Comparison of migratory tendency in European Quail *Coturnix c. coturnix*, domestic Japanese Quail *Coturnix c. japonica* and their hybrids

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Since the 1970s, the decline of the occidental populations of European Quail *Coturnix c. coturnix*, a partial migrant Galliform species, has driven the release of domestic Japanese Quail *Coturnix c. japonica* into the wild as game birds. Recent experiments suggest that reproductive isolating mechanisms have not developed to prevent hybridization between European and Japanese Quail. To assess the potential impact of hybridization between the subspecies in the wild, this study aims to compare the migratory characteristics of captive European Quail, domestic Japanese Quail, F1 hybrids and a backcross. In a laboratory experiment, birds hatched in summer and reared under a natural photoperiod were transferred during winter to an artificial photoperiod (light–dark) of 14 : 10 h. Behavioural (migratory restlessness, crowing activity in males) and physiological (sexual development, fat accumulation, body mass) measures were recorded. Domestic Japanese Quail showed no migratory tendency in response to the increased day length. F1 hybrids showed rapid sexual development and few of them exhibited the typical profile of a migrant bird. Backcrosses showed great variation in their response, comparable with those of the European Quail. Therefore, hybridization could lead to an increased proportion of quail showing sedentary rather than migratory behaviour. Furthermore, hybrids that do show migratory behaviour have the potential to facilitate Japanese gene flow into areas where the release of domestic Quail as game birds is not yet practised.

During the past century, significant declines have been noted in European bird populations, and long-distance migrants have been affected in particular (Berthold et al. 1998). Different factors may be involved in the decline of different species. Changes in agricultural practices, together with habitat destruction, have noticeably affected birds breeding in Europe, and, since the early 1970s, wintering conditions have deteriorated because of the persistent drought that has affected countries in the Sahel region of Africa. Furthermore, recent global climatic warming may have enhanced the process of residency (Berthold et al. 1998). Indeed, milder autumns and winters and earlier springs may have reduced the normally high winter mortality of resident birds. In partial migrant populations (i.e. populations that include some individuals that do and some that do not migrate from the same breeding area; Terril & Able 1988), the proportion of residents increases, short-distance migrants travel less far, migrants return sooner to the breeding grounds and breeding begins earlier. This may increase competition and lead to a progressive loss of breeding sites for long-distance migrants, which arrive at the breeding grounds last. All this may result in a gradual restructuring of the European avifauna in favour of the residents, and partial and short-distance migrants, to the detriment of the long-distance migrants (Berthold et al. 1998). This appears to be the case for the Common or European Quail *Coturnix c. coturnix*, a partial migrant Phasianid subspecies with a breeding range that...
extends from the Atlantic to Lake Baikal and from the Arctic Circle to the tropics (Johnsgard 1988, Del Hoyo et al. 1994, Guyomarc’h et al. 1998). A decline in European Quail numbers in the western Palearctic has been observed over the last few decades (Guyomarc’h et al. 1998). This decline has led to the double listing of this subspecies in the Bonn convention (Annexe II, migrant species non-protected, but in an unfavourable conservation status) and the Berne convention (Annexe III, game bird under regulated exploitation). European Quail tend to become mainly resident in countries between 28°N and 38°N: southern Portugal to southern Morocco (Fontoura et al. 2000).

The decline of the European Quail in northern latitudes has stimulated the release of domestic Japanese Quail Coturnix c. japonica as game birds in different European countries (Rodriguez-Tejieiro et al. 1993, Guyomarc’h et al. 1998). The Japanese Quail exists in the wild in Asia (Johnsgard 1988, Del Hoyo et al. 1994), but is best known in its domestic form in Europe, Asia, North America and India, where it is farmed for meat and egg production; it is also commonly used in laboratories (Mills et al. 1997). Attempts to establish Japanese Quail in North America by releasing domestic birds were unsuccessful (Labisky 1961, Wetherbee & Jacobs 1961, Howes 1964), although populations of introduced birds have been established in Hawaii (Schwartz & Schwartz 1949, Nichols 1991).

