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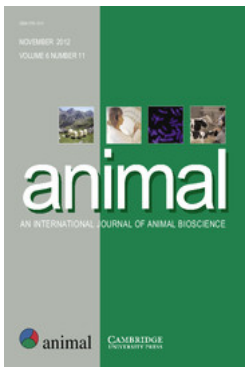

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Inheritance of duration of fertility in female common ducks (*Anas platyrhynchos*) inseminated in pure breeding or in inter-generic crossbreeding with Muscovy drakes (*Cairina moschata*)

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*Ducks (common, Muscovy and mule ducks) are the third most important bird species in animal production for human consumption worldwide. Our study aimed to improve the efficiency of mule duck breeding, thus contributing to the efficiency of food production in general. In the common duck, females can be bred either with males of the same species (i.e. in pure breeding (PB) subscript p) or in inter-generic crossbreeding (CB; subscript c) with Muscovy drakes to produce the hybrid mule duck. The aim of the present study was to estimate the genetic parameters of several indicators of duration of fertility, considered to be a trait of the female duck, within and between breeding schemes and, in particular, to estimate the purebred–crossbred genetic correlation (rg_{pc}). These indicators were maximum duration of fertility (*MD*), that is, the time interval between insemination and the last fertilised egg, the number of fertile eggs (*F*) and of hatched ducklings (*H*) after a single artificial insemination (AI), and the fertility rate over days 2 to 12 after AI ($F_{2,12}$), taking three sub-periods ($F_{2,4}$, $F_{5,8}$, $F_{9,12}$) into account. A total of 494 females and 2655 inseminations were involved. PB resulted in longer duration of fertility ($MD_p = 8.1$ v. $MD_c = 6.4$ days). Heritability (h^2) was higher for MD_p (estimate ± s.e.: 0.27 ± 0.04) than for MD_c (0.15 ± 0.04), but both traits were highly correlated with each other ($rg_{pc} = 0.85 \pm 0.07$). F_p and F_c had similar heritability (h^2 around 0.24) and displayed a high genetic correlation (0.78 ± 0.07). The same was true for H_p and H_c (h^2 around 0.17 and $rg_{pc} = 0.88 \pm 0.05$). The heritability estimates were 0.24 ± 0.03 for $F_{2,12p}$ and 0.20 ± 0.04 for $F_{2,12c}$, with a 0.80 ± 0.07 genetic correlation between each other. Permanent environmental effects influenced MD_p far less than MD_c, F_p less than F_c, but H_p and H_c to the same extent. The high values for rg_{pc} (>0.78) indicated that the same genes are involved in the duration of fertility for both PB and CB. Unlike CB, initial fertility for PB ($F_{2,4p}$) was not correlated to overall fertility rate and to duration of fertility and probably involves different genes, if any. In both breeding schemes, indirect selection on F would be better than direct selection on H to improve H, and easier to implement than selection on MD. Moreover, any gain in one breeding scheme will have its correlated counterpart in the other one, because of the high values of rg_{pc}.*

Keywords: common duck, hybridisation, duration of fertility, heritability, genetic correlation

Practical implications

The common duck can be bred either in pure breeding (PB) or in crossbreeding (CB) using the semen of Muscovy drakes to produce the mule duck. Because of the short duration of the fertile period (DFP), particularly in CB, it is necessary to inseminate the females twice a week. Selection for increased DFP might be a solution to reduce the insemination frequency and hence labour costs and animal handling, thus improving animal welfare. Our results demonstrate (in PB) or confirm (in CB) that DFP can be improved by selection due to fairly high heritability values and that gains in one breeding scheme will result in correlated gains in the other one due to high values of the purebred–crossbred genetic correlations.

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Introduction

Female birds can store spermatozoa for prolonged periods in specialised sites located in the lower and upper oviduct (Fujii and Tamura, 1963; Michel, 1987) allowing the fertilisation of several eggs during the days following a single mating or artificial insemination (AI; Zavaleta and Ogasawara, 1987). As a consequence, females may lay fertile eggs for periods of variable length. Each period, which can be defined as 'duration of fertile period' (DFP), is itself dependent on a

variety of male and female traits. As a consequence, other factors directly associated with the fertile period (e.g. the maximum duration of fertility (*MD*), as defined by Lake, 1975) vary extensively between and within species.

