Does restocking with Japanese quail or hybrids affect native populations of common quail Coturnix coturnix?

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ABSTRACT

Natural populations of the common quail Coturnix coturnix may hybridize in the wild with non-native individuals (Japanese quail Coturnix japonica or hybrids) as a result of restocking for hunting purposes. Several laboratory studies suggest that this could lead to a decline in the impulse to migrate in the common quail, and a drop in the frequency of phenotypes showing this tendency. This could lead to an increase in common quail populations in North Africa and a decrease in Europe. This paper provides new data on the proportion of hybrids in Catalonia (Northeast Spain) over 24 years (1983–2006) 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 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, indicating that restocking poses no serious conservation problems at present. However, 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 suggested. Moreover, further studies are needed to clarify the extent of this conservation problem.

Introduction
Hybridization, understood as the interbreeding of individuals from what are believed to be genetically distinct populations, regardless of the taxonomic status of such populations (Rhymer and Simberloff, 1996), has recently been viewed in two different ways (Allendorf et al., 2001). First, as a natural, not uncommon and probably underestimated process (Endler, 1998; Mallet, 2005), that can generate genetic variation, functional novelty and new species (Arnold, 1997). A paradigmatic example of this approach may be the study by Grant and Grant (1992) using Darwin’s finch populations on the Galapagos Islands. However, Seehausen (2004) pointed out that interspecies hybridization is controversial; some consider it an important mechanism of 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 would render the hybrids an evolutionary dead end. Second, hybridization has been 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 which brings previously isolated species into contact (Levin et al., 1996; Rhymer and Simberloff, 1996). This displacement of native populations may occur either by competitive exclusion or by introgression. In the latter case, displacement of native taxa by non-native taxa can occur very rapidly (i.e. in less than five generations; Huxel, 1999). Hybridization has reportedly led to many conservation problems among birds (Rhymer and Simberloff, 1996). The case of the white-headed duck (Oxyura leucocephala) threatened by the introduced North American ruddy duck (O.jamaicensis) 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 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
Central Asia (Gallego et al., 1997), and it could become an endangered species if hybridization and introgression occurred with the introduced Japanese quail Coturnix japonica. Its geographical range encompasses from the British Isles to Lake Baikal, and the Arctic Circle to the tropics (Del Hoyo et al., 1994; Johnsgard, 1998; Guyomarc’h et al., 1998). It is now considered (Johnsgard, 1998; Clements, 2000) an allospecies of the Japanese quail, which is distributed in most parts of Russia and East Asia, including Japan, Korea, China and India. Although the breeding distribution of these two species is mostly allopatric (Fig. 1), there are small areas of sympathy in the Baikal region in Russia (Izmailov, 1967; Fefelov, 1998) and in the Kentei region in Mongolia (Kozlova, 1932). In spite of this, no natural hybridization has been reported (Moreau and Wayre, 1968; Del Hoyo et al., 1994; Guyomarc’h et al., 1998). However, Barilani et al. (2005) have suggested such a possibility on the basis of mtDNA and 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 the field due to restocking with Japanese quail or hybrids in some Mediterranean countries for hunting purposes (Spain, Rodríguez-Teijeiro et al., 1993; Portugal and France until 2002, Guyomarc’h, 2003; Boutin, pers. comm.; Italy, Galli, 2003 and Greece, Thomaides, pers. comm.). The wild species (common quail and Japanese quail) are morphologically very similar. As reported in Guyomarc’h (2003) and in Barilani et al. (2005), there are some criteria which allow the differentiation of the two species: length of the folded wing with respect to the tarsus length, the shape of the feathers in the malar fields of the chin, the existence of a suspended moult in the common quail, crowing call structure of males and the temperament of sexually mature males. However, since 1910 (Yamashina, 1961) the original wild Japanese quail has undergone a domestication and selection process in Europe, Asia, North America and India.
(Dere´gnaucourt et al., 2005) for egg and meat production (Yamashina, 1961; Mills et 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 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 that Japanese quails and hybrids are better adapted to captivity, and are more productive. The case of red-legged partridges Alectoris rufa and rock partridges A. graeca is similar, as reported in Nadal (1992). Reproductive barriers (either pre-zygotic or/and post-zygotic) between the species do not seem to be strong enough to prevent hybridization. In the pre-zygotic case, it is well known that the habitat requirements of Japanese quail and common quail are almost identical (Taka-Tsukasa, 1941). Moreover, Dere´gnaucourt and Guyomarc’h (2003) have shown that, in captivity, common quail 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 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 a partial discrimination in mate choice. However, field experiments with funnel traps have shown that Japanese quail females can attract common quail males (Puigcerver et al., 2000), even more than common quail females can (pers. obs.). Finally, a decoy with 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 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 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
backcrosses were also obtained. This potential for hybridization in the wild may be
favoured by restocking campaigns. Thousands of hybrid quails were sold each year until
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).
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
this introgression constitute a real threat to the native populations of common quail?
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
migratory impulse during its domestication process (Dere´gnaucourt et al., 2005).
According to these authors, as released hybrid quails have a lower frequency of
migratory phenotypes (Dere´gnaucourt et al., 2004), they could mate with the
longdistance migrant common quail phenotypes that still arrive north of 40_N. This
could cause a decrease in the migratory tendency of common quail populations, and,
consequently, a dramatic decrease in the number of long migrant individuals arriving in
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
genetic pollution throughout the entire distribution area, and notably towards the
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
the impulse to migrate in quails, as well as to a drop in the frequency of phenotypes still
showing this tendency, leading to an increase in North African common quail
populations and a decrease in European ones. If this hypothesis were true, a rapid
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
fertile and mate both with other hybrids and with parental individuals (Allendorf et al., 2001). After a few generations, this process would result in a hybrid swarm in which essentially all individuals are of hybrid origin (Huxel, 1999; Allendorf et al., 2001), 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 40\_N is needed in order to establish the changing proportion of hybrids detected in wild populations of common quail. A more realistic idea of the actual dimension of this 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 Spain), (b) to provide data concerning the proportion of hybrids found in several breeding areas in this region during 24 years (1983–2006), and (c) to provide a diagnosis of how restocking with Japanese quail or hybrids affects native populations of 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 issue are proposed.

