*, once considered part of the Torquatus group, is a distinct group according to mtDNA data. Subspecies with an asterisk were not included in this study. Subspecies abbreviations used in Figure 1.

Subspecies group: subspecies

Colchicus: <i>persicus</i> (PER), <i>talischensis</i> (TAL), <i>colchicus</i> (COL), <i>septentrionalis</i> *
Principalis–Chrysomelas: <i>principalis</i> (PRI), <i>zarudnyi</i> *, <i>chrysomelas</i> *, <i>bianchii</i> (BIA), <i>zerafschanicus</i> *, <i>shawii</i> (SHA)
Tarimensis: <i>tarimensis</i> (TAR)
Mongolicus: <i>mongolicus</i> (MON), <i>turcestanicus</i> *
Torquatus: <i>satscheunensis</i> (SAT), <i>pallasi</i> (PAL), <i>suehschanensis</i> (SUE), <i>torquatus</i> (TOR), <i>kiangsuensis</i> (KIA), <i>rothschildi</i> *, <i>karpowi</i> (KAR), <i>strauchi</i> (STR), <i>elegans</i> (ELE), <i>vlengalii</i> (VLA), <i>hagenbecki</i> (HAG), <i>edzinensis</i> *, <i>alaschanicus</i> (ALA), <i>sohokhotensis</i> *, <i>decollatus</i> (DEC), <i>takatsukasae</i> (TAK), <i>formosanus</i> (FOR).

many studies of closely related avian taxa, the nuclear genes provided no information on relationships of subspecies owing to the insufficient time of isolation for coalescence owing to their greater effective population size of nuclear loci (Zink and Barrowclough 2008).

To provide a check on the accuracy of the sequences, we compared the *cyt b* sequences of Liu et al. (2010) and Kayvanfar et al. (2017), both of which included several subspecies in the *torquatus* group (*pallasi*, *karpowi*, *torquatus*, *kiangsuensis*, *strauchi*, *satscheunensis*). When we analyzed the pooled sequences, we produced a phylogenetic tree (not shown) that separated 2 groups of sequences by lab group. We discovered 6 base positions (93, 96, 234, 342, 408, 426) in which the Kayvanfar et al. (2017) sequences contained a “C,” whereas the Liu et al. (2010) sequences showed an “A” for individuals KY246228–KY246295. Our sequences matched those in Liu et al. (2010); the erroneous base positions caused the separation of sequences by lab group. When we queried the authors of Kayvanfar et al. (2017), we were sent a corrected data set that included more individuals and subspecies (21), albeit without the first 100 base pairs of the *cyt b* gene from the original data of Kayvanfar et al. (2017); we used their corrected data in our analyses.

DNA Extraction

We obtained muscle or heart tissue samples from both wild and captive pheasants in both Nebraska and South Dakota (**Fig. 1**) in 2016 and 2017; wild birds were hunter-harvested and checked for toe clips or holes in nares that would be present on liberated captive-bred birds. We extracted DNA using a DNeasy Blood and Tissue Kit (Qiagen, Venlo, Netherlands) following manufacturer instructions or a standard phenol-chloroform protocol, modified to increase DNA yield during ethanol precipitation by incubating samples in an ice bath overnight at 0°C rather than at -20°C. We designed primers pc3_cytb_L (5'-TGTAACCGA CGGCCAGTTCCTTCGCCCTTACAATCCTCAT-3') and pc3_cytb_H (5'-CAG-GAAACAGCTATGACGCTG GAGAGAAAGGTTTAAGTC-3') to amplify the *cyt b* gene in a single pass. We carried out polymerase chain reactions (PCR) in volumes of 25 µL consisting of 9.5 µL molecular grade water, 12.5 µL GoTaq Green Mastermix (Promega, Madison WI, USA), 1 µL of each primer at a concentration of 10 nmol, and 1 µL of DNA template. Polymerase chain reaction conditions consisted of 36 cycles (30 sec at 95°C, 10 sec at 68.2°C, and 1 min at 72°C) with initial denaturation at 95°C for 3 minutes and final extension at 72°C for 7 minutes. PCR purification and DNA sequencing was carried out at Genewiz (Cambridge, MA, USA) with each sample being sequenced in forward and reverse directions using M13F(-21) and M13R primers. We edited sequence.ab1 files in SEQUENCHER 4.7 (Gene-codes Inc., Ann Arbor, MI, USA) and checked for stop codons. We used MEGA version 7 (<http://www.megasoftware.net/>) to produce alignments and check sequence for stop codons (Kumar et al. 2018).