The introduction of foreign species may lead to the disappearance of a native species: introduced animals may be carriers of diseases, especially if they are captive-born; they may compete with the native species for resources such as habitat and food; and, in some cases, they may compete for sexual partners. This may result in hybridization (Randler 2002, e.g. Potts 1988, Rhymer et al. 1994, Hoysak & Ankney 1996, Hughes 1996, Rhymer & Simberloff 1996, Negro et al. 2001). Interbreeding between the European Quail and the domestic Japanese Quail may constitute yet another example. Indeed, elsewhere, we have demonstrated that postzygotic reproductive isolating mechanisms have not been established between the two subspecies; we were able to produce hybrids readily: F₁, F₂ and backcrosses (Derégnaucourt et al. 2002). In addition, prezygotic mechanisms may not be strong enough to prevent hybridization (Derégnaucourt & Guyomarc’h 2003).

When hybridization occurs beyond the first generation, drastic demographic changes may occur that may lead to the development of a hybrid population and, in the worst case, to the disappearance of the native species (Huxel 1999). It is known that the migratory behaviour of many bird species, including Quail, has a genetic component (Gwinner 1986, Guyomarc’h & Guyomarc’h 1995, Guyomarc’h & Belhamra 1998) and that it is, to a large extent, inherited (Berthold 1988, Pulido et al. 1996). Crossing birds with different migratory tendencies, such as different strains from the same species, or different species, results in intermediate patterns of movements in terms of migratory direction and/or distance (Berthold 1998). Thus, crossing birds with different migratory tendencies may result in demographic changes within natural populations.

A study of sexual development in the domestic Japanese Quail has shown that they lack many of the behavioural and physiological characteristics shown by the migratory birds when kept in captivity (Guyomarc’h 1985). Hunters have been aware of this loss of migratory impulse in domestic strains since the 1970s; their goal has been to establish a sedentary game bird that does not disperse from the release sites (Rizzoni & Lucchetti 1972). Thus, hybridization between the rare long-distance migrant European Quail that still arrive in Europe with the non-migrant domestic Japanese Quail may modify the migratory patterns of wild populations of quail. In addition, the survival of hybrid quail will depend on their abilities to survive in the wild. Long-distance migration is an adaptation to winter conditions of northern and central Europe where, with the exception of isolated observations (Guyomarc’h et al. 1998), European Quail are generally not observed outside the breeding season and, presumably, would not survive. To address the potential effects of hybridization on natural quail populations, the aim of this study was to compare the sexual and migratory characteristics of hybrid birds with those of European and domestic Japanese Quail.

**METHODS**

**Subjects**

Thirty-six female and 26 male European Quail (EUR) were randomly selected from a captive stock maintained in our laboratory. The founders were wild migratory birds caught in France (1983/84), Spain (1992) and Portugal (1997). The use of biometrical measures (wing length, tarsus length and their ratio), sonographic analysis of male mating call structure and the high proportion of long-distance...
migratory birds (Saint Jalme 1990, Belhamra 1997) ensured that our breeding population was representative of a wild population.

We used 16 male and 12 female Japanese Quail (JAP) of a domestic strain selected for meat and egg production (Agronomic Research National Institute, Nouzilly, France).

We then used these strains of European and Japanese Quail to produce hybrid birds (F₁, F₂ and backcrosses) (Derégnaucourt et al. 2002). Because we did not have space to house birds of all possible hybrid combinations, we decided to use only one F₁ cross (mother Japanese × father European: F₁), and a backcross (mother F₁ × father European: BC₁).

As the sex ratio is male biased at the beginning of the breeding season in Europe (Puigcerver 1991, Mur 1994), these crosses are those most likely to occur in the field. Therefore, we randomly selected (1) 22 males and 26 females from the F₁ cross, and (2) 22 males and 22 females from the BC₁ cross.