**Materials and methods**

Nine breeding areas of Catalonia (Northeast Spain, Fig. 2) were studied in a north–south gradient, and at different heights above the sea level (from 381m to 1200 m). Non-irrigated winter cereal crops (mainly wheat and barley) and irrigated ones (mainly alfalfa, vetch and meadow) were covered. The area is suitable for the study because Spain is home to approximately 425,000 breeding pairs of quail (almost 60\% of those in Europe, Gallego et al., 1997) and because Catalonia is situated above 40\_N, clearly 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
1995 this practice was forbidden (article 13, Diari Oficial de la Generalitat de Catalunya 7th June 1995) with one exception: restocking is permitted in “special intensive hunting areas”, where Japanese quail and hybrids may be released throughout the year.

Monitoring started in the breeding season of 1983. Hybrids were phenotypically detected for the first time during the breeding season of 1990 (Rodríguez-Teijeiro et al., 1993). During the breeding seasons from 1983 to 2006 (from late March to early April–late July to early August) census, capture and ringing campaigns 3–5 days aweek 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. 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 approached the plot where the individual was crowing, extended a net over the cereals and tried to capture the male with the aid of a magnetic female common quail decoy. This method stimulates male song (a common quail, a Japanese quail or a hybrid) and the male usually approaches the decoy emitting its sexual call. Once the individual was 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 possible silent males to sing and then it was proceeded to capture as before. It is well known that common quail and Japanese quail have an almost total overlap of the two 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, 1973). Hybrid calls are intermediate and show a higher variability (Deregnacourt et al., 2001). Learning plays no role in the development of vocalizations (Konishi and Nottebohm, 1969; Baptista, 1996). For these reasons, the structure of male songs may 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 males detected by song were captured (Gallego et al., 1993, present study) and it was possible to identify both species and hybrids by their crowing call during the capture process. However, paired males do not usually respond to the female decoy, so sampling was carried out mainly on single males. Analyses were conducted on the captured common quail males instead of those included in the census, to avoid pseudo-replication. However, for Japanese quails and hybrids, some males included in the 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 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) and nuclear DNA markers (microsatellites) was used, together with Bayesian admixture 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 researcher who carried out laboratory analyses did not know the previous classification (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 song structure (10) had Japanese quail mtDNA; however, Bayesian admixture analysis as implemented in STRUCTURE (Pritchard et al., 2000) showed that a further 10 individuals phenotypically classified as common quails showed admixed microsatellite genotypes. Therefore, although all individuals showing a Japanese quail or hybrid song structure were confirmed as non-native quails by molecular analyses, an underestimation of 50% of the total number of non-native individuals is expected when applying the phenotype method.
**Results**