Following chicken and turkey, ducks are the third most important bird species in animal production for human consumption worldwide, and duck meat production has sharply risen over the last decades (Pingel, 2009). Two major species are concerned, the common duck (*Anas platyrhynchos*) and the Muscovy duck (*Cairina moschata*), as well as their hybrid, the so-called 'mule duck'. The mule duck is traditionally important in Taiwan for meat production and its production has dramatically increased in France since the 1990s for the production of *foie gras*. The mule duck combines the high reproductive rate and the early development of the common duck dam (usually a Pekin duck), and the high proportion of muscle of the Muscovy sire (Ricard, 1988; Pingel, 1990). Mule ducks therefore have great potential for providing duck meat for worldwide food production. AI was the key technology that led to the success of mule duck production, greatly improving the fertility level (Tai and Tai, 2001).

Female common ducks can thus be bred either in pure breeding (PB) or in inter-generic crossbreeding (CB) with Muscovy drakes. Fertility levels observed after CB generally remain lower than those observed after PB. The main difference between the two breeding schemes lies in the persistence of fertility after a single AI rather than in the initial fertility (Brun *et al.*, 2005 and 2008). In the INRA44 experimental strain of common duck, half initial fertility, an indicator of persistence, was reached on day 5.5 after AI in CB *v.* 7.5 in PB, and the *MD* was evaluated at 6.4 days in CB *v.* 8.1 days in PB (Sellier *et al.*, 2005; Brun *et al.*, 2005 and 2008). In commercial flocks, this shorter duration of fertility in CB justifies the need for frequent AI (e.g. two AIs per week) in order to maintain fertility rates at acceptable levels. Increasing the duration of fertility in commercial flocks of CB would therefore make it possible to reduce AI frequency and, as a consequence, labour costs and animal handling, thus improving animal welfare.

Authors who have studied the possibility of improving the duration of fertility by selection have primarily focused on the female component: Pingel (1990), Beaumont (1992) and Brillard *et al.* (1998) for the laying hen, and Tai *et al.* (1994), Poivey *et al.* (2001) and Cheng *et al.* (2002 and 2009) for the common duck. In the case of ducks bred by CB, selection can dramatically improve the number of fertile eggs after a single insemination (Cheng *et al.*, 2002 and 2009).

Meanwhile, the expressions of the duration of fertility in PB or CB can be considered, at least *a priori*, as two different traits due to marked differences between the two breeding schemes. The objective of the present study was to estimate their heritability and the purebred–crossbred genetic correlation as indicators of the extent of their genetic similarity. This would also make it possible to predict the direct and the correlated responses to selection on one of them. Several characteristics of fertility duration have been analysed: the *MD*, the number of fertile eggs and the number of hatched ducklings following a single insemination, and the fertility rate over days 2 to 12 post insemination. Moreover, the latter trait has been analysed by considering three sub-periods, days 2 to 4, 5 to 8 and 9 to 12 after AI, respectively.

Material and methods

Birds and breeding methods

This study was performed over a 3-year period at the INRA Experimental Farm for Waterfowl in Artiguères (south-western France). It involved three successive generations of INRA44 female ducks. The INRA44 strain is a synthetic strain of common duck initially obtained by crossing Tsaiya and Pekin grandparent stocks. Each year of the experiment, a total of 180 common duck females, 36 common drakes (INRA44) and 36 Muscovy drakes (ST4 Compact, Gourmaud selection) were individually caged and then raised under standard conditions. The 494 females studied were the progeny of a total of 34 sires and 128 dams. The females were divided into two groups each year, with the same sires and dams, and subjected to the two breeding schemes. Females were inseminated during three periods of their reproductive cycle (27 to 35 weeks, 39 to 43 weeks and 49 to 56 weeks of age). Within each period, the first group of females was initially inseminated with semen from the same species (PB) and, 3 weeks later, with semen from Muscovy drakes (CB). The second group was inseminated under the exact same conditions, except that the genetic origin of the semen was reversed. Six insemination batches were thus performed each year, resulting in a total of 18 AI batches over the 3-year period. A total of 1368 and 1287 fertile periods were recorded in PB and CB, respectively. Inseminations were performed with a pistol, after cloacal reversion, with pooled semen from several males, with 175 ± 25 million spermatozoa per dose. Eggs were collected from the 2nd to the 22nd day after AI, stored for 1 week at 16°C and then incubated under standard conditions for common or mule duck eggs (Sellier *et al.*, 2005). Fertility was assessed by candling (UV lamp) on day 6 of incubation.