**Experimental procedures**

After hatching (June and July), the birds were held in groups of ten individuals in indoor pens in the laboratory (ten birds per pen), under natural day lengths until the wintering phase in December when the photoperiod had reached approximately 9.5 : 14.5 h of light–dark (LD) (Rennes, France, 48°N). All birds were sexually regressed at the beginning of the breeding season in Europe (Puigcerver 1991, Mur 1994), these crosses are those most likely to occur in the field. Therefore, we randomly selected (1) 22 males and 26 females from the F₁ cross, and (2) 22 males and 22 females from the BC₁ cross.

**Physiological state of the birds**

The physiological state of the birds was checked every 10 days. Sexual development was assessed by measuring the length of the cloacal vent (Sachs 1969). In addition, we noted the appearance of cloacal foam in males and egg laying activity in females. The width of the pectoral lipid band (viewed through the skin) was also measured. This is a good indicator of a European Quail’s fat accumulation because there is a positive correlation between this measure and the total body fat content (Guyomarc’h et al. 1990). In addition, this is an indicator of the migratory state because Saint Jalme (1990) observed a positive correlation between the width of this band and the level of migratory restlessness in a laboratory experiment. Here, we investigated whether this could be a valuable indicator of migratory activity in both Japanese and hybrid Quail. The two morphological measures were taken with callipers to the nearest 0.1 mm. Body mass of the birds was measured with an electronic balance (precision of 0.1 g). Measurements were performed at approximately the same time of day on each day of sampling.

**Migratory restlessness**

The quail is a nocturnal migrant (Guyomarc’h et al. 1998). ‘Zugunruhe’ or migratory restlessness is the extra activity performed by captive birds during the migratory season (Berthold 1993). It has been shown that the pattern of timing and amount of migratory restlessness is a reliable measure of migratory activity in the wild in several species of migrant birds (Berthold 1973, Gwinner & Czelschlik 1978, Pulido et al. 2001), including quail (Hémon et al. 1986). Throughout the experiment, the activity of each bird was recorded continuously by using infrared detectors. Movements of the bird cut a horizontal infrared beam: the signal was amplified and transmitted to an Amiga computer. The numbers of cuts were recorded sequentially every 12 min. After analysis by custom-made software, we obtained actograms, i.e. representation of the activity of each bird for each day (Fig. 1, cf. Guyomarc’h & Guyomarc’h 1992).

We counted the number of nights of migratory restlessness during the 60 days of the experiment for each bird. In addition, we measured the level of activity (i.e. number of cuts of the infrared beam) per night of migratory impulse.

**Classification of the etho-physiological phenotypes**

We classified etho-physiological phenotypes using the sexual state of the birds and their daily patterns of activity, but not by the width of the lipid band, because although this is a good indicator of migratory tendency in European Quail, it has not been validated for Japanese and hybrid Quail.
In order to create a typology of daily profiles, levels of activity for each bird were measured during different parts of the daily cycle (Fig. 1, LD 14 : 10 h, lights switched on at 06:00 h and off at 20:00 h): P1, 17:00–20:00 h; P2, 20:00–23:00 h; P3, 24:00–03:00 h; P4, 03:00–06:00 h; P5, 06:00–09:00 h. We defined four profiles focused on nocturnal activity: (1) P2 + P3 + P4 < 200 beam cuts: an exclusively diurnal bird (Fig. 1A); (2) P2 + P3 + P4 > 200, three options: (2.1) the level of activity was maximum in P2 (beginning of the night, Fig. 1B), (2.2) the level of activity was maximum in P3 (middle of the night, Fig. 1C) and (2.3) the level of activity was maximum in P4 (end of the night, Fig. 1D).

Following previous experiments on European Quail in the field (Hémon et al. 1986) and in the laboratory (Saint Jalme 1990), we could interpret these behaviours in different ways. Males could show these four profiles whatever their sexual development. The expression of profiles B, C and D could be interpreted as migratory restlessness in males in sexual quiescence (C and D are often present during the first days of migratory restlessness but disappear rapidly). The situation was more complex in sexually mature males. Some birds showed sexual development at the end of the migratory phase and continued to show a peak in nocturnal activity at the beginning of the night. We interpreted this as migratory restlessness. This profile of activity in sexually mature males could also be interpreted as being associated with nomadic movement during the breeding season (Berthold 1993). Other individuals showed a D profile during gonadal development. This activity, maximal at the end of the night, could be related to crowing activity that occurs in anticipation of sunrise in the wild (Guyomarc’h & Thibout 1969, Hémon et al. 1986), and subsequently was not considered as migratory restlessness. The expression of the C profile could be interpreted in one of two ways: (1) a delayed start of migratory restlessness during the night, or (2) an anticipation of the sunrise activity linked with crowing behaviour. We therefore considered this to be the preferred option of mature males when P2 > P4, and the second option when P2 < P4. The four profiles can be observed in females in sexual quiescence. Only the A profile was shown by females engaged in egg laying.

