1 Does restocking with Japanese quail or hybrids affect

2 native populations of common quail Coturnix coturnix?

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4 A B S T R A C T

5 Natural populations of the common quail Coturnix coturnix may hybridize in the wild 6 with non-native individuals (Japanese quail Coturnix japonica or hybrids) as a result of 7 restocking for hunting purposes. Several laboratory studies suggest that this could lead 8 to a decline in the impulse to migrate in the common quail, and a drop in the frequency 9 of phenotypes showing this tendency. This could lead to an increase in common quail 10 populations in North Africa and a decrease in Europe. This paper provides new data on 11 the proportion of hybrids in Catalonia (Northeast Spain) over 24 years (1983–2006) 12 showing how restocking with Japanese quail or hybrids affects native populations of common quail. The first hybrids were detected in 1990 with an estimate of 4.65% of 13 14 non-native individuals during the breeding season of wild common quail populations. No increase in non-native or hybrid numbers was detected during the study period, 15 indicating that restocking poses no serious conservation problems at present. However, 16 17 this may change in the near future, either with or without changes in the current scenario. A prudent policy with regard to restocking with non-native individuals is 18 suggested. Moreover, further studies are needed to clarify the extent of this conservation 19 20 problem.

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<sup>22</sup> Introduction

Hybridization, understood as the interbreeding of individuals from what are believed to 24 be genetically distinct populations, regardless of the taxonomic status of such 25 populations (Rhymer and Simberloff, 1996), has recently been viewed in two different 26 ways (Allendorf et al., 2001). First, as a natural, not uncommon and probably 27 underestimated process (Endler, 1998; Mallet, 2005), that can generate genetic 28 variation, functional novelty and new species (Arnold, 1997). A paradigmatic example 29 of this approach may be the study by Grant and Grant (1992) using Darwin's finch 30 populations on the Galapagos Islands. However, Seehausen (2004) pointed out that 31 interspecies hybridization is controversial; some consider it an important mechanism of 32 33 evolution while others argue against an important role for it, because hybridization frequently results in a reduction in fitness (Mayr, 1963, 1992; Mallet, 2005), and that 34 would render the hybrids an evolutionary dead end. Second, hybridization has been 35 36 viewed as a process contrary to conservation, in which non-indigenous species displace natives. It occurs either through introduction by humans or through habitat modification 37 38 which brings previously isolated species into contact (Levin et al., 1996; Rhymer and 39 Simberloff, 1996). This displacement of native populations may occur either by competitive exclusion or by introgression. In the latter case, displacement of native taxa 40 by non-native taxa can occur very rapidly (i.e. in less than five generations; Huxel, 41 1999). Hybridization has reportedly led to many conservation problems among birds 42 (Rhymer and Simberloff, 1996). The case of the white-headed duck (Oxyura 43 leucocephala) threatened by the introduced North American ruddy duck (O.jamaicensis) 44 45 is a recent example in Europe (Owen et al., 1986; Hughes, 1996a,b; Mun oz-Fuentes et al., 2007). The common quail Coturnix coturnix is a small phasianid migratory species 46 47 with an unfavourable conservation status in Europe (SPEC 3) and a depleted status (Burfield, 2004) at present. The species is found in the Western Palearctic, West and 48