Traits analysed

MD = maximum duration of fertility, that is, time lapse between the day of AI and the day when the last fertile egg was laid.

As the probability of obtaining one fertile egg was extremely low after 12 days following the day of AI, irrespective of the breeding scheme, analyses of the other traits were limited to eggs laid between days 2 and 12 following AI. These traits were:

F = number of fertile eggs from days 2 to 12 after AI.

H = number of hatched ducklings from days 2 to 12 after AI.

$F_{2,12}$ = fertility rate from days 2 to 12 after AI.

In order to analyse the change in fertility after AI, the period of its observation was subdivided into three sub-periods and fertility rates were calculated for each sub-period:

$F_{2,4}$, $F_{5,8}$, $F_{9,12}$ = fertility rate from days 2 to 4, 5 to 8 and 9 to 12, respectively.

$F_{sim} = 0.5$ ($F_{2,4} + F_{2,5}$) is the fertility rate at a simulated frequency of two AIs per week.

As each trait may be measured in PB or in CB, the subscript p or c specifies the trait, depending on the case.

Data analysis

Inseminations followed by the absence of at least one fertile egg were eliminated from the analyses, considering that this result was more a consequence of missed semen deposition rather than because of the birds *per se*. The very low repeatability of the variable 'presence/absence of fertile eggs' supports this hypothesis. Ducks with less than eight eggs laid over the 21 days of egg collection (laying rate $<$38%) were also excluded, considering that such ducks with low laying performances did not allow precise determination of their duration of fertility. The above-described limitations resulted in the exclusion of a total of 3.4% of the raw data.

Phenotypic correlations between variables were calculated within breeding schemes as the residual correlations of the multivariate option of the GLM procedure of Statistical Analysis Systems Institute (SAS) (2001), using the MANOVA statement. The model included the fixed effect of the insemination batch (18 levels).

Within breeding schemes, repeatability estimates were calculated using Proc Mixed of SAS (2001), with a linear model that included the random effect of the duck and the fixed effect of the insemination batch. Repeatability was estimated as the ratio of the duck variance to the total variance.

Genetic parameters were estimated with a multitrait animal model, using the restricted maximum likelihood method, with the VCE 4.2 software package (Neumaier and Groeneveld, 1998). The statistical model included the fixed effect of the insemination batch and two random effects: the additive genetic value of the duck and the permanent environmental effect.

Results

The basic statistics of the traits studied here can be found in Table 1. The results confirmed that the duration of fertility is longer in PB than in the inter-generic CB. For example, the *MD* in PB was 8.08 days *v.* 6.40 days in CB. Overall fertility over days 2 to 12 was 61% in PB and 43% in CB.

Change in egg fertility after AI

Overall fertility was broken down into early ($F_{2,4}$), intermediate ($F_{5,8}$) and late fertility ($F_{9,12}$). F_{sim}, the fertility rate at a simulated frequency of two AIs per week, is another indicator of early fertility. Phenotypic correlations of fertility between these sub-periods are given in Table 2 for each breeding scheme. The pattern of correlations between sub-periods was quite similar in PB and CB. It revealed a low phenotypic link, if any, between the early ($F_{2,4}$) and later fertility, and particularly with $F_{9,12}$, an indicator of persistency. Correlations between $F_{5,8}$ and $F_{9,12}$ were themselves limited to $\sim$0.30 values in both breeding schemes. The breeding schemes differed, however, in terms of the correlation of each component with the overall fertility. Early fertility (F_{sim}, for example) had a higher correlation to overall fertility in CB ($r = 0.58$) than in PB ($r = 0.35$). In contrast, late fertility was more correlated to overall fertility in PB ($r = 0.69$) than in CB ($r = 0.50$).