Moreover, each individual could show different daily profiles during the experiment. Therefore, we proposed a hierarchical classification of the responses to increasing day length as follows. (1) Birds that showed nocturnal activity during sexual quiescence: ‘migrant birds’. Some of the males classified as ‘migrant birds’ could maintain a migratory restlessness during gonadal development. (2) Birds that exhibited migratory restlessness only when they developed sexually: ‘nomads’. This phenotype was only shown by some males and never observed in females. (3) Birds that developed sexually and never showed migratory restlessness: ‘sedentary birds’.

**Statistical analysis**

The two subspecies of Palearctic quail are sexually dimorphic, with females larger than males (Guyomarc’h et al. 1998), and etho-physiological differences between
sexes have been reported (Saint Jalme & Guyomarc’h 1995, Guyomarc’h & Belhamra 1998). We therefore performed analyses on the sexes separately. The domestic Japanese Quails that we used were larger than the European Quails from our laboratory strain, as shown by tarsus length (values are reported as mean ± se throughout) (JAP: males: 33.2 ± 0.2 mm, n = 24, females: 33.2 ± 0.2 mm, n = 15; EUR: males: 27.6 ± 0.1 mm, n = 44, females: 27.8 ± 0.1 mm, n = 66). The hybrids were intermediate in size between the two parental strains (tarsus length, F₁: males 30.0 ± 0.2 mm, n = 39, females 30.2 ± 0.2 mm, n = 54; BC₁: males 28.3 ± 0.2 mm, n = 35, females 28.6 ± 0.2 mm, n = 24; Derégnaucourt 2000). We back transformed all residuals to a normalized European Quail tarsus length estimate for use in figures by adding residuals to the mean of log European Quail tarsus length and was especially pronounced for JAP (day 0: 3.3 ± 0.1 mm, day 10: 5.3 ± 0.2 mm) and BC₁ (day 0: 3.4 ± 0.1 mm, day 10: 4.3 ± 0.1 mm) (Spjøtvoll–Stoline post-hoc test, 0.7 < absolute mean difference < 2, P < 0.001), whereas sexual development was more progressive for EUR (i.e. no significant differences were observed between a particular measure and those performed either 10 days before or 10 days after). Twenty days after the lengthening of the photophase, 100% of JAP (16/16) and F₁ (22/22), 73% of BC₁ (16/22) and 35% of EUR (9/26) showed a developed cloacal gland, which indicated that they were physiologically able to reproduce. During the same period, more than 70% of JAP and F₁ males started crowing whereas fewer than 40% of EUR and BC₁ did so.

As in males, changes in the length of cloacal vent differed between the groups of females (Fig. 2, repeated-measures ANOVA, F₁8,555 = 3.71, P < 0.001). A significant increase was observed between day 0 and day 10 in all the groups (Spjøtvoll–Stoline post-hoc test, 0.8 < absolute mean difference < 2, P < 0.002), and was especially pronounced for JAP (day 0: 3.4 ± 0.2 mm, day 10: 6.1 ± 0.4 mm). This increase was also significant between day 10 and day 20 for F₁ and BC₁ (F₁, day 10: 5.3 ± 0.3 mm, day 20: 6.9 ± 0.4 mm; BC₁, day 10: 4.3 ± 0.2 mm, day 20: 6.2 ± 0.4 mm; Spjøtvoll–Stoline post-hoc test, absolute mean differences for F₁: 1.6, BC₁: 1.9, P < 0.001). These results are linked to the increasing number of egg-laying females during the experiment. After 20 days of the experiment, 100% of JAP (12/12), 80% of F₁ (21/26), 70% of BC₁ (15/22) and 30% of EUR (11/36) had laid. Some females never laid during the experiment: nine EUR (25%), five BC₁ (23%) and one F₁ (4%).

