Anim. Res. 52 (2003) 125–140

DOI: 10.1051/animres:2003010

Original article

Analysis of laying traits in first cycle geese in two production systems

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(Received 10 January 2002; accepted 4 February 2002)

Abstract — The phenotypic relationships between the components of the number of eggs per goose in the first laying cycle were estimated in two systems: S1 consisted of geese used for fatty liver production (Grey Landes) and reared in mating pens with natural lighting; S2 consisted of meat production geese, reared in individual cages under controlled lighting conditions. Criteria of the laying rhythm were defined and estimated, according to the phenomenon of laying clutches. A clutch was defined as the number of eggs separated by an interval of 48 h at most. Intervals greater than 48 h were defined as pauses. Differences between the two systems (S1 vs. S2) were obvious for all traits investigated, with dramatic effects on the total number of eggs (37.8 vs. 72.0), the laying duration (92.3 vs. 156.2 d), the average clutch length (4.4 vs. 7.7 eggs), the average pause duration, the percent of productive time and the within clutch interval between consecutive eggs (41 vs. 43 h). The difference in total egg number between S1 and S2 production systems appeared to be due to a difference in clutch length rather than to a difference in the number of clutches. Except for the correlations involving the number of clutches and other components of egg production (number of eggs, laying intensity or pause duration), the two systems showed a great similarity in the pattern of phenotypic correlations between component traits of total egg production. High positive correlations were found between total egg number and its components, laying duration and laying rate. Correlations between egg number and characteristics of clutches were also similar across systems, except for the number of clutches: egg number was positively correlated with clutch length and negatively with pause duration.

goose / laying / clutch / production system

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Résumé — Analyse des caractères de ponte d'oies en premier cycle dans deux systèmes de production. Les relations phénotypiques entre différentes composantes de la ponte d'oies en premier cycle sont estimées dans deux systèmes : le système S1 consiste en oies à gaver (Landaises grises) élevées en parquets extérieurs et soumises à la photopériode naturelle ; S2 consiste en oies à rôtir élevées en cages individuelles et en conditions lumineuses contrôlées. Les composantes du rythme de ponte sont estimées selon la notion de 'série de ponte', définie comme l'ensemble des œufs avec un intervalle maximum de 48 h entre deux œufs consécutifs. Un intervalle de plus de 48 h est défini comme une pause. Les deux systèmes diffèrent pour la plupart des caractères analysés, avec une différence spectaculaire (S1 vs. S2) pour le nombre total d'œufs (37,8 vs. 72,0), la durée de ponte (92,3 vs. 156,2 j), la longueur moyenne des séries (4,4 vs. 7,7 oeufs), la durée moyenne des pauses, le pourcentage de temps productif et l'intervalle moyen entre deux œufs consécutifs d'une série (41 vs. 43 h). La différence de nombre d'oeufs entre les systèmes S1 et S2 apparaît plus liée à une différence de longueur de séries qu'à une différence de nombre de séries. A l'exception des corrélations entre nombre de séries d'une part et certaines composantes de la production d'oeufs (nombre d'œufs, intensité de ponte et durée de pause), les deux systèmes montrent une grande similitude dans les corrélations phénotypiques entre les composantes du nombre total d'œufs. Une corrélation positive élevée est trouvée entre le nombre d'oeufs et ses composantes de durée et d'intensité de ponte. Les corrélations entre le nombre d'œufs et les caractéristiques des séries (à l'exception du nombre de séries) sont semblables dans les deux systèmes : positive avec la longueur moyenne des séries, négative avec la durée moyenne des pauses.

oie / ponte / série de ponte / système de production

1. INTRODUCTION

The goose is a species with interesting biological characteristics, such as a high juvenile growth rate, a good adaptation to free range and grazing, and a high dietary quality of meat [18]. Genetic diversity of the domestic goose consists in an array of specialised breeds, for production of meat or fatty liver. The limiting factor of goose production remains, however, the egg production, which is very dependent on lighting conditions. When exposed to natural day length, geese exhibit a short and seasonal laying period, which restricts gosling production to the spring season. An artificial control of the lighting conditions can be done in closed buildings in order to extend gosling production all over the year [23] or to increase the laying duration [17, 19, 26, 27].