Central Asia (Gallego et al., 1997), and it could become an endangered species if 49 50 hybridization and introgression occurred with the introduced Japanese quail Coturnix japonica. Its geographical range encompasses from the British Isles to Lake Bai" kal, 51 and the Arctic Circle to the tropics (Del Hoyo et al., 1994; Johnsgard, 1998; 52 Guyomarc'h et al., 1998). It is now considered (Johnsgard, 1998; Clements, 2000) an 53 allospecies of the Japanese quail, which is distributed in most parts of Russia and East 54 Asia, including Japan, Korea, China and India. Although the breeding distribution of 55 these two species is mostly allopatric (Fig. 1), there are small areas of sympatry in the 56 Bai kal region in Russia (Izmailov, 1967; Fefelov, 1998) and in the Kentei region in 57 Mongolia (Kozlova, 1932). In spite of this, no natural hybridization has been reported 58 (Moreau and Wayre, 1968; Del Hoyo et al., 1994; Guyomarc'h et al., 1998). However, 59 Barilani et al. (2005) have suggested such a possibility on the basis of mtDNA and 60 61 nuclear DNA analyses of a small sample (five individuals). Despite this apparent lack of natural hybridization, there are several reasons to think that hybridization may occur in 62 63 the field due to restocking with Japanese quail or hybrids in some Mediterranean countries for hunting purposes (Spain, Rodri'guez-Teijeiro et al., 1993; Portugal and 64 France until 2002, Guyomarc'h, 2003; Boutin, pers. comm.; Italy, Galli, 2003 and 65 Greece, Thomaides, pers. comm.). The wild species (common quail and Japanese quail) 66 are morphologically very similar. As reported in Guyomarc'h (2003) and in Barilani et 67 al. (2005), there are some criteria which allow the differentiation of the two species: 68 length of the folded wing with respect to the tarsus length, the shape of the feathers in 69 70 the malar fields of the chin, the existence of a suspended moult in the common quail, 71 crowing call structure of males and the temperament of sexually mature males. 72 However, since 1910 (Yamashina, 1961) the original wild Japanese quail has undergone a domestication and selection process in Europe, Asia, North America and India 73

(Dere'gnaucourt et al., 2005) for egg and meat production (Yamashina, 1961; Mills et 74 75 al., 1997) which has led to a marked increase in size and weight. More recently, a strain has been developed on farms for restocking. By rearing wild common and Japanese 76 77 quail hybrids, breeders have obtained hybrid strains that are virtually indistinguishable from the native common quail. The reason why common quail are not bred in farms is 78 that Japanese quails and hybrids are better adapted to captivity, and are more 79 productive. The case of red-legged partridges Alectoris rufa and rock partridges A. 80 graeca is similar, as reported in Nadal (1992). Reproductive barriers (either pre-zygotic 81 or/and post-zygotic) between the species do not seem to be strong enough to prevent 82 hybridization. In the pre-zygotic case, it is well known that the habitat requirements of 83 Japanese quail and common quail are almost identical (Taka-Tsukasa, 1941). Moreover, 84 Dere'gnaucourt and Guyomarc'h (2003) have shown that, in captivity, common quail 85 86 females emit the greatest number of rally calls in response to mating calls from conspecific males, the lowest number to mating calls produced by Japanese quail males 87 88 and an intermediate number to mating hybrid males. On the other hand, Japanese quail females produce similar responses to all types of mating calls. Thus, quails present only 89 a partial discrimination in mate choice. However, field experiments with funnel traps 90 have shown that Japanese quail females can attract common quail males (Puigcerver et 91 92 al., 2000), even more than common quail females can (pers. obs.). Finally, a decoy with 93 the sexual call of a common quail female is able to attract not only common quail males, but also Japanese quail males and hybrids in the field (pers. obs.). With regard to 94 95 post-zygotic barriers, it is well documented that in captivity hybridization between common and Japanese quail occurs (Dere'gnaucourt et al., 2002). No differences have 96 97 been found between the average fertility, hatch and survival rates of eggs and chicks from hybrid pairs compared with those from the pure common quail. F2 and 98

backcrosses were also obtained. This potential for hybridization in the wild may be 99 100 favoured by restocking campaigns. Thousands of hybrid quails were sold each year until 101 the late 1990s by professional game breeders in Spain, France and Italy for restocking prior to the opening of the hunting season (Guyomarc'h, 2003; Puigcerver et al., 2004). 102 103 Therefore, it seems clear that hybridization and introgression of Japanese quail DNA may occur in wild native populations of common quail. One question that arises is: May 104 this introgression constitute a real threat to the native populations of common quail? 105 106 Some laboratory findings seem to support this possibility. According to Guyomarc'h (2003), the common quail is a partial migratory species. The Japanese quail lost its 107 migratory impulse during its domestication process (Dere'gnaucourt et al., 2005). 108 According to these authors, as released hybrid quails have a lower frequency of 109 migratory phenotypes (Dere'gnaucourt et al., 2004), they could mate with the 110 111 longdistance migrant common quail phenotypes that still arrive north of 40\_N. This 112 could cause a decrease in the migratory tendency of common quail populations, and, 113 consequently, a dramatic decrease in the number of long migrant individuals arriving in 114 Europe. What is more, as the frequency of migratory phenotypes in hybrid quails is considerably lower (though not yet completely eliminated) there is danger of spreading 115 genetic pollution throughout the entire distribution area, and notably towards the 116 117 African wintering zones and favourable habitats in the Maghreb. Thus, restocking practices may have contributed (or may contribute in the near future) to a lessening of 118 the impulse to migrate in quails, as well as to a drop in the frequency of phenotypes still 119 showing this tendency, leading to an increase in North African common quail 120 121 populations and a decrease in European ones. If this hypothesis were true, a rapid 122 increase in the proportion expected, because once hybridization has begun (as Dere'gnaucourt et al., 2002 suggest), it is difficult to stop, especially if hybrids are 123

