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Finnish native grey partridge (*Perdix perdix*) population differs clearly in mitochondrial DNA from the farm stock used for releases

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The mitochondrial DNA (mtDNA) control region I (CR1) of 138 wild and 36 captive grey partridges (*Perdix perdix*) was sequenced. Representing two major mitochondrial DNA lineages that differed by 15 nucleotide substitutions (3.7%), the Finnish lineage dominated in the wild, whereas the European lineage dominated in the captive stock. Most individuals represented a single haplotype in each lineage. Nucleotide and haplotype diversities were high in mixed subpopulations with individuals of both lineages. Analysis of molecular variance (AMOVA) showed that when the captive stock was excluded, about 80% of the total variation could be explained by the variation within subpopulations. When captive stock was included, 67% of the variation was explained by the variation between subpopulations. According to Φ_{ST} values, captive stock differed from the wild subpopulations. These results clearly show that the native stock in Finland differs in mtDNA CR1 from the farm stock. In the area of large-scale captive rearing and releasing, only one bird represented the same mitochondrial lineage as the farm stock. It is evident that released farm birds have left only minor marks in the native population in Finland.

Introduction

Captive rearing and releasing of game birds is traditionally carried out for game management purposes with the main aim of increasing the size of the game bag, i.e. the number of birds harvested. Besides hunting purposes, captive rearing and releasing have been used as tools for conservation of endangered species (IUCN 1987, Nesbitt & Carpenter 1993, Cade & Temple 1995).

The grey partridge (*Perdix perdix*) is a species common to cultivated farmlands in temperate climate. Its distribution covers large areas in Europe and Asia from Ireland to the Ural Mountains. The worldwide decline in the number of the grey partridges is well documented. A marked decline in its distribution range has occurred during the last century, mostly at the beginning of the 1950s as a result of modern agricultural practices (for review *see* Potts 1986).

In Finland, the grey partridge reaches the edge of its northernmost distribution range. The population has decreased from approximately 15 000 pairs in the 1950s (Merikallio 1958) to approximately 4000 pairs in the early 1990s (Koskimies 1992). The present population size is

unknown, but it is estimated to be between 4000 and 10 000 pairs (J. Bisi pers. comm.). According to Kivirikko (1948: 418–423), the grey partridge arrived in Finland from the southeast at the beginning of the 1800s, although the earliest observations were already reported in 1690 (Merikallio 1958). The first introductions for hunting purposes were conducted in the middle of the 18th century (Merikallio 1958), with birds imported from Sweden (Kreuger 1950).

The grey partridge is listed in Annex II/1 of the Birds Directive (79/409/EEC) Article 7 (http://www.europa.eu.int/comm/environment/nature/legis.htm). Species referred to in Annex II/1 may be hunted with respect to certain regulations in EU Member States. Accordingly, the grey partridge is still legal game in Finland, even though it is classified as a near-threatened species (Rassi *et al*. 2001). Finland is divided into 15 Game Management Districts, and as stated by the Hunting Law in Finland (Law no. 615/1993, decree no. 664), grey partridge can be hunted in six Game Management Districts, whereas special permission is required in the remaining Districts. Several Game Management Associations and Hunting Clubs have voluntarily protected the grey partridge.

The European grey partridge can be divided into two mitochondrial DNA (mtDNA) lineages (Liukkonen-Anttila *et al*. 2002), consistent with two subspecies, *P. p. perdix* and *P. p. lucida* (Potts 1986). The colonisation of Europe occurred from two different glacial refugia, from the east (Balkans/Caucasus) and from the west (Pyrenees) (Liukkonen-Anttila *et al*. 2002). The *perdix* lineage is widely found in Europe, for example in France, Germany, Italy, Poland and the UK. The *lucida* lineage birds are found in Finland, Greece, Kazakhstan and Ireland. In Estonia, Bulgaria (Liukkonen-Anttila *et al*. 2002), Russia and Ukraine (T. Liukkonen unpubl. data) populations are mixed, but this structure is assumed to be man-made rather than natural, because birds of unknown origin have been released into these areas. The two different mtDNA lineages will be hereafter referred to as "European" and "Finnish".