The present study was aimed at identifying the main components of the first cycle of egg production for geese placed in two housing systems. In addition to the usual criteria, such as sexual maturity, laying rate and laying persistency calculated at the flock level [14, 25, 32], this study investigates individual variations underlying the laying curve of a flock. Furthermore, we propose to describe the characteristics of the laying rhythm by analogy with the phenomenon of laying clutches, well described in the laying hen as reviewed by Sauveur [24]. The possibility to identify laying clutches in the goose was first proposed by Stasko et al. [29, 30]. Since ovulation generally follows the oviposition of the previous egg [24], the normal interval between successive ovipositions, in the case of normal-shelled eggs, should be longer than the duration of egg formation, estimated to vary from 42 to 44 h in the White Roman geese [7]. Recently, a cyclic variation in the plasma levels of progesterone was identified in the goose [6], with a periodicity much longer than 24 hours. Based on this information, a definition of the laying clutch in the Geese will be proposed. A set of numerical criteria will also be defined in order to provide a detailed phenotypic analysis of the laying rhythm and laying intensity. These criteria will be calculated on two data sets obtained from geese placed in two contrasted production systems: on the one hand, geese for fatty liver production exposed to natural lighting conditions, and, on the other hand, meat-type geese housed in cages with controlled lighting conditions. The phenotypic correlations obtained for laying traits and the calculated criteria will be compared across the two production systems, in order to check their generality and improve the knowledge of the mechanisms of egg production in geese. The mean values will also be compared across the two systems but, due to the confounding between the breed type and management system, differences between systems will not be interpreted.

2. MATERIALS AND METHODS

The production system will be defined by the combination of a strain and management system. The INRA strain '7' [21] is maintained at the 'Unité Expérimentale sur les Palmipèdes à Foie Gras' (Waterfowl Experimental Unit) at Artiguères, in the south-west of France, the Landes region, and corresponds to system S1. The meat type synthetic strain is selected on the number of goslings by the private breeder, Gourmaud Sélection S.A., in the west of France, the Vendée region, and corresponds to system S2. The main characteristics of both systems are described in Table I. The variation in lighting conditions in S2, which were aimed at determining an optimum lighting programme, is detailed in Table II.

Egg production was recorded according to the Palmi software [3] on a daily basis. Some egg abnormalities (double-yolked, abnormally small i.e. lighter than 110 g, porous-shelled) were recorded.

The usual laying traits to be analysed were the number of eggs in the first laying cycle (NE), the age at the first egg (AF), the laying duration (DU, the number of days between the first and the last laid egg), and the individual laying intensity (I = NE/DU, expressed in percentage).

The definition of the laying clutch was based on two types of information: the distribution of intervals between two consecutive eggs, and the physiology of egg formation. Previous work by Stasko et al. [30] established that the mean interval between consecutive eggs was 36.3 hours in Landaise geese, and 36.6 hours in a commercial strain. In the present data set, the mode of the distribution of intervals between consecutive eggs was found to be 2 days, whatever the production system (Fig. 1); all geese showed a proportion of eggs separated by two days (around 50%) higher than the proportion of eggs separated by one day (around 30%). Recent data on plasma progesterone in geese showed a single pre-ovulatory peak within an interval of 46 to 48 h separating two ovipositions, the peak took place 12 to 13 h before ovulation [6] which suggested that hormonal secretions did not follow a 24 hours rhythm. Furthermore, the duration of egg formation was estimated to vary from 42 to 44 h in white Roman geese [7], which does not match easily with a 24 hour rhythm of egg laying. Taking this information into account, we defined the laying clutch in geese as the number of eggs separated by an interval which may reach 48 h at the most. Intervals greater than 48 h were defined as pauses, which interrupt the clutch. The laying rhythm was thus characterised by the number of clutches (NS), the average length of clutches (LS, in number of eggs or DS, in number of days), the maximum clutch length (LSmax) and the average pause duration (DP). In the case of good layers, the value of LSmax was less affected than LS by the occurrence of internal ovulations or unrecorded eggs. Based upon

Table I. Characteristics of the two production systems studied.

	System 1	System 2
Data analysed	5 generations (1993-98). 884 geese	5 generations (1995-1999). 646 geese
Genetic type	Strain INRA 7 of Landaise geese used for fatty liver production	Synthetic strain (private breeder) used for meat production
Origin	Experimental population closed since 1961, subdivided into 2 lines from 1975 to 1991, merged again in 1992	A cross in 1995 between a strain of Polish geese and a strain of rhenan geese
Rearing conditions	Closed sheds with run; feeding ad libitum until 12 weeks then restricted to 550 kcal·day^{-1} until 26–30 weeks.	Free range (1000 geese per ha); grazing + suppl. feeding ad libitum until 12 weeks then restricted until the age of 30–34 weeks.
Adult housing	Open breeding pens with pond; Natural lighting; Trap nesting	Individual cages from 30–34 weeks of age on; closed building; lighting programme: 10 to 11 h light per 24 h (see Tab. II)
Feeding	From 26–30 weeks on until onset of laying, restricted to 700 kcal·day^{-1} then ad libitum	Ad libitum during laying
Reproduction	1 gander × 5 geese in natural mating	Artificial insemination (pedigree during replacement; else with pooled semen)
Laying period	February to June	February to July (22 to 24 weeks)
Hatching period	3 to 5 hatches March to May	2 hatches April to May

Table II. Lighting conditions used in S2 as compared to natural lighting conditions in S1.