fertile and mate both with other hybrids and with parental individuals (Allendorf et al., 124 2001). After a few generations, this process would result in a hybrid swarm in which 125 essentially all individuals are of hybrid origin (Huxel, 1999; Allendorf et al., 2001), 126 127 leading to a collapse of the migratory common quail population. However, there is no empirical evidence in the wild that quail populations in European breeding areas above 128 40 N is needed in order to establish the changing proportion of hybrids detected in wild 129 populations of common quail. A more realistic idea of the actual dimension of this 130 131 potential wild common quail conservation problem will be had. The aims of this study are: (a) to provide data concerning the extent of restocking in Catalonia (northeast 132 Spain), (b) to provide data concerning the proportion of hybrids found in several 133 breeding areas in this region during 24 years (1983-2006), and (c) to provide a 134 diagnosis of how restocking with Japanese quail or hybrids affects native populations of 135 136 common quail. Moreover, whether restocking with Japanese quail or hybrids is a conservation problem for the common quail is discussed and future studies to clarify the 137 138 issue are proposed.

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# 140 Materials and methods

Nine breeding areas of Catalonia (Northeast Spain, Fig. 2) were studied in a north-south 141 142 gradient, and at different heights above the sea level (from 381m to 1200 m). Nonirrigated winter cereal crops (mainly wheat and barley) and irrigated ones (mainly 143 alfalfa, vetch and meadow) were covered. The area is suitable for the study because 144 Spain is home to approximately 425,000 breeding pairs of quail (almost 60% of those in 145 146 Europe, Gallego et al., 1997) and because Catalonia is situated above 40\_N, clearly 147 indicating that birds that arrive there are phenotypically long range migrants. Moreover, historically hundreds of thousands of farm quails have been restocked in Catalonia. In 148

1995 this practice was forbidden (article 13, Diari Oficial de la Generalitat de Catalunya 149 7th June 1995) with one exception: restocking is permitted in "special intensive hunting 150 areas", where Japanese quail and hybrids may be released throughout the year. 151 Monitoring started in the breeding season of 1983. Hybrids were phenotypically 152 detected for the first time during the breeding season of 1990 (Rodri'guez-Teijeiro et 153 al., 1993). During the breeding seasons from 1983 to 2006 (from late March to early 154 April-late July to early August) census, capture and ringing campaigns 3–5 days aweek 155 156 in different breeding areas in Catalonia were carried out (Fig. 2). The breeding areas sampled ranged from 1 to 3 km2. Censuses were carried out from sunrise to sunset. 157 158 Transects were specifically designed for each area and every 200–300m the advertising call of common quail males was listened for. When one was heard, researchers 159 approached the plot where the individual was crowing, extended a net over the cereals 160 and tried to capture the male with the aid of a magnetic female common quail decoy. 161 This method stimulates male song (a common quail, a Japanese quail or a hybrid) and 162 163 the male usually approaches the decoy emitting its sexual call. Once the individual was 164 under the net, it was scared; the bird tried to fly and was then caught, trapped in the net. If no singing male was detected, the female decoy was still reproduced as it stimulates 165 possible silent males to sing and then it was proceeded to capture as before. It is well 166 167 known that common quail and Japanese quail have an almost total overlap of the two 168 repertoires, except for the crowing call (Guyomarc'h and Guyomarc'h, 1996), which is quite different and stereotyped in time structure in the two species (Schleidt and Shalter, 169 170 1973). Hybrid calls are intermediate and show a higher variability (Dere'gnaucourt et 171 al., 2001). Learning plays no role in the development of vocalizations (Konishi and 172 Nottebohm, 1969; Baptista, 1996). For these reasons, the structure of male songs may 173 be a powerful criterion for identifying common quail, hybrid and Japanese quail males