In Finland, many release programmes have been carried out to strengthen natural populations of the grey partridge. However, the survival of captive-reared birds after release into the wild is reported to be poor (Putaala & Hissa 1998). Siivonen (1957) suggested that differences in the genetic adaptation of subspecies to the specific climatic conditions in their original range could be a partial explanation for the failed introductions. As subspecies have evolved as a consequence of isolation and genetic adaptation of populations to local conditions, failed introductions could have resulted from maladaptive traits that have been introduced into the wild when birds of "wrong" origin have been released.

Interest in managing grey partridge populations and willingness to conserve the Finnish subspecies have recently increased in Finland. Based on these interests, I wanted to (1) examine the genetic structure of the native grey partridge population in Finland, (2) compare mitochondrial DNA sequences of wild and captive birds with each other, and (3) find guidelines for future management of the grey partridge in Finland. The need for information about the composition of the captive and wild population is obvious, if releases will be made in the future.

Material and methods

Sampled birds and laboratory methods

A total of 174 Finnish grey partridges were sampled for this study, 138 wild birds and 36 farm birds (sampling locations are given in Fig. 1). Some samples were obtained from harvested birds during the hunting season. However, most of the samples were collected from the wild as carcasses and moulted feathers (one feather/carcass from one place/year is one individual). Feather samples (n = 44) were also taken from trapped birds. Samples obtained from the harvested and farm birds were collected in 1999–2003 and samples from the wild in 1999–2004. Trapped birds were sampled in 2000–2001.

The farm bird samples were collected from four different farm stocks (Fig. 1), of which two are still used for releases (C3, C4), and two (C1, C2) were used in the past (less than 10 years ago). Farm birds have been imported mostly from Sweden, Denmark and France, but the exact sources or numbers of imported birds from different countries is unknown. Captive stock C1 was based on the captive stock C2 and altogether 15

birds were sampled from these stocks. From C3 three birds and from C4 18 birds were sampled.

DNA extraction, PCR and sequencing procedures were carried out as described in Liukkonen-Anttila *et al*. (2002, 2004). The first 408 nucleotides of the control region, i.e. the control region 1 (CR1) were amplified. This is the most variable of the three domains of the CR in the grey partridge. Negative controls — samples without specimen DNA — were used to detect possible contamination. Some of the unique samples were sequenced with both the forward and the reverse primer. Sequences have been deposited in GenBank (accession numbers AY601123–AY601153).

Sequence comparisons and statistical analysis

Sequence alignment was done by eye using Sequencher (ver. 4.0.5, Gene Codes Corp.) and BioEdit Sequence Alignment Editor (ver. 7.0.0). The first 20 nucleotides were ignored due to an incompleteness in sequencing. The minimum-spanning network (Fig. 2) was drawn manually based on segregating sites (Appendix), Arlequin ver. 2.0 (Schneider *et al*. 2000), and Treeview ver. 1.6.6 (Page 2000).

The sequence data were divided into five subpopulations (Fig. 1): "North Ostrobothnia" (n = 26), "South Ostrobothnia" (n = 90), "South-West" (n = 13), "South" (n = 9), and "Captive" (n = 36). Because grey partridges do not regularly move long distances (breeding dispersal distance of radio-tagged wild females is on average 3.1 km ± 0.5 km, Putaala & Hissa 1998), subpopulations were designed as in Fig. 1 to ensure that they are separate units. All captive bird samples were pooled into one captive population.

MEGA ver. 2.1 (Kumar *et al*. 2001) was used to compute Tajima-Nei distances (Tajima & Nei 1994) between and within subpopulations. Nucleotide diversity (π, Nei 1987: eq. 10.5), haplotype diversity ($\hat{h}$, Nei 1987: eqs. 8.4, 8.12), and Tajima's D's (Tajima 1989) were calculated with DNAsp ver. 4.0 (Rozas & Rozas 1999). Tukey-Kramer test (Box 9.11, Sokal & Rohlf 1995) was used for pairwise comparisons of diversity parameters between subpopulations.