Table 1 *Basic statistics of the traits analysed in PB and in CB*

	PB		CB	
Traits	*n*	Mean (s.d.)	*n*	Mean (s.d.)
MD (days)	1316	8.08 (1.88)	1248	6.40 (2.19)
F (eggs)	1316	5.90 (1.98)	1248	4.15 (1.84)
H (ducklings)	1236	4.80 (2.06)	1145	3.43 (1.79)
$F_{2,12}$ (%)	1316	61 (17)	1248	43 (18)
$F_{2,4}$ (%)	1295	95 (16)	1229	88 (23)
$F_{5,8}$ (%)	1300	78 (27)	1236	47 (33)
$F_{9,12}$ (%)	1300	18 (24)	1234	5 (14)
F_{sim} (%)	1295	95 (15)	1229	86 (22)

PB = pure breeding; CB = crossbreeding; *MD* = maximum duration of fertility; *F* and *H* = number of fertile eggs and of hatched ducklings after a single insemination; AI = artificial insemination; $F_{2,12}$, $F_{2,4}$, $F_{5,8}$ and $F_{9,12}$ = fertility rates over days 2 to 12 after AI, 2 to 4, 5 to 8 and 9 to 12, respectively; F_{sim} = fertility rate at a frequency of two AIs/week.

Phenotypic correlations between various DFP-related traits

The phenotypic correlations between DFP traits (Table 3) were generally high and were very similar for both PB and CB: between *MD* and *F*, 0.75 and 0.73, respectively; between *MD* and *H*, 0.57 and 0.59, respectively; and between *F* and *H*, 0.82 and 0.84, respectively.

As a duck repeats a given trait three times in its reproductive cycle, the correlation between these repeated performances (repeatability) can be estimated. All estimates were in the range of 0.22 to 0.35. Again, the repeatability estimates were quite close in both breeding schemes: for *MD*, 0.29 and 0.32 in PB and CB, respectively; for *F*, 0.31 and 0.35, respectively; and for *H*, 0.30 and 0.22, respectively.

Genetic variability: comparison between PB and CB

The heritability for *MD* (Table 3) in PB (0.27) was significantly higher than in CB (0.15). The number of fertile eggs after a single insemination had similar heritability estimates in PB and in CB (0.25 and 0.23, respectively). Overall fertility rates ($F_{2,12}$) had the same pattern of heritability (0.24 and 0.20, respectively; Table 2). The number of hatched ducklings also had similar heritability estimates in both breeding schemes (0.19 in PB and 0.16 in CB).

Regarding MD_p and, to a lesser extent, F_p, the permanent environmental effects (Table 4) had little impact on the total variance (3% and 8%, respectively). The contribution was higher for the other traits studied, amounting to 10% to 17%. In particular, *MD* was more highly influenced by permanent environmental effects in CB than in PB. On the other hand, H_p and H_c were very similar with respect to the balance of the heritable *v.* non-heritable part of the variance because of the

Table 2 *Parameters of fertility rates in different sub-periods after AI: (1) within a breeding scheme (upper and middle part of the table): heritability (diagonal), phenotypic correlations (under diagonal) and genetic correlations (above diagonal); (2) pure-bred–crossbred genetic correlations (lower part of the table)*

PB	$F_{2,4p}$	F_{simp}	$F_{5,8p}$	$F_{9,12p}$	$F_{2,12p}$
$F_{2,4p}$	0.01 ± 0.01	–	0.15 ± 0.50	−0.56 ± 0.26	−0.30
F_{simp}	0.97	0.01 ± 0.01	0.49 ± 0.40	−0.37 ± 0.29	0.00 ± 0.001
$F_{5,8p}$	0.08	0.18	0.16 ± 0.04	0.89 ± 0.06	0.97
$F_{9,12p}$	0.01	0.02	0.29	0.28 ± 0.09	0.96
$F_{2,12p}$	0.29	0.35	0.78	0.69	0.24 ± 0.03
CB	$F_{2,4c}$	F_{simc}	$F_{5,8c}$	$F_{9,12c}$	$F_{2,12c}$
$F_{2,4c}$	0.04 ± 0.03	–	1	0.76 ± 0.25	1.00 ± 0.01
F_{simc}	0.95	0.06 ± 0.03	1.00 ± 0.01	0.74 ± 0.22	0.95 ± 0.08
$F_{5,8c}$	0.18	0.33	0.14 ± 0.04	0.98 ± 0.12	1.00
$F_{9,12c}$	0.05	0.07	0.29	0.09 ± 0.03	0.94 ± 0.08
$F_{2,12c}$	0.48	0.58	0.84	0.50	0.20 ± 0.04
PB and CB relationship	$F_{2,4c}$	F_{simc}	$F_{5,8c}$	$F_{9,12c}$	$F_{2,12c}$
$F_{2,4p}$	−0.87				
F_{simp}		−0.56 ± 0.59			
$F_{5,8p}$			0.80 ± 0.08		
$F_{9,12p}$				0.80 ± 0.10	
$F_{2,12p}$					0.80 ± 0.07