(Guyomarc'h and Guyomarc'h, 1996; Collins and Goldsmith, 1998). Almost 50% of 174 males detected by song were captured (Gallego et al., 1993, present study) and it was 175 possible to identify both species and hybrids by their crowing call during the capture 176 process. However, paired males do not usually respond to the female decoy, so 177 sampling was carried out mainly on single males. Analyses were conducted on the 178 captured common quail males instead of those included in the census, to avoid pseudo-179 replication. However, for Japanese quails and hybrids, some males included in the 180 181 census which were detected for several days at the same crop and which were therefore considered to be the same individual were also taken into account. During the breeding 182 183 season of 1998 an analysis to detect possible bias in estimating numbers of Japanese quail or hybrid males by their song structure was carried out. Mitochondrial (mtDNA) 184 and nuclear DNA markers (microsatellites) was used, together with Bayesian admixture 185 186 analyses to assess species distinction and identify hybrids in the wild (Barilani et al., 2005). Ninety-two captured individuals were used in a blind design in which the 187 188 researcher who carried out laboratory analyses did not know the previous classification 189 (common quail, Japanese quail or hybrid) conducted by field.Results clearly showed (Barilani et al., 2005) that all the Japanese quail or hybrids classified on basis of their 190 song structure (10) had Japanese quail mtDNA; however, Bayesian admixture analysis 191 192 as implemented in STRUCTURE (Pritchard et al., 2000) showed that a further 10 193 individuals phenotypically classified as common quails showed admixed microsatellite 194 genotypes. Therefore, although all individuals showing a Japanese quail or hybrid song 195 structure were confirmed as non-native quails by molecular analyses, an 196 underestimation of 50% of the total number of non-native individuals is expected when 197 applying the phenotype method.

## 199 **Results**

200 Hunting order plans, which have been obligatory in Catalonia since 1990, allow us to know the number of farm quails restocked in the last seventeen years. From them (Dep. 201 202 de Medi Ambient, Generalitat de Catalunya, unpublished data) it is known that more than one million farm quails were restocked in Catalonia in the period 1990-2006 203 (Table 1). These individuals were restocked throughout the year and a few days before 204 the opening of the hunting period (mid August). On average, 68,295 farm quails were 205 206 restocked per year. As shown in Table 2, during the breeding seasons of 1990-2006, a total of 5213 males were included in the census, of which 46% were captured; censused 207 208 and captured individuals are strongly correlated (r = 0.85, n = 17, p = 0.00002). Only 2.32% of captured males were Japanese quail or hybrids, and non-native captured 209 individuals (r = 0.06, n = 17, p = 0.83). However, this is an underestimation as a 210 211 proportion of hybrids emit their advertising song with the same structure as native 212 common quail males and they are, therefore, virtually indistinguishable from common 213 quail males. From the 1998 sample, when phenotypical identifications with those 214 provided by molecular analyses were compared, a more reliable estimation of 104 hybrids and Japanese quails (4.65% of the total quails captured, see Table 2) can be 215 suggested. The number of restocked individuals shows a marginally significant 216 217 correlation with the number of non-native quails captured (r = 0.47, n = 17, p = 0.056). The Japanese quails and hybrids found in the analysed samples represent 0.0067% of 218 the total number of restocked individuals. The proportion of Japanese quails and hybrids 219 220 remains fairly constant in spite of the huge number of farm quails released during the period 1990–2006 (Fig. 3); no significant trend was observed in captured ( $r^2 = 0.026$ , 221 222 F1,15 = 0.395, p = 0.539) or in estimated non-native quails (r2 = 0.029, F1,15 = 0.449, p = 0.513). 223