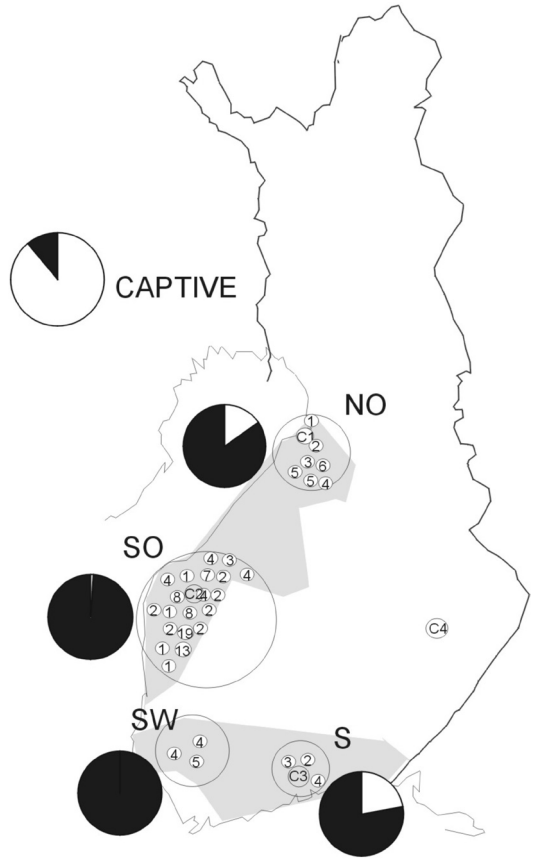

Fig. 1. Distribution range (grey area) and sampling locations (n given in the circle) of the grey partridge (*Perdix perdix*) in Finland. NO = "North Ostrobothnia", SO = "South Ostrobothnia", SW = "South-West", S = "South", C1–C4 indicate captive stocks. In pie diagrams the proportion of Finnish lineage haplotypes is given in black and European lineage haplotypes in white. Outside the map proportion of the haplotypes in the captive stock.

Pairwise Φ_{ST}s (estimated using the haplotype frequencies and Tajima-Nei distances), the Exact test of differentiation (Raymond & Rousset 1995), and the analysis of molecular variance (AMOVA, Excoffier *et al*. 1992) were calculated with Arlequin ver. 2.00.

Results

The length of the mitochondrial control region (CR) of the grey partridge is 1151 nucleotides, of which 408 nucleotides were sequenced. Two