Changes in the width of the lipid band and body mass

In males, a significant difference was observed between the groups in the width of the pectoral lipid band during the experiment (Fig. 2, repeated-measures ANOVA, F₁8,492 = 3.48, P < 0.001). The width of the lipid band of JAP was higher than that of the other groups at day 0 but the difference was significant only with EUR (JAP: 8.6 ± 0.2 mm; EUR: 5.5 ± 0.5 mm; Spjøtvoll–Stoline post-hoc test, absolute mean difference = 3.1, P < 0.001). The width of the lipid band fluctuated significantly for EUR and BC₁ during the experiment: we observed significant differences between the measurements at day 0 and each of the other measurements performed.

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Spjøtvoll–Stoline post-hoc test, $0.5 < \text{absolute mean difference} < 4.2, P < 0.001$). This was not the case for JAP and $F_1$, in which the width of the pectoral band did not show significant changes ($0.05 < \text{absolute mean difference} < 2, P > 0.05$ for the same comparisons). The maximal gain (i.e. difference between the measure of the width of the lipid band at day 0 and its maximal value) differed significantly between the groups (ANOVA, $F_{3,82} = 7.1, P < 0.001$). EUR males had accumulated significantly more pectoral fat than JAP (EUR: $5.1 \pm 0.7$ mm; JAP: $1.3 \pm 0.4$ mm; Spjøtvoll–Stoline post-hoc test, absolute mean difference $= 3.8, P = 0.001$). Other comparisons between the four groups revealed no significant differences.

Figure 2. Changes in length of cloacal vent, width of lipid band and body mass in quail exposed to a light–dark photoperiod of 14 : 10 h for 60 days. Data points correspond to mean values. Error bars (se) have been added to the upper mean and to the lower mean at each time point. EUR: European Quail; JAP: Japanese Quail; $F_1$: mother JAP × father EUR; $BC_1$: backcross mother $F_1$ × father EUR.
Body mass increased in all groups of males at the beginning of the experiment, and decreased after day 40 in EUR. However, no significant difference between any of the groups was observed during the experiment (Fig. 2, repeated-measures ANOVA, \( F_{18,492} = 1.52, P = 0.08 \)).

In females, the width of the lipid band differed significantly between the groups over the course of the experiment (Fig. 2, repeated-measures ANOVA, \( F_{18,552} = 2.65, P < 0.001 \)). In JAP, we observed an increase throughout the experiment but no significant differences were observed between measurement days. Lipid band width increased at the beginning of the experiment for other groups and then decreased after day 40 in EUR (day 40: 11.0 ± 0.7 mm, day 50: 9.0 ± 0.8 mm; absolute mean difference = 2, \( P < 0.001 \)) and \( F_1 \) (day 40: 11.3 ± 0.9 mm, day 50: 9.6 ± 0.9 mm; absolute mean difference = 1.7, \( P > 0.05 \)) and at day 50 in BC₁ (day 50: 12.0 ± 1.0 mm, day 60: 10.6 ± 1.0 mm; absolute mean difference = 1.4, \( P > 0.05 \)). We observed no significant difference between the groups for the maximum level of pectoral fat accumulation during the experiment (EUR: 4.2 ± 0.6; BC₁: 5 ± 1.0; \( F_1 \): 3.4 ± 0.8; JAP: 3.2 ± 0.4; ANOVA, \( F_{3,92} = 1.09, P = 0.3581 \)).

Changes in body mass differed between the groups during the experiment (Fig. 2, repeated-measures ANOVA, \( F_{18,552} = 11.53, P < 0.001 \)). It increased significantly between day 0 and day 10 in JAP females (day 0: 77.1 ± 1.5 g, day 10: 101.4 ± 1.7 g; Spjøtvoll–Stoline post-hoc test, absolute mean difference = 24.3, \( P < 0.001 \)), and was more progressive for females of other groups. This increase was mainly linked to the increasing number of females that reached sexual maturity (oviduct development, weight of the eggs in formation).