### 225 **Discussion**

The low hybridization rates found in Catalonia seem to contradict the predicted rapid 226 collapse of the migratory common quail population and the occurrence of a hybrid 227 swarm, especially when tens of thousands of domesticated Japanese quail and hybrids 228 are annually released as game birds into the mating areas of the common quail. 229 Restocked birds are phenotypically detectable Japanese quail or F1 hybrids, whereas 230 undetected hybrids are backcrosses (unpublished data). This difference would tend to 231 232 rule out the possibility that the low numbers of hybrids found was due to an increase in underestimation over the years. Then, if there is no increase in the number of 233 phenotypically detectable F1 hybrids, an increase in their corresponding backcrosses 234 would be unlikely. Restocking with Japanese quails or hybrids does not have severe 235 effects on wild common quail populations, as shown by their stable low capture rate 236 237 over the last 17 years. There are several possible explanations for this apparent paradox. 238 First, captured Japanese quail or hybrid individuals correspond to those restocked 239 mainly in August, just before the opening of the hunting season, that is, individuals that have survived the winter. Alternatively, they could be non-native or hybrid individuals 240 restocked throughout the year in intensive special hunting areas. The low proportion of 241 Japanese quails or hybrids captured (less than 5%) clearly suggests an extremely high 242 243 mortality rate of released individuals, badly adapted to the wild and lacking the ability to defend themselves against cold, antipredator behaviour and the ability to forage for 244 245 and select food (Guyomarc'h, 2003). This hypothesis is supported by data found in farm-reared red-legged partridges, where the global survival rate of 20 radio-tagged 246 247 individuals was 15% three months after the release (Duarte and Vargas, 2004). 248 Furthermore, hunting practices may be an important mortality factor for these restocked individuals; Guyomarc'h (2003) reports that, in a 64 000 ha sampling area of Haute-249

Garonne, 4950 quails were hunted and 75% of them were restocked individuals. 250 Therefore, if the mortality rate were very high for non-native species, then natural 251 conditions and hunting pressure would "clean" natural native species populations and 252 253 would strongly reduce the risk of genetic pollution, maintaining hybrid population at residual levels. This first explanation implies a lack of hybridization in field conditions; 254 there is a correlation between the number of quails captured and the census, clearly 255 indicating that the number captured is dependent on the size of the population, which 256 257 may vary greatly from year to year (Puigcerver et al., 2004). If non-native quails were the result of hybridization in the wild, a density dependence would also be expected, 258 259 however, results show no dependence on the density of the population. Furthermore, there is a marginal correlation with the number of restocked individuals suggesting that 260 non-native quails detected in the study areas could be restocked ones. However, if this 261 262 hypothesis holds, how can it explain the lack of hybridization in natural conditions? It is 263 well documented that many species not known to hybridize in nature can readily be 264 crossed in captivity, merely by placing a male of one species with a female of another one, as reported in Pierotti and Annett (1993). Therefore, it is possible that in spite of a 265 lack of reproductive barriers in captivity, there could be unknown ecological or 266 behavioural constraints for crosses in nature. A second possibility is that hybridization 267 268 between Japanese quails or hybrids and native common quails occurs in nature, but at a very low rate. It is well known that hybridization should be more common in areas 269 where one of the two species is rare (Randler, 2002), as is the case in the area studied. 270 271 The lack of hybrid swarms could be explained by a combination of a high mortality rate 272 for restocked individuals, difficulty for non-native quails to mate with common quails, 273 and a high chick mortality rate among mixed pairs. Duarte and Vargas (2004) reported 274 that on release of twenty farm-reared red-legged partridges (ten males and ten females),

only two radiotagged females paired with wild males, and only one farmreared female 275 finally nested and hatched 11 chicks, which showed a chick mortality rate of 91%. Only 276 one chick out of 20 restocked individuals survived and grew to adult size. A third non-277 278 exclusive and less likely possible explanation for the presence of non-native quails in Catalonia is that hybrids which still maintain their condition of long range migrant 279 phenotypes come from Africa. The admixed quails from Senegal found by Barilani et 280 al. (2005) may be a surprise initially, but according to Guyomarc'h (2003), releasing 281 282 Japanese quails inWest Africa (Senegal) has been a common practice since the 1990s because of the decrease in migratory phenotypes. However, as hybridization favours 283 284 sedentarization, it is not considered very likely. Focusing on the conservation aspect, at present the reservation of the genetic integrity of native species is an international 285 preoccupation (IUCN, 1998) due to recent alarming estimates of biodiversity loss 286 287 (Gaston et al., 2003). Particularly, restocking common quail populations with farm 288 reared Japanese quail or hybrids is considered to have negative conservation effects 289 (Europarl, 2002; Guyomarc'h, 2003), in spite of the lack of empirical data. Results 290 indicate that under the scenario described (high hunting pressure, hybrids probably poorly adapted to natural conditions, etc.) the potential and suggested conservation 291 problem arising from restocking with Japanese quail or hybrids does not exist. 292 293 However, even though this scenario may not change for a long time, it should not be 294 forgotten that in biotic invasions, the progression from non-native species to invader often involves a delay or lag phase (which may last some decades) followed by a phase 295 296 of rapid exponential increase in both numbers and distribution that continues until the 297 species reaches the bounds of its new range and its population growth rate slackens 298 (Mack et al., 2000). For this reason, in spite of opinions suggesting that conservationists need not raise the alarm every time populations exchange genes (Rhymer and 299