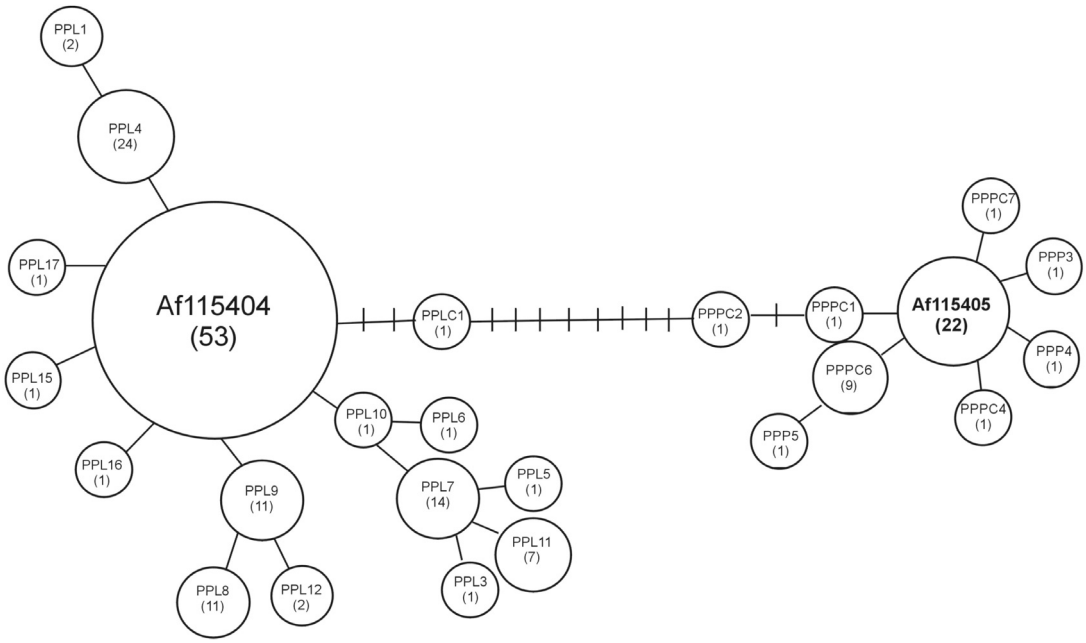

Fig. 2. The minimum spanning network of the sampled Finnish grey partridges (*Perdix perdix*). Each line between two cross-bars or two circles indicates one point mutation. The size of the circle refers to the sample size (*n* is given under haplotype name). PPL-haplotypes = Finnish, wild, PPLC = Finnish, captive, PPP = European, wild and PPPC = European, captive.

major mtDNA haplotype lineages, as described earlier by Liukkonen-Anttila *et al*. (2002), were detected.

The dominant Finnish haplotype differed from the dominant European haplotype by 15 nucleotides (3.7%, Fig. 2). Each lineage included one core haplotype (Fig. 2). The Finnish lineage dominated in the wild population (131/138 birds, 94.9%, Appendix), whereas the European lineage dominated in the captive stock (32/36 birds, 88.9%, Appendix).

The CR1 sequences exhibited 12 variable sites (2.9%, 6 transitions, 4 transversions and 3 indels/deletions) in the Finnish lineage and 10 (2.5%, 6 transitions and 4 indels/deletions) in the European lineage (Appendix). The Finnish core haplotype (GenBank accession number AF115404, Liukkonen-Anttila *et al*. 2002) was observed in 53 wild individuals (38.4% of all wild bird samples) and it dominated in the "South-Ostrobothnia" population (42/90 individuals). Four birds of this haplotype were also found in the subpopulations "North Ostrobothnia" and "South" and three in "South-West". An additional 14 Finnish haplotypes were found among the wild, and one was identified among the farm birds. Five European haplotypes were found among the farm, and three among the

Table 1. Tajima-Nei mean net distances (± SE) between populations above diagonal, within-population distances on the diagonal (in boldface) and between-population distances below the diagonal for the grey partridge (*Perdix perdix*) in Finland (for abbreviations *see* Fig. 1).

	NO	SO	SW	S	C
NO	**0.01005 ± 0.00260**	0.00118 ± 0.00065	0.00085 ± 0.00024	–0.00026 ± 0.00042	0.01528 ± 0.00424
SO	0.00739 ± 0.00211	**0.00236 ± 0.00101**	0.00008 ± 0.00006	0.00057 ± 0.00019	0.02361 ± 0.00624
SW	0.00690 ± 0.00191	0.00229 ± 0.00120	**0.00205 ± 0.00150**	0.00073 ± 0.00024	0.02359 ± 0.00632
S	0.01230 ± 0.00305	0.00928 ± 0.00225	0.00928 ± 0.00231	**0.01506 ± 0.00367**	0.01321 ± 0.00346
C	0.02431 ± 0.00660	0.02880 ± 0.00774	0.02861 ± 0.00772	0.02474 ± 0.00640	**0.00800 ± 0.00208**

wild birds in addition to the dominating European haplotype (GenBank accession number AF115405, Liukkonen-Anttila *et al*. 2002).

The largest between-population distances (0.02880 ± 0.00774, 0.02861 ± 0.00772, 0.02474 ± 0.002310, and 0.02431 ± 0.00660) were found between the wild and "Captive" subpopulations (Table 1). The highest nucleotide (0.01554 ± 0.00586) and haplotype diversities (0.794 ± 0.067) were found in the "South" and "North-Ostrobothnia" populations, respectively (Tukey-Kramer: $p < 0.05$), where individuals representing both lineages were found (Table 2). The lowest nucleotide (0.00233 ± 0.00070) and haplotype (0.525 ± 0.053) diversities were found in "South Ostrobothnia" (Tukey-Kramer: $p < 0.05$, Table 2). The significantly negative Tajima's D in "South Ostrobothnia" ($D = –2.37037$, $p < 0.01$) and in the whole population ($D = –1.83351$, $p < 0.05$) is characteristic of an expanding population (Table 2).