AI = artificial insemination; PB = pure breeding; CB = crossbreeding; $F_{2,4}$, $F_{5,8}$, $F_{9,12}$ and $F_{2,12}$ are the fertility rates for days 2 to 4, 5 to 8, 9 to 12 and 2 to 12 after AI, respectively; F_{sim}(=0.5 ($F_{2,4}$ + $F_{2,5}$)) is the fertility rate at a simulated frequency of two AI per week. The subscripts p and c correspond to PB and CB, respectively.
Genetic correlations without standard errors correspond to non-convergent analyses.

Table 3 *Estimates (±s.e.) of heritability (diagonal), genetic correlations (above diagonal) and phenotypic correlations (under diagonal) for* MD, F *and* H *for* PB *(subscript p) and for CB (subscript c)*

	MD_p	F_p	H_p	MD_c	F_c	H_c
MD_p	0.27 ± 0.04	0.98 ± 0.01	0.92 ± 0.06	0.85 ± 0.07		
F_p	0.75	0.25 ± 0.05	0.89 ± 0.05		0.78 ± 0.07	
H_p	0.57	0.82	0.19 ± 0.04			0.88 ± 0.05
MD_c				0.15 ± 0.04	0.97 ± 0.03	0.96 ± 0.04
F_c				0.73	0.23 ± 0.05	0.97 ± 0.02
H_c				0.59	0.84	0.16 ± 0.03

MD = maximum duration of fertility; *F* = the number of fertilised eggs; *H* = the number of hatched ducklings; PB = pure breeding; CB = crossbreeding.

female duck. For H_p, their respective proportions of the total variance were 19% *v.* 13%; for H_c, they were 16% *v.* 10%.

The genetic correlations between *MD*, *F* and *H* were high in both breeding schemes, all estimates being >0.89. The correlations for permanent environmental effects between traits were also high in both breeding schemes, except between MD_p and H_p.

Rates of early fertility ($F_{2,4}$ and F_{sim}) had a vey low heritability in both breeding schemes with, however, a trend for higher values in CB (0.04 and 0.06 *v.* 0.01 and 0.01; Table 2). In contrast, a higher heritability was observed for intermediate fertility ($F_{5,8}$) in both breeding schemes and for late fertility ($F_{9,12}$) in PB. The pattern of the genetic correlations between initial and later fertility seems to depend on the breeding scheme: an independence of initial fertility with later fertility was observed in PB, whereas high positive correlations (>0.74) were found in CB. As a consequence, initial fertility was genetically unlinked to overall fertility in PB, whereas it was highly correlated in CB ($rg = 0.95$). Intermediate and late fertility rates were highly correlated to each other in both breeding schemes.

Genetic and permanent environmental correlations between the same traits expressed in PB and in CB

The genetic correlations between the expression of the same trait in PB and in CB were high for the three traits analysed, *MD*, *F* and *H*, in the range of 0.78 to 0.88 (Table 3). This parameter is referred to as the purebred–crossbred genetic correlation in the text and written as rg_{pc}. The overall fertility rate ($F_{2,12}$) also displayed a high value for rg_{pc} (means ± s.e.: 0.80 ± 0.07; Table 2).

Table 4 *Estimates (±s.e.) of the ratio of permanent environmental variance to total variance (diagonal) and correlations between traits for permanent environmental effects (above diagonal) for* MD, F *and H for* PB *(subscript p) and for CB (subscript c)*

	MD_p	F_p	H_p	MD_c	F_c	H_c
MD_p	0.03 ± 0.03	0.80 ± 0.19	0.41 ± 0.18	0.57 ± 0.28		
F_p		0.08 ± 0.04	0.74 ± 0.11		0.91 ± 0.04	
H_p			0.13 ± 0.03			0.88 ± 0.05
MD_c				0.18 ± 0.03	0.92 ± 0.04	0.78 ± 0.05
F_c					0.14 ± 0.04	0.88 ± 0.06
H_c						0.10 ± 0.03

MD = maximum duration of fertility, *F* = the number of fertilised eggs; *H* = the number of hatched ducklings; PB = pure breeding; CB = crossbreeding.