**Expression of the different etho-physiological phenotypes**

The majority of EUR (23/26, 88%) and BC₁ (13/22, 59%) males presented a ‘migrant’ behavioural profile (Fig. 3). Only four of 22 (18%) \( F_1 \) showed the same phenotype, and nine (41%) exhibited nocturnal activity characteristic of ‘nomad’ birds. One male JAP showed this phenotype, but most (15/16, 94%) did not show migratory restlessness and were classified as ‘sedentary’.

In females, the proportions of migrant and sedentary females differed significantly between the four groups (Fig. 3, \( \chi^2 = 23.1, df = 3, P < 0.001 \)). The majority of EUR (29/36, 81%) and BC₁ (13/22, 59%) showed migratory restlessness. Ten \( F_1 \) females out of the 26 (38%) and one female JAP out of 12 showed the same behaviour. Most of the JAP (11/12, 92%) developed sexually without exhibiting

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**Figure 3.** Distribution of birds of different groups in relation to their response to increased day length. The total number of birds used for the experiment is shown in parentheses. EUR: European Quail; JAP: Japanese Quail; \( F_1 \): mother JAP × father EUR; BC₁: backcross mother \( F_1 \) × father EUR.
nocturnal activity and were classified as ‘sedentary’. Some of the females started egg-laying at the beginning of the experiment, and then showed gonadal regression and nocturnal activity (EUR: 4/29; BC1: 3/22). Others interrupted a long period of migratory activity by a phase of egg laying (EUR: 1/29; BC1: 1/22; F1: 5/10).

**Level of migratory restlessness**

In males, 19 out of 26 (73%) EUR and 14 out of 22 (64%) BC1 showed more than 30 nights of migratory restlessness during the experiment, whereas only three out of 13 (23%) F1 did so. We observed a significant difference between groups in the number of active nights (Fig. 4, Kruskal–Wallis, $H = 10.139$, $df = 2$, $P = 0.0063$). EUR and BC1 showed more nights of migratory restlessness than F1 (Spjøtvoll–Stoline post-hoc test, absolute mean differences: EUR vs. H1: 16.1, BC1 vs. H1: 16.4, $P < 0.05$). No significant difference was observed between EUR and BC1. The relationship between the total number of nights of migratory restlessness and the total number of cuts of the infrared beam was high for the three groups (Spearman, EUR: $n = 24$, $Rho = 0.565$, $P = 0.0068$; BC1: $n = 18$, $Rho = 0.583$, $P = 0.0133$; F1: $n = 13$, $Rho = 0.863$, $P = 0.0028$). In addition, we observed that the difference was significant in the mean number of cuts per night (Fig. 4, Kruskal–Wallis, $H = 13.833$, $df = 2$, $P = 0.001$). F1 males presented lower levels than EUR and BC1 (Spjøtvoll–Stoline post-hoc test, absolute mean differences: EUR vs. H1: 1084, BC1 vs. H1: 1161, $P < 0.05$). No significant difference was observed between EUR and BC1.

In females, no significant difference was observed between EUR, BC1 and F1 birds regarding the number of nights during which migratory activity occurred (Kruskal–Wallis, $H = 1.856$, $df = 2$, $P = 0.3948$). Nevertheless, only two out of ten (20%) F1 birds showed more than 30 nights of migratory restlessness, whereas 10 out of 29 (35%) EUR and six out of 13 (46%) BC1 did. We found a statistically significant difference when we compared the mean number of cuts of the infrared beam per night (Fig. 4, Kruskal–Wallis, $H = 11.293$, $df = 2$, $P = 0.0035$). EUR females were more active than the F1 females during the nights of migratory restlessness (Spjøtvoll–Stoline post-hoc test, absolute mean difference = 1961, $P < 0.05$). No significant difference was observed between BC1 and the other two groups. The correlation between the total number of nights of migratory restlessness and the total number of cuts of the infrared beam was high for the three groups (Spearman, EUR: $n = 29$, $Rho = 0.818$, $P < 0.0001$; BC1: $n = 13$, $Rho = 0.922$, $P = 0.0014$; F1: $n = 10$, $Rho = 0.924$, $P = 0.0056$).
Relationships between the width of the lipid band and migratory restlessness