Simberloff, 1996) and that this exchange may even have positive effects (Grant and 300 Grant, 1992; Endler, 1998; Mallet, 2005; Tompkins et al., 2006), it is very important to 301 adopt a vigilant attitude towards this hypothetical problem and observe its evolution 302 carefully in the near future. A prudent policy to prevent biological invasions 303 fromoccurring when possible is also suggested, together with a re-analysis of the extent 304 of this potential conservation problem. Finally, as there is no direct evidence of field 305 interbreeding of released farm-reared quails with wild ones, new radiotracking studies 306 307 carried out with farm restocked quails are strongly suggested, to establish whether the lack of reproductive barriers seen under laboratory conditions applies in the field. These 308 should be combined with studies concerning assortative mating and the breeding 309 success in natural conditions of different mates (non-native female with native male, 310 native female with non-native male, native couple, non-native couple). 311

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Fig. 1 – Breeding areas of the common quail (vertical lines) and the Japanese quail (horizontal lines), showing the area of populations' overlap.



407	
408	Table 1 – Restocked farm quails (Japanese quail or hybrids) in Catalonia from 1990 to 2006 (percent of the total restocked quails is
409	given in parenthesis)total restocked quails is given in parenthesis)
110	given in parentiesis), our resconce quaries is given in parentiesis)
111	Var / No. of restantial individuals
411	real/No. of restocked individuals
415	1990 17,550 (1.5)
415	1991 2430 (0.2)
414	1992 27,425 (2,4)
415	1993 10,271 (0.9)
419	1994 33,742 (2.9)
417	1995 37,997 (3.3)
410	1996 94,838 (8.2)
419	1997 49,947 (4.3)
420	1998 90,406 (7.8)
444	1999 93,984 (8.1)
422	2000 80,217 (6.9)
423	2001 93,006 (8)
424	2002 114,100 (9.8)
4425	2003 153,600 (13.2)
420	2004 115,500 (9.9)
44/	2005 81,500 (7)
428	2006 64,500 (5.6)
429	Total 1,161,013
431 432	Source: Hunting order plans (Dep. de Medi Ambient, Generalitat de Catalunya, unpublished data)
433	Table 2 – Summary of censused and captured quails in the study areas from 1990, year in which the first Japanese quail or
454	nybrid was detected in the field
/135	Veer/Cansured/Contured/Common quoil/Japanese quoil/Hybrids/Japanese quoil + hybrids/Estimation (%) (Japanese quoil +
426	Let i i i
430	nyonas)
437	
430	
439	1992 222 114 114 0 0 0 0 1002 191 00 77 0 2 7 5
770	
772	1974 136 100 104 1 1 2 3.6 1005 270 125 123 0.2 3 2
443	1995 210 125 125 20 2 3.2
	1007 431 195 191 13 4 4 3
<u>ảả</u> ś	1997 391 105 115 115 2 5 8 7
446	1999 243 178 174 4 0 4 4 5
447	2000 422 206 201 2 3 5 4 9
448	2001 26 14 113 10 1 18
449	2002 352 150 146 4 0 4 5 3
45Ŏ	2003 203 105 99 1 5 6 11 4
451	2004 551 238 238 0 0 0
452	2005 443 163 160 0 3 3 3.7
453	2006 261 78 76 0 2 2 5.1
454	Total 5213 2393 2341 27 25 52 4.7
455	Common quails, non-native quails (Japanese quails and/or hybrids) and a more reliable estimation from molecular analyses are reported.