Concerning the components of $F_{2,12}$, rg_{pc} was not different from zero for initial fertility, whereas it was >0.80 for intermediate, late and overall fertility (Table 2).

The correlations of permanent environmental effects for the expression of one trait in PB and in CB were as high as the genetic correlations, except for the correlation between MD_p and MD_c (0.57 ± 0.28).

Discussion

Comparison with other species

Genetic parameters for PB can be compared with those available in other poultry species, which are, in fact, restricted to the laying hen. Our heritability estimate for MD_p (0.27 ± 0.04) is close to the realised heritability of 0.21 obtained by Pingel (1990), based on seven selection generations, but higher than the estimates of 0.15 obtained by Beaumont *et al.* (1992) when averaged over estimation methods and generations. Our heritability estimate for H_p (0.19) is close to the one (0.18) estimated by Beaumont (1992). The very high genetic correlations between *MD*, *F* and *H* found in our study were also observed by Beaumont (1992).

Comparison with other studies in duck hybridisation

Our estimates of heritability for duration of fertility in common ducks inseminated with semen from Muscovy drakes tended to be lower than those obtained by Poivey *et al.* (2001) in two strains (selected and control) of Tsaiya common ducks in the course of a selection experiment: for MD_c, 0.15 *v.* 0.25 on average over the two Tsaiya strains; for F_c, 0.23 *v.* 0.28; and for H_c, 0.16 *v.* 0.18. Our estimates of the genetic correlations between these traits were higher than 0.96, whereas the estimates from Poivey *et al.* (2001) ranged from 0.82 to 0.96, depending on the strain and the pair of traits considered.

Variance components and genetic correlations for PB v. CB

Duration of fertility traits was expressed in two breeding schemes, PB and CB. The genes controlling these traits were thus expressed in two different biological environments, able to induce genetic-by-environment interactions. Such interactions can be expressed by a different h^2 depending on the environment and by a purebred–crossbred genetic correlation different from 1 (Brun, 1982).

In the present study, the heritability for *MD* is significantly higher in the case of PB. Another fertility trait investigated in a closely related strain, the fertility rate over 4 weeks with two inseminations per week, showed the reverse pattern, with a higher heritability for CB (Brun and Larzul, 2003). The insemination rate of two AIs per week, however, put the maximum fertility in the 3- to 4-day period after AI to the test, rather than its persistence. The trend observed in our experiment for a higher heritability of $F_{2,4}$ and F_{sim} for CB makes it possible to reconcile the two studies.

In contrast to heritability, the part of variance of *MD* because of permanent environmental effects was higher for CB. We are tempted to attribute this to the difficulty to control AI in hybridisation. The success of insemination with semen from another species would be more sensitive to the place where the semen is deposited than with semen from the same species. However, the repeatability estimates (encompassing genetic and permanent environmental variances) are similar in both breeding schemes, which do not support such an interpretation.

Surprisingly, and despite a high genetic correlation with *MD*, the traits *F* and *H* showed no such heritability difference between PB and CB, nor such an unbalance between genetic additive and permanent environmental variances. We have found no explanation for these results so far.

As of this time, the only study concerning the purebred–crossbred relationship in common duck reproduction (Brun and Larzul, 2003) reported a low value of rg_{pc} for fertility with two AIs/week (rg_{pc} = 0.49). Our corresponding value (i.e. rg_{pc} for F_{sim}) was even smaller and not different from zero (−0.56 ± 0.59). The high values obtained in the present study for rg_{pc} of MD and the other DFP-related traits were unexpected. First, the high differences in the mean values of DFP traits between the two breeding schemes suggested quite different traits. Second, the existence of a species-specific barrier to sperm transport in the vagina, along with the existence of surface antigenicity of the sperm membrane revealed in the chicken (Steele and Wishart, 1992) could result in interactions between the female duck genital tract and the sperm type, and thus give a value different from 1 for rg_{pc}. The discrepancy between the fairly low value of rg_{pc} for fertility in two AIs/week and the high value after a single AI confirms that we are dealing with two different traits, the former involving initial fertility and

the latter specifically involving the persistence of fertility. In laying hens divergently selected for duration of fertility, Brillard *et al.* (1998) showed that fertility persistence was linked to the sperm storage capacity of the hens, with more sperm storage tubules in the high line, a histo-anatomical trait. If such a trait was involved in the duck, this could explain the high rg_{pc} found in the current study for duration of fertility. This high value was confirmed by the 'realised correlation' observed in a selection experiment on another criterion of DFP (Brun *et al.*, 2006). The selection criterion was the number of live mule embryos obtained at the limited rate of one insemination per week. This high value suggests that many of the same genes are involved in the duration of fertility for both PB and CB.