Phylogenetic Analysis

To depict the genetic placement of Midwest pheasants in the context of relationships among subspecies across most of the native range (Kayvanfar et al. 2017), we used a Median Joining network analysis (Bandelt et al. 1999) as implemented in POPART (<http://popart.otago.ac.nz/index.shtml>; Leigh and Bryant 2015) based on our *cyt b* haplotypes for Midwest pheasants combined with *cyt b* plus CR data from Kayvanfar et al. (2017; we entered missing data "?" for Midwest birds for CR). We also constructed a maximum likelihood tree using Garli 2.01 (Zwickl 2006;

Figure 1. Network showing genetic relationships of mtDNA haplotypes for the common pheasant, including subspecies from native range (open circles) and Midwest, USA (colored circles, labeled NE for Nebraska and SD for South Dakota, USA). The USA samples were obtained in 2016 and 2017. See text for haplotypes shared among subspecies. Filled black circles represent unsampled haplotypes. Size of circle is proportional to sample size as shown in the inset. Abbreviations for subspecies in Table 1.

<http://www.bio.utexas.edu/faculty/antisense/garli/Garli.html>) using independent partitions for CR and cyt *b* with 1,000 bootstrap replicates as implemented in the CIPRES Science Gateway (<http://www.phylo.org/>; Miller et al. 2010). We plotted the geographic distribution of wild and captive harvested birds as a function of their lineage assignment. We note that no sequences were available for the subspecies *septentrionalis*, *zarudnyi*, *chrysomelas*, *zerafschanicus*, *turcestanicus*, *rothschildi*, *edzinensis*, and *sohokhotensis* (Table 1). All new sequences from this work are deposited in Genbank (MN390814-390971).

Results

Genetic Relationships of Midwestern Ring-Necked Pheasants

We obtained cyt *b* data for 158 individuals, which revealed 14 haplotypes. The network revealed that many subspecies share haplotypes, although the overall structure separated the *Torquatus*, *Colchicus*, *Mongolicus*, *Tarimensis*, and *Principalis* subspecies groups, as well as a group recognized by Kayvanfar et al. (2017) consisting of the subspecies *P. c. elegans* (previously considered part of the *Torquatus* group; Fig. 1). The same general relationships were found in the maximum likelihood phylogenetic hypothesis (not shown). Pheasants from the Midwest sorted into the broad *Colchicus* and *Torquatus* groups (Fig. 1); individuals from the *colchicus* group share haplotypes with *colchicus*, *persicus*, and *talischensis* subspecies, and individuals from the *Torquatus* group share haplotypes with the subspecies *decollatus*, *formosanus*, *karpowi*, *pallasi*, *strauchi*, *suehschanensis*, *takatsukasae*, and *torquatus*. ALA 2945 is the same haplotype as that found in individuals representing ALA ($n = 2$), HAG (6), KIA (6), SAT (9), STR (5), SUE (3), and VLA (10; Fig. 1). Haplotype COL 5765 is the same haplotype as that found in individuals representing COL (2), PER (6), and TAL (1). PRI 5788 is the same haplotype as that found in 8 other PRI. DEC 4424 is the same haplotype as that found in individuals representing FOR (8), KAR (6), PAL (7), STR (1), SUE (1), TAK (2), and TOR (4). DEC 4425 is the same haplotype as that found in individuals representing DEC (5) and TOR (2). PER 5780 is the same haplotype as that found in individuals representing TAL (3). BIA 1733 includes 10 BIA and 16 SHA. All other native haplotypes that represent

>1 individual include only that subspecies. Thus, there appeared to be 2 main mitochondrial lineages represented among Midwest pheasants. The groups *mongolicus*, *principalis*, *tarimensis*, and *elegans* were not found in our sample of Midwest birds.

Representation of Two Clades of Pheasants in the Midwest

We discovered that wild pheasants (those without obvious signs of captivity noted above) most closely related to the eastern China group (e.g., *Torquatus* group) were 3 times more common than those from northern Eurasia (e.g., *Colchicus* group; **Fig. 2**). In our captive population from Nebraska, the groups were in equal frequency, whereas in the captive sample from South Dakota, the ratio was closer to that observed in the wild (**Table 2**). The geographic distribution of the major haplotype groups in wild birds showed considerable variation in both states (Fig. 2). Although the captive facility in South Dakota has 28%

Figure 2. Lineage membership of Midwest, USA, pheasants in wild and 3 captive (triangles) samples. A “C” refers to the northern Eurasian lineage (*Colchicus* group) and a “T” refers to the eastern China lineage (*Torquatus* group). Numbers indicate relative proportions of major groups. A dot without explanation indicates a single wild individual. Samples were obtained from Nebraska and South Dakota, USA, in 2016 and 2017.

Table 2. Distribution of 2 mitochondrial clades of ring-necked pheasants in captive and wild populations in South Dakota (SD) and Nebraska (NE), USA, taken in 2016 and 2017.

<i>Origin</i>	<i>Captive NE</i>	<i>Captive SD</i>	<i>Wild NE</i>	<i>Wild SD</i>
Torquatus	18	23	34	35
Colchicus	19	9	9	11

Colchicus individuals, only one wild-harvested bird was taken near that facility (blue dot in Fig. 2), with the others farther east and south. Near the captive site in central Nebraska, with 66% Colchichus birds, only 2 were found nearby (green dots in Fig. 2).