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. 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 (Table 1). These individuals were restocked throughout the year and a few days before the opening of the hunting period (mid August). On average, 68,295 farm quails were 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 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 individuals ($r = 0.06$, $n = 17$, $p = 0.83$). However, this is an underestimation as a proportion of hybrids emit their advertising song with the same structure as native common quail males and they are, therefore, virtually indistinguishable from common quail males. From the 1998 sample, when phenotypical identifications with those 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 suggested. The number of restocked individuals shows a marginally significant 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 the total number of restocked individuals. The proportion of Japanese quails and hybrids 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 ($r^2 = 0.026$, $F_{1,15} = 0.395$, $p = 0.539$) or in estimated non-native quails ($r^2 = 0.029$, $F_{1,15} = 0.449$, $p = 0.513$).
Discussion

The low hybridization rates found in Catalonia seem to contradict the predicted rapid collapse of the migratory common quail population and the occurrence of a hybrid swarm, especially when tens of thousands of domesticated Japanese quail and hybrids are annually released as game birds into the mating areas of the common quail. Restocked birds are phenotypically detectable Japanese quail or F1 hybrids, whereas undetected hybrids are backcrosses (unpublished data). This difference would tend to 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 phenotypically detectable F1 hybrids, an increase in their corresponding backcrosses would be unlikely. Restocking with Japanese quails or hybrids does not have severe effects on wild common quail populations, as shown by their stable low capture rate over the last 17 years. There are several possible explanations for this apparent paradox. First, captured Japanese quail or hybrid individuals correspond to those restocked 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 restocked throughout the year in intensive special hunting areas. The low proportion of Japanese quails or hybrids captured (less than 5%) clearly suggests an extremely high 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 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 individuals was 15% three months after the release (Duarte and Vargas, 2004). 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-
Garonne, 4950 quails were hunted and 75% of them were restocked individuals.

Therefore, if the mortality rate were very high for non-native species, then natural conditions and hunting pressure would “clean” natural native species populations and 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; there is a correlation between the number of quails captured and the census, clearly indicating that the number captured is dependent on the size of the population, which 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, 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 non-native quails detected in the study areas could be restocked ones. However, if this hypothesis holds, how can it explain the lack of hybridization in natural conditions? It is well documented that many species not known to hybridize in nature can readily be 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 lack of reproductive barriers in captivity, there could be unknown ecological or behavioural constraints for crosses in nature. A second possibility is that hybridization 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 where one of the two species is rare (Randler, 2002), as is the case in the area studied. The lack of hybrid swarms could be explained by a combination of a high mortality rate for restocked individuals, difficulty for non-native quails to mate with common quails, and a high chick mortality rate among mixed pairs. Duarte and Vargas (2004) reported 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
finally nested and hatched 11 chicks, which showed a chick mortality rate of 91%. Only
one chick out of 20 restocked individuals survived and grew to adult size. A third non-
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
phenotypes come from Africa. The admixed quails from Senegal found by Barilani et
al. (2005) may be a surprise initially, but according to Guyomarc’h (2003), releasing
Japanese quails in West Africa (Senegal) has been a common practice since the 1990s
because of the decrease in migratory phenotypes. However, as hybridization favours
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
preoccupation (IUCN, 1998) due to recent alarming estimates of biodiversity loss
(Gaston et al., 2003). Particularly, restocking common quail populations with farm
reared Japanese quail or hybrids is considered to have negative conservation effects
(Europarl, 2002; Guyomarc’h, 2003), in spite of the lack of empirical data. Results
indicate that under the scenario described (high hunting pressure, hybrids probably
poorly adapted to natural conditions, etc.) the potential and suggested conservation
problem arising from restocking with Japanese quail or hybrids does not exist.
However, even though this scenario may not change for a long time, it should not be
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
of rapid exponential increase in both numbers and distribution that continues until the
species reaches the bounds of its new range and its population growth rate slackens
(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
Simberloff, 1996) and that this exchange may even have positive effects (Grant and Grant, 1992; Endler, 1998; Mallet, 2005; Tompkins et al., 2006), it is very important to adopt a vigilant attitude towards this hypothetical problem and observe its evolution carefully in the near future. A prudent policy to prevent biological invasions from occurring when possible is also suggested, together with a re-analysis of the extent of this potential conservation problem. Finally, as there is no direct evidence of field interbreeding of released farm-reared quails with wild ones, new radiotracking studies 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 should be combined with studies concerning assortative mating and the breeding success in natural conditions of different mates (non-native female with native male, native female with non-native male, native couple, non-native couple).