Fertility rates at different sub-periods after AI showed the same trend in both breeding schemes: low heritability values in the early period but higher ones in the intermediate and late ones. The number of days of egg collection taken into account (3 days in the early period *v.* 4 days for the other two) could explain part of the difference. Another part of the difference could be because of the fact that later fertility put duration of fertility to the test, with the higher heritability of histo-anatomical traits, whereas early fertility did not and thus displayed low heritability values, as is the rule for fertility traits in animal species (David, 2008). It seems, however, that initial fertility has a somewhat different status depending on the breeding scheme: initial fertility was less correlated to later and to overall fertility in PB than in CB, both in terms of phenotypic and genetic correlations. The particular status of initial fertility appeared again through the purebred–crossbred genetic correlation. Although the estimation of genetic correlations involving initial fertility in PB may be partly hampered by its very low additive genetic variance and heritability, the phenotypic correlation remains significant. In other words, PB initial fertility is not at all linked to duration of fertility, whereas it tends to be in CB. How can this be interpreted at the biological level? In PB, initial fertility would not be limited by the female sperm storage capacity, as in the case of CB, or only later on after insemination in both breeding schemes.

Our results demonstrate that selection for increased duration of fertility is possible, regardless of the breeding scheme. In order to improve *H*, the higher heritability of *F* and its high genetic correlation with *H* would make indirect selection on *F* more profitable than direct selection on *H*. Moreover, such a strategy would be easier to implement than direct selection on the number of hatched ducklings as fertility is assessed earlier, at candling instead of hatching. Moreover, any gain in one breeding scheme will result in correlated gains in the other one because of high values of the purebred–crossbred genetic correlation.

Conclusion

The variability of DFP-related traits was analysed in common duck females bred by PB or by CB. Although trait expression was dramatically influenced by the breeding scheme, their phenotypic and genetic variability were quite similar in both breeding schemes. The purebred–crossbred genetic correlations were high for all traits, suggesting that most of the genes that influence duration of fertility in both PB and CB are the same. Noticeable differences between the two breeding schemes, however, were observed: (1) *MD* was more influenced by permanent environmental effects in CB; and (2) the initial fertility (obtained over days 2 to 4 after insemination) was independent of duration of fertility in PB, whereas it showed some link in CB.

Our results either confirm (CB) or demonstrate (PB) that duration of fertility can be improved by genetic selection because of fairly high heritability values. In both breeding schemes, the number of eggs fertilised after a single insemination can be used as the selection criterion with a favourable correlated response on the number of hatched ducklings. Moreover, any gain in one breeding scheme will have its correlated counterpart in the other one.

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References

Beaumont C 1992. Genetic parameters of the duration of fertility in hens. Canadian Journal of Animal Science 72, 193–201.

Beaumont C, Millet N, Le Bihan-Duval E, Kipi A and Dupuy V 1992. Comparison of various characteristics of duration of fertility in hens. British Poultry Science 33, 649–661.

Brillard JP, Beaumont C and Scheller MF 1998. Physiological responses of hens divergently selected on the number of chicks obtained from a single insemination. Journal of Reproduction and Fertility 114, 111–117.

Brun JM 1982. Interactions géniteur × population des partenaires. I. – Définition d'indicateurs. Annales de Génétique et Sélection Animale 14, 463–480.

Brun JM and Larzul C 2003. Inheritance of reproductive traits of female common ducks (*Anas Platyrhynchos*) in pure breeding and in inter-generic crossbreeding with Muscovy ducks (*Cairina Moschata*). British Poultry Science 44, 1–6.

Brun JM, Mialon-Richard MM, Dubos F and Guy G 2006. Réponses à une sélection sur la durée de la période fertile (évaluée sur la survie de l'embryon) de la cane commune inséminée avec de la semence de Barbarie. Conference at the 7èmes Journées de la Recherche sur les Palmipèdes à Foie Gras, Arcachon, France, 4 pp.