Levels of Variability

Samples from the native range in Eurasia (Kayvanfar et al. 2017) are considerably more variable than those from the Midwest (haplotype diversity [h] = 0.8, nucleotide diversity (π) = 0.0023 for *Torquatus* group (n = 44); h = 0.73 and π = 0.0078 for *shawi*, *tarimensis*, *mongolicus* (n = 15). Of course, it is possible that captives have been released in the native range as well. In our midwestern samples, values for the *Torquatus* group were h = 0.687, π = 0.0011 (n = 45) and for the *Colchicus* group, h = 0.07, π = 0.0001 (n = 27). Levels of variability were not computed for captive versus wild birds because the values would depend on the ratio of the 2 groups in the sample.

Discussion

Prior to our study, it was unknown which mitochondrial lineages were represented in the Midwest, USA (Baxter and Wolfe 1973). Although many of the subspecies in the *Colchicus* and *Torquatus* groups are not supported by the molecular data gathered to date (Kayvanfar et al. 2017), this is not unusual for avian subspecies (Zink 2004). The 5 main groups (Madge and McGowan 2002; plus *P. c. elegans*) are discernable from the mtDNA data. Thus, the mtDNA data allow placing individual birds into one of the major groups. We found that pheasants in the Midwest are derived from 2 different morphological groups from the

ancestral lineage, one from northern Eurasia (*Colchicus* or black-necked pheasant group) and the other from eastern China (*Torquatus* or gray-rumped or ring-necked group). The Midwest birds are not closely related to the groups *Principalis*, *Tarimensis*, or *Elegans*. Although greater geographic sampling will be needed for a definitive conclusion, if birds from the subspecies *mongolicus* were introduced, none appeared to have persisted in Nebraska or South Dakota (a few Midwest birds are close to *hagenbecki*, however). There were no differences in genetics between captive and wild pheasants, only in the frequency of the 2 lineages, especially in wild-harvested birds, where there were 3 times as many birds from the eastern China lineage.

The reason for the greater representation of the eastern China birds in the wild population is unclear. It is possible that they survive better outside of captivity or are better adapted to Midwestern habitats and climate. Madden and Whiteside (2014) suggest that behavioral traits of pheasants play a role in whether they were harvested or not, and potentially, the 2 main groups of Midwestern pheasants could exhibit different behavioral temperaments. That is, even if not numerically more prevalent, it is possible that the eastern China birds are less wary and perhaps more easily shot by hunters (Madden and Whiteside 2014). Although we have no data to support this, Robertson et al. (1993) noted that birds released from game farms tend to be weaker flyers and attain lower heights when flushed, owing to greater mass; therefore, any mass difference between *colchicus* and *torquatus* birds could affect their probability of being shot. It is also possible that the ratio of the 2 lineages in wild harvested birds reflects the lineage composition of local hatcheries or released birds. The representation of the 2 lineages in the South Dakota captive sample is intermediate between the Nebraska captives and wild samples. It is generally thought that captive-raised hens have low persistence (owing either to low survival, low reproduction, or both) in the wild (Robertson et al. 1993, Musil and Connelly 2009, Madden et al. 2018). Whereas, survival of roosters is less clear, although T. Runia (South Dakota Game, Fish, and Parks, personal communication, 2 May 2019) found that captive-roosters released in South Dakota in the autumn experience very low survival. It will require further sampling to determine if a discrepancy between the ratio of the 2 lineages in captive and wild populations holds over larger areas and samples. Nonetheless, it is difficult to explain why the 2 lineages are not equally represented in

the wild. We consider “wild” birds individuals that were hatched in the wild, but we speculate that they have ≥ 1 parent from a captive facility in the past few generations. It is worth recalling that all wild pheasants in North America have a captive parent somewhere in their genealogy.

We also note that our genetic marker was mitochondrial DNA, which does not recombine. Thus, mtDNA preserved lineage identity, but obscured the extent of hybridization between groups, the latter of which would be revealed in the nuclear genome. To date we have established that 2 matrilineal lines exist in Midwestern pheasants and are apparently unequally represented in wild samples, for unknown reasons. If matrilineal lineages initially were present in different frequencies, genetic drift might lead to fixation of a single lineage, which as yet has not happened. It is likely that differing regimes of selective breeding and subsequent release of captive-raised birds has resulted in the maintenance of ≥ 2 lineages in the wild population. It remains to be determined if the nuclear genomes are completely homogenized with only the nonrecombining matrilineal lines remaining to document the historical legacy of the North American introductions. We are pursuing multilocus nuclear comparisons and searching for potential adaptive reasons for the apparent differential survival of the eastern China maternal lineage.

Management implications The existence of multiple mtDNA lineages has not been previously identified in wild and captive populations of ring-necked pheasants. If different mitochondrial lineages persist better in natural environments, captive breeding should focus on those lineages, so that direct releases of captive bred birds or accidental escapees from game farms will have the greatest chance of increasing wild populations. If a link among body size, mtDNA lineage, and captive heritage influences the probability of harvest, these factors could determine how breeders produce stock for release into the wild.

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