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REFERENCES


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

Fig. 2 – Breeding sites of the common quail where the study was carried out. (1) Alp (1100m above sea level, 42° 11.4'E, 53.4'N). (2) Fortia' (8m above sea level, 42° 14.1'E, 53.4'N). (3) Sant Boi de Lluc'ane's (810m above sea level, 42° 2.9'E, 3.5'N). (4) Folgueróles (552m above sea level, 41° 56.5'N, 12.9'E). (5) Calaf (680m above sea level, 41° 44.3'N, 30.9'E). (6) Vilanova de Segrià' (255m above sea level, 41° 42.9'N, 37.3'E). (7) Santa Maria de Miralles (628m above sea level, 41° 29.9'E, 32.3'E). (8) Figuerola del Camp (494m above sea level, 41° 22.5'N, 15.6'E). (9) Pla de Santa Maria (381m above sea level, 41° 22.1'N, 17.8'E).
Table 1 – Restocked farm quails (Japanese quail or hybrids) in Catalonia from 1990 to 2006 (percent of the total restocked quails is given in parenthesis/total restocked quails is given in parenthesis)

<table>
<thead>
<tr>
<th>Year/ No. of restocked individuals</th>
<th>1990 17,550 (1.5)</th>
<th>1991 2430 (0.2)</th>
<th>1992 27,425 (2.4)</th>
<th>1993 10,271 (0.9)</th>
<th>1994 33,742 (2.9)</th>
<th>1995 37,997 (3.3)</th>
<th>1996 94,838 (8.2)</th>
<th>1997 49,947 (4.3)</th>
<th>1998 90,406 (7.8)</th>
<th>1999 93,964 (8.1)</th>
<th>2000 80,217 (6.9)</th>
<th>2001 93,006 (8)</th>
<th>2002 114,100 (9.8)</th>
<th>2003 153,600 (13.2)</th>
<th>2004 115,500 (9.9)</th>
<th>2005 81,500 (7)</th>
<th>2006 64,500 (5.6)</th>
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<td>Total 1,161,013</td>
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Source: Hunting order plans (Dep. de Medi Ambient, Generalitat de Catalunya, unpublished data)

Table 2 – Summary of censused and captured quails in the study areas from 1990, year in which the first Japanese quail or hybrid was detected in the field

| Year/ Censured/ Captured/ Common quail/ Japanese quail/ Hybrids/ Japanese quail + hybrids/ Estimation (%) (Japanese quail + hybrids) | 1990 365 181 179 2 0 2 2.2 | 1991 220 105 105 0 1 1 1.9 | 1992 222 114 114 0 0 0 0 | 1993 181 80 77 0.3 3 7.5 | 1994 138 106 104 1 1 2 3.8 | 1995 270 123 123 2 0 2 3.2 | 1996 356 149 141 6 2 8 10.7 | 1997 431 185 181 3 1 3 4.4 | 1998 289 115 110 3 2 5 8.7 | 1999 243 178 174 4 0 4 4.5 | 2000 422 206 201 2 3 5 4.9 | 2001 266 114 113 1 0 1 1.8 | 2002 352 150 146 4 0 4 5.3 | 2003 203 105 99 1 5 6 11.4 | 2004 551 238 238 0 0 0 0 | 2005 443 163 160 0 3 3 3.7 | 2006 261 78 76 0 2 2 5.1 | 2007 521 239 234 1 2 7 25 52.4.7 |
| Total 5213 2393 2341 27 25 52.4.7 | Common quails, non-native quails (Japanese quails and/or hybrids) and a more reliable estimation from molecular analyses are reported.