Brun JM, Richard MM, Marie-Etancelin C, Rouvier R and Larzul C 2005. Le canard mulard: déterminisme génétique d'un hybride intergénérique. INRA Productions Animales 18, 295–308.

Brun JM, Mialon-Richard MM, Sellier N, Batellier F and Brillard JP 2008. Duration of fertility and hatchability of the common duck (*Anas Platyrhynchos*) in pure- or crossbreeding with Muscovy drakes (*Cairina Moschata*). Theriogenology 69, 983–989.

Cheng YS, Rouvier R, Poivey JP, Tai JJL, Tai C and Huang SC 2002. Selection responses for the number of fertile eggs of the Brown Tsaiya duck (*Anas Platyrhynchos*) after a single insemination with pooled Muscovy (*Cairina Moschata*) semen. Genetics Selection Evolution 34, 597–611.

Cheng YS, Rouvier R, Poivey JP, Liu HL, Huang SC, Huang YC, Liao CW, Tai JJL, Tai C and Poivey JP 2009. Eleven generations of selection for the duration of fertility in the intergeneric crossbreeding of ducks. Genetics Selection Evolution 41, 32–43.

David I 2008. Analyse génétique et modélisation de la production de semence et de la réussite de l'insémination artificielle en ovin. PhD, AgroParisTech.

Fujii S and Tamura T 1963. Location of sperms in the oviduct of the domestic fowl with special reference to storage of sperms in the vaginal gland. Journal of the Faculty of Fisheries and Animal Husbandary, Hiroshima University 5, 145–163.

Lake PE 1975. Gamete production and the fertile period with particular reference to domesticated birds. Symposia of the Zoological Society of London 35, 225–244.

Michel G 1987. Sperm storage in the oviduct of domestic poultry with emphasis on sperm nests near the uterovaginal junction. Anatomia Histologia Embryologia 16, 254–258.

Neumaier A and Groeneveld E 1998. Restricted maximum likelihood estimation of covariances in sparse linear models. Genetics Selection Evolution 30, 3–16.

Pingel H 1990. Genetic of growth and meat production in waterfowl. In Poultry breeding and genetics (ed. RD Crawford), pp. 691–704. Elsevier, Amsterdam, The Netherlands.

Pingel H 1990. Duration of fertility – an inheritant character. In Control of fertility in domestic birds (ed. INRA), pp. 33–39. Les Colloques de l'INRA no. 54. INRA Publishing, Versailles, France.

Pingel H 2009. Waterfowl production for food security. Conference at the 4th World Waterfowl Conference, Thrissur, India, 6pp.

Poivey JP, Cheng YS, Rouvier R, Tai C, Wang CT and Liu HL 2001. Genetic parameters of reproductive traits in Brown Tsaiya ducks artificially inseminated with semen from Muscovy drakes. Poultry Science 80, 703–709.

Ricard FH, de Carville H and Marché G 1988. Etude comparative de la composition anatomique des canards de barbarie, Pékin et mulard. In La génétique du canard de Barbarie (*Cairina moschata*) et du mulard (ed. R Rouvier), pp. 75–99. Les Colloques de l'INRA no. 42. INRA Publishing, Versailles, France.

Statistical Analysis Systems Institute (SAS) 2001. SAS/STAT. User's guide, version 8.02. SAS Institute Inc., Cary, NC, USA.

Sellier N, Brun JM, Richard MM, Batellier F, Dupuy V and Brillard JP 2005. Comparison of fertility and embryo mortality following artificial insemination of common duck females (*Anas Platyrhynchos*) with semen from common or Muscovy (*Cairina Moschata*) drakes. Theriogenology 64, 429–439.

Steele MG and Wishart GJ 1992. Evidence for a species-specific barrier to sperm transport within the vagina of the chicken hen. Theriogenology 38, 1107–1114.

Tai C, Rouvier R and Poivey JP 1994. Heritabilities for duration of fertility traits in Brown Tsaiya female duck (*Anas Platyrhynchos*) by artificial insemination with pooled Muscovy (*Cairina Moschata*) semen. British Poultry Science 35, 377–384.

Tai C and Tai JJL 2001. Future prospects of duck production in Asia. The Journal of Poultry Science 38, 99–112.

Zavaleta D and Ogasawara F 1987. A review of the mechanism of the release of spermatozoa from storage tubules in the fowl and turkey oviduct. Worlds Poultry Science Journal 43, 132–139.