The analysis of molecular variance showed that 79.8% of the total variation was explained by the variation within subpopulations (df = 134), and 20.2% by the variation between subpopulations (df = 3). When the captive stock was included in the analysis, 67.0% of the variation was explained by the variation between (df = 4) and 33.0% by the variation within the subpopulations (df = 169). According to the significant pairwise Φ_{ST}s (permutation test: $p < 0.05$) the captive stock is differentiated from all wild populations. In addition, "South Ostrobothnia" is differentiated from "North Ostrobothnia" and "South", and "South-West" from "North Ostrobothnia". The Exact test of differentiation supported the differentiation of captive stock from all wild subpopulations (Table 3).

When the captive stock was compared with the entire wild population, 75% of the variation was explained by the variation among populations (df = 1), and 25% within populations, i.e. among individuals. The Φ_{ST} was 0.74873 and the populations were significantly differentiated from each other. The Exact test of differentiation supports this result.

The minimum-spanning network (Fig. 2) included two cores, one for the European (AF115405) and one for the Finnish lineage (AF115404). Some common haplotypes were found (PPL4, PPL7, PPL8, PPL9 and PPPC6, Appendix), but several unique haplotypes were also identified (PPL1, PPL3, PPL5, PPP3, PPP4, PPP5, Appendix). The distribution of all haplotypes among wild subpopulations is given in the Appendix. The haplotype composition of different captive stocks is given in Table 4.

Discussion

Mitochondrial DNA variation in Finnish grey partridge populations

The grey partridge population in Finland is divided into two clearly differentiated mtDNA lineages (Liukkonen-Anttila *et al*. 2002, and the present study). Most wild birds represent the Finnish lineage, whereas farm birds represent the European lineage. The difference between these two lineages is similar to the difference between Finnish and European capercaillie *Tetrao urogallus* (Liukkonen-Anttila *et al*. 2004).

The difference between the wild and captive subpopulations was obvious and supported by the high between-population Tajima-Nei distances. The captive population included mostly European haplotypes whereas "South-West" contained only Finnish haplotypes. Subpopulations

Table 2. The sample size (N), nucleotide (π) and haplotype ($\hat{h}$) diversities, number of haplotypes, Tajima's D and its significance (p) for the grey partridge (*Perdix perdix*) in Finland (for abbreviations *see* Fig. 1).

	N	π	SD	$\hat{h}$	SD	Number of haplotypes	Tajima's D	p
NO	26	0.01089	0.00282	0.794	0.067	8	0.18307	> 0.10
SO	90	0.00233	0.00070	0.525	0.053	11	–2.37037	< 0.01
SW	13	0.00316	0.00058	0.795	0.085	6	1.03125	> 0.10
S	9	0.01554	0.00586	0.722	0.159	5	–0.25460	> 0.10
C	36	0.00777	0.00228	0.698	0.067	10	–0.76728	> 0.10
All wild	138	0.00489	0.00103	0.639	0.035	21	–1.83351	< 0.05

"South Ostrobothnia" and "North Ostrobothnia" were mixed but with a majority of Finnish haplotypes. Diversity parameters were low in "South Ostrobothnia", which contained mainly Finnish core haplotype birds, whereas high nucleotide diversities were found in subpopulations "North Ostrobothnia" and "South", which contained both lineages. If we compare these parameters with those obtained from the capercaillie (Liukkonen-Anttila *et al*. 2004), the diversity values are of the same magnitude except in mixed subpopulations "North Ostrobothnia" and "South" (Liukkonen-Anttila *et al*. 2004).

Population structuring and differentiation within and among subpopulations

The significantly negative Tajima's *D* in "South Ostrobothnia", and the population as a whole, indicated an expanding population (Aris-Brosou & Excoffier 1996). However, this pattern is likely to be ancient, because the decline of the population is ongoing and well documented.