We excluded from the analysis a single JAP male that showed migratory restlessness. Its profile of fat accumulation did not differ from those of the other males of this cross. There was a significant correlation between fat accumulation and the number of nights of activity for EUR (Fig. 5, Spearman, $n = 26$, $Rho = 0.4939$, $P = 0.0103$). Such relationships were not observed for BC1 ($n = 22$, $Rho = 0.2512$, $P = 0.2595$) and F1 birds ($n = 22$, $Rho = 0.0848$, $P = 0.7075$).

In females, a significant correlation between fat accumulation and the number of nights of migratory restlessness was observed for the females of the three groups (Fig. 5, Spearman, EUR: $n = 36$, $Rho = 0.468$, $P = 0.004$; BC1: $n = 22$, $Rho = 0.633$, $P = 0.0015$; F1: $n = 26$, $Rho = 0.573$, $P = 0.0022$). This correlation was not observed in JAP females because they showed fat accumulation levels similar to those of the other groups but only one bird showed migratory restlessness.

DISCUSSION

When reproductive isolating mechanisms are not established, interbreeding between two species may lead to the production of hybrids with intermediate characteristics both of morphology and of behaviour (Grant & Grant 1992). Our study demonstrates that a minority of F1 hybrids derived by crossing domestic Japanese Quail, which have lost the migratory impulse, with the European Quail, a partial migrant, present migratory tendencies. These results suggest that introduction of domestic Japanese Quail in Europe and subsequent hybridization with the native European Quail may modify the migratory patterns of the natural populations of quail.

The results obtained in the European Quail agree with those from previous studies (Saint Jalme 1990). Although most individuals showed migratory
restlessness – but varying greatly between individuals in duration and/or intensity – we observed that only some developed sexually in the first days after the increase in day length. As suspected by Rizzoni and Luccetti (1972) and Guyomarc’h (1985), the migratory impulse of the domestic Japanese Quail has been eliminated by breeders. Nevertheless, we observed vestigial migratory restlessness in a female, and in a male that was sexually mature. This strain has been selected for meat and egg production for over 100 generations. It would be of interest to repeat this experiment to compare other strains of domestic Japanese Quail with their wild counterparts.

We observed a low migratory drive in the F1 hybrids. Ten females out of the 26 showed migratory restlessness, and only three of them showed more than 20 nights of activity. Whereas 13 males out of 22 exhibited nocturnal activity, only four showed the phenotype of a truly sexually regressed migrant bird. The BC1 backcross birds showed results similar to those of the European Quail in all criteria: proportion of migrant birds and intensity of nocturnal restlessness. In addition, we observed similar results in an analysis of the male mating call structure, which is thought to be under a strong genetic influence; BC1 males produced calls similar to those of the European Quail (Derégnaucourt et al. 2001). Backcrossing presumably restores the genome sufficiently close to its original form to produce behaviour near that typical of the species to which the hybrid was backcrossed. The results from our hybrid F1 and BC1 crosses agree with other studies involving crossing strains of birds with different sexual and migratory trends, demonstrating a strong genetic influence (Berthold & Querner 1981, Helbig 1991, Berthold 1998).

These results enable us to speculate about the future of European populations of quail. The geographical separation of the two subspecies has certainly induced morphological, physiological and behavioural differences in adaptation to environmental conditions, as has already been shown for other bird species (Klaassen 1995; O’Connor 1996, Prats et al. 1996). Such changes may have occurred during the domestication process of the Japanese Quail as well (Sossinka 1982): adaptive capacities such as feeding selectivity, resistance to climatic conditions and anti-predatory behaviours may have altered. As in captive-bred game birds released legimitately, such as the Common Pheasant Phasianus colchicus (Mayot et al. 1997) and the Red-legged Partridge Alectoris rufa (Havet & Biadi 1990, Mauvy et al. 1992), we might expect the majority of quail released into the wild to survive for only a short period. Nevertheless, tens of thousands of domestic quail are released in Europe each year. Released quail could mate with the rare long-distance migrant European Quail that still arrives north of the 40°N. The rapid sexual development shown by Japanese and hybrid Quail in this experiment confers a selective advantage to these birds in spring compared with any long-distance migrant European Quail that arrive on their breeding grounds later in the season. As reproductive isolating mechanisms have not evolved to prevent hybridization between the subspecies (Derégnaucourt et al. 2002, Derégnaucourt & Guyomarc’h 2003), interbreeding is likely to lead to the formation of a hybrid population.

Artificial selection in the laboratory has demonstrated that the incidence of migratory activity could change rapidly over few generations. In a captive population of European Quail, migrants and non-migrants were selectively bred in a two-way experiment (Guyomarc’h & Belhamra 1998). After two generations of selection, 38% of the birds from the non-migrant line expressed migratory restlessness compared with 98% in the migrant line (Belhamra 1997). Thus, as in the Blackcap Sylvia atricapilla (Berthold 1988), it would take only a few generations to turn a partially migrant population into either a completely migratory or an exclusively non-migrant one. Such selection has certainly occurred during the domestication process of the Japanese Quail. Because birds have been selected for high sexual drive, their migratory tendency has been counterselected. As in other partial migrant species (Berthold et al. 1998), selective environmental pressure against long-distance migratory phenotypes, such as extension of favourable breeding areas in the Maghreb together with the drought of Sahelian countries, may have favoured the short-distance migratory European Quail (Guyomarc’h et al. 1998). In addition, Pulido et al. (1996) postulated that the transition from migratory to resident behaviour is not only driven by selection favouring resident birds but also by selection for lower migratory activity. Both aspects, residency and lower migratory activity, were observed in F1 hybrids during our experiment. This selection on two aspects of the same trait may enable extremely rapid evolutionary changes to occur in migratory behaviour (Pulido et al. 1996). Thus, the introduction of non-migrant Japanese Quail, and then subsequent hybridization with European Quail, may rapidly enhance the process of residency of natural
hybridization between European Quail and Japanese Quail

populations of quail in the middle part of their breeding range.

Despite sporadic observations of quail being present in the breeding grounds in winter (Guyomarc'h et al. 1998), trophic and climatic conditions would certainly not favour the survival of non-migratory hybrids in these areas. In the European Quail, fat accumulation constitutes a good indicator of the migratory tendency (Saint Jalme 1990). This was not the case for the F₁ and BC₁ hybrids (in males) and the domestic Japanese Quail (both sexes): some exhibited fat accumulation comparable with the European subspecies but they did not engage in migratory activity. However, if the quantity of fat is not a good indicator, the quality of the lipids could be a better one. Gonçalves et al. (2001) have shown that the composition of fatty acids changed during the annual cycle in European Quail. These results may enable resident quail to be distinguished from migrant birds in southern Europe during spring and autumn. It would be interesting to repeat this experiment with domestic Japanese Quail and hybrids. If fat accumulation occurs in Japanese and hybrid quail in autumn, it may contribute to their survival in Europe during winter, especially in southern Europe. If non-migrant hybrids increasingly represent the offspring of the rare long-distance migrant European Quail that still arrive in the northern latitudes, a rapid decrease in the numbers of returning migratory quail north of the 40°N would be expected. The presence of quail in this zone would be maintained only by continual releases of commercially raised game birds. Nothing is known about the mechanisms of migratory orientation in quail, but the few hybrids that show migratory activity may be able to leave the release locations and reach areas where such releases are not practised, particularly the favourable habitats in the Maghreb, which currently constitute the ‘natural reservoir’ of the occidental populations of European Quail. The migratory European Quail may become one of the most endangered Galliforms of the western Palearctic if the release of Japanese and hybrid Quail as game birds is not banned in every country.

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