According to the results from the pairwise Φ_{ST} values (Table 3), the Finnish grey partridge population was somewhat structured and the differentiation resulted from the existence of two distinct mtDNA lineages in the population. All wild subpopulations differed from the captive population. "North Ostrobothnia", which contained haplotypes of both lineages (22 Finnish/4 European), differed from "South Ostrobothnia" (89 Finnish/1 European) and "South-West" (only Finnish haplotypes). "South Ostrobothnia" also differed from "South", which was a mixed subpopulation (seven Finnish and two European haplotypes). However, the sample size for "South" was too low to make any strong conclusions about its structure.

When only wild subpopulations were included in the AMOVA, 20.2% of the total variation could be explained by the variation between subpopulations, but when the captive population was included in the analysis, 67.0% of the variation was explained by the variation between subpopulations. The captive stock population differed significantly from all wild subpopulations, with the majority of birds in it being of European origin.

The minimum-spanning network showed that the Finnish lineage included two separate clusters, but no clear geographical structure was found. The pattern of one core, some common, and several unique haplotypes is similar to that found in the Finnish capercaillie populations (Liukkonen-Anttila *et al*. 2004). The existence of haplotype PPL9 both in the wild population and in the C4 stock may reveal a wild ancestor in this captive stock.

Released birds are of foreign origin

The two mtDNA lineages found in Europe for the grey partridge (Liukkonen-Anttila *et al*. 2002) are consistent with two subspecies. This study differentiated the Finnish native population *P. p. lucida* from the farm stock *P. p. perdix* indicating that releases in Finland have mainly been conducted with birds of non-native (European)

Table 3. Pairwise Φ_{ST}s (significant values in boldface) and significance of Exact test of differentiation (significant differences are indicated with asterisks) below diagonal between the grey partridge (*Perdix perdix*) populations in Finland (for abbreviations *see* Fig. 1).

	NO	SO	SW	S
NO				
SO	**0.31126**			
SW	**0.11034**	0.03349		
S	0.01368	**0.25154**	0.09857	
C	**0.59498***	**0.84653***	**0.74592***	**0.56824***

Table 4. The distribution of different haplotypes of the grey partridge (*Perdix perdix*) among the captive stocks C1–C4.

Haplotypes	C1 (*n* = 5)	C2 (*n* = 10)	C3 (*n* = 3)	C4 (*n* = 18)
PPP	4	9	3	4
PPPC1	1			
PPPC2				1
PPPC4		1		
PPPC6				8
PPPC7				1
PPL				1
PPL9				2
PPLC1				1

origin. The seven European birds found in the wild in this study could be explained by introductions. In "North Ostrobothnia", European birds were found from the area where research releases were conducted during 1991–1995 (Putaala & Hissa 1998) with farm stock of European haplotypes (C1). In "South Ostrobothnia", one European bird was found in the area where intensive introductions with European haplotype farm birds were carried out during the last fifty years (C2). The population "South" consisted of seven Finnish and two European birds. The area where these birds were shot is an area of active releasing, even today, and the farm stock consists of birds of European origin (C3). The fourth farm stock (C4) included mainly European haplotypes but also four birds representing Finnish haplotypes.

The original aim of captive rearing and releasing of the grey partridges in Finland has been to increase the amount of game. Recently, however, it has become a priority to strengthen natural populations and to reintroduce the species into areas where it has disappeared. Fortunately, survival of released grey partridges has been poor (Putaala & Hissa 1998). It is noteworthy that despite the frequent releases of birds representing the European lineage into the subpopulation "South Ostrobothnia", only one bird (1/90) of this lineage was found in this area. As suggested by Siivonen (1957), the failure of introductions could be due to the maladaptation of the European grey partridges to the climatic conditions of the release areas in Finland. Although the survival of the released partridges seems to be poor, it is possible that some released birds survive in the wild and later breed. Therefore, the origin of released birds should be compatible with the wild birds of the releasing area (Ruokonen *et al*. 2000, Palkovacs *et al*. 2004). To release animals of foreign origin is against the general policy in Finland.

Will a farm stock of native origin birds solve all the problems?

Captive rearing should be considered from the point of view of natural selection. Individuals better adapted to the environment will have survival and reproductive advantage over individuals less well adapted. However, the selection pressure against individuals in captivity and for those in the wild are not the same. Tame birds breed better and are favourable for use as farm stock. As a result, because European grey partridges have been captive-bred in Finland for generations, it has become obvious that the farm stock is well suited to life in aviaries. These birds breed easily and produce a great amount of offspring. In contrast, if wild birds are taken into farms to "renew blood", they are generally unsuccessful because of stress and fear of human presence, thus being pruned out of the farm stock.

Genetic adaptation to captive conditions is recognised as a severe problem if captive populations are used for reintroductions (Woodworth *et al*. 2002, Gilligan & Frankham 2003). To avoid genetic adaptation to captive conditions and to preserve genetic variation in the farm stock are major challenges in captive rearing. To some extent captive stock may be "improved" by taking in individuals from the wild (Theodorou & Couvet 2004), but this may not always be possible or expedient. In general, the negative consequences of introducing captive individuals into the wild may be reduced if three conditions are met. The time of captive rearing should not exceed 20 generations, the number of introduced animals should be one or two per generation (this is not possible with the grey partridge, birds are released in flocks), and the size of the captive population should be large, more than 20 individuals (Theodorou & Couvet 2004).

In Finland, it has become increasingly desirable to only captive-rear birds of native origin. Captive-rearing itself includes many pitfalls that have to be solved to produce "good-quality" birds for reintroductions. In this study, I clearly show one pitfall in captive-rearing, the possibility of genetic difference between the wild and the captive stocks. To introduce alien species or subspecies is not considered reasonable from a conservation perspective. This has already been taken into account in the management of the grey partridge at a national level, and the national management plan for the species explicitly recognizes this problem. Hopefully, the Finnish farm stock will in time be comprised only of birds of Finnish origin. However, habitat protec-

tion and improvement of the environment, as well as hunting restrictions, will remain of high importance in the conservation of the Finnish grey partridge populations. Closely monitored experimental releases could give essential information about the value of introductions to wild populations, and in the future, all releases should be carefully controlled.

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Appendix. The variable sites in the Finnish grey partridge (*Perdix perdix*) mitochondrial DNA control region 1 (CR1) sequences (for abbreviations *see* Figs. 1 and 2).

Finnish	**.12233333344 714704888911 403809169817**	**NO**	**SO**	**SW**	**S**
Wild					
Finnish, AF115404 (53)	**TGTACTCTTCCC**	4	42	3	4
PPL1, AY601123 (2)	.....G.....-		2		
PPL3, AY601125 (1)	....T..-G..-		1		
PPL4, AY601126 (24)	..........-		19	3	2
PPL5, AY601127 (1)	....T.AC....			1	
PPL6, AY601128 (1)	......AC....			1	
PPL7, AY601129 (14)	....T..C....	12	2		
PPL8, AY601130 (11)	....T......-		6	4	1
PPL9, AY601131 (11)	....T.......	2	9		
PPL10, AY601132 (1)	.......C....		1		
PPL11, AY601133 (7)	....T..C...-	1	5	1	
PPL12, AY601134 (2)	....T....T..	2			
PPL15, AY601137 (1)	..........-.		1		
PPL16, AY601138 (1)	.T..........	1			
PPL17, AY601139 (1)	...G........		1		
		22	89	13	7
Captive					
Finnish, AF115404 (2)	.....				
PPLC1, AY601141 (1)	C.C......T..				
PPL9, AY601131 (1)	....T.......				
European	**1122333334 7855088991 5979067897**				
Captive					
European, AF115405 (19)	GCAGTC-TCC				
PPPC1, AY601147 (1)	.T........				
PPPC2, AY601148 (1)	AT.A......				
PPPC4, AY601150 (1)	..G.......				
PPPC6, AY601152 (9)	.......C..				
PPPC7, AY601153 (1)	.....-....				
Wild					
European, AF115405 (4)	....	2	1		1
PPP3, AY601144 (1)	......T...	1			
PPP4, AY601146 (1)	....C.....	1			
PPP5, AY601145 (1)	.......C--				1
		4	1		2
	TOTAL	26	90	13	9