<table>
<tr><th rowspan="2">Week</th><th colspan="5">Year</th><th rowspan="2">Natural light</th></tr>
<tr><th>1995</th><th>1996</th><th>1997</th><th>1998</th><th>1999</th></tr>
<tr><td>49</td><td>8h</td><td>8h</td><td>8h</td><td>8h</td><td>8h</td><td>8h23</td></tr>
<tr><td>52</td><td>|</td><td>|</td><td>|</td><td>|</td><td>9h</td><td>8h13</td></tr>
<tr><td>53</td><td></td><td></td><td></td><td></td><td>9h30</td><td></td></tr>
<tr><td>1</td><td>|</td><td>8h30</td><td>|</td><td>|</td><td>10h</td><td>8h18</td></tr>
<tr><td>2</td><td>8h</td><td>9h30</td><td>9h</td><td>9h</td><td>10h30</td><td>8h28</td></tr>
<tr><td>3</td><td>8h30</td><td>10h30</td><td>10h</td><td>10h</td><td>|</td><td>8h42</td></tr>
<tr><td>4</td><td>9h30</td><td>11h30</td><td>10h30</td><td>|</td><td>|</td><td>9h</td></tr>
<tr><td>5</td><td>10h30</td><td>|</td><td>|</td><td>|</td><td>|</td><td>9h19</td></tr>
<tr><td>6</td><td>11h</td><td>|</td><td>|</td><td>|</td><td>|</td><td>9h40</td></tr>
<tr><td>10</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>11h13</td></tr>
<tr><td>15</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>13h22</td></tr>
<tr><td>20</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>15h15</td></tr>
<tr><td>25</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>16h05</td></tr>
<tr><td>30</td><td>-</td><td>|</td><td>|</td><td>|</td><td>|</td><td>15h22</td></tr>
<tr><td>31</td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>15h00</td></tr>
<tr><td>32</td><td></td><td>-</td><td>|</td><td>-</td><td>-</td><td>14h40</td></tr>
<tr><td>34</td><td></td><td></td><td>-</td><td></td><td></td><td>14h00</td></tr>
</table>

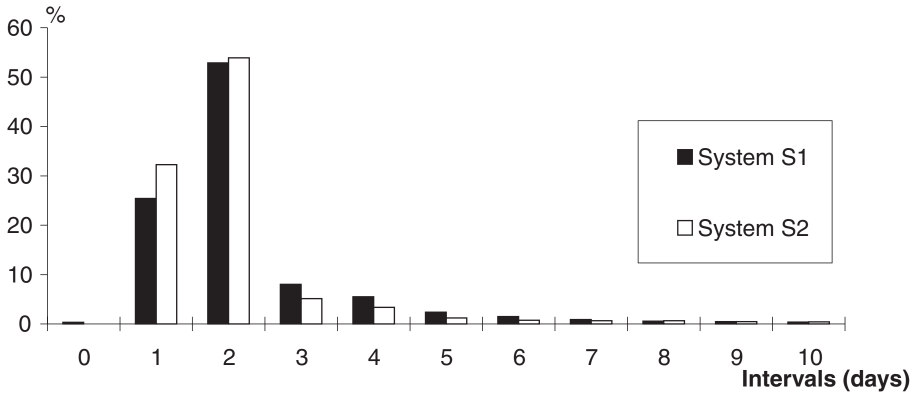

Figure 1. Distribution of intervals between 2 consecutive eggs.

these definitions, it was possible to calculate the mean within-clutch interval between two consecutive eggs, t2o, the within-clutch laying intensity, Is, and the percentage of productive time, PP, as:

t2o = DS/(LS-1); Is= LS/DS; PP = I/Is.

Egg weight was recorded in both systems but in a different way: in S1, the eggs were weighed individually along the entire laying cycle, whereas in S2, the mean egg weight was determined at the peak of laying. Double-yolked eggs were excluded from the analysis of egg weight. Body weight was also recorded in a different way: it was measured at the onset of lay, between 36 and 43 weeks of age, in S1, whereas it was measured when the geese were placed in cages, between 30 and 35 weeks of age, in S2. Depending on the system, egg weight and body weight may be different traits, which should be remembered when discussing their genetic correlations with other traits.

The analysis of variance was done in two steps, using the GLM procedure of SAS® [22]:

– a first analysis was aimed at estimating the effects of the production system, the model included the fixed effect of the production system, and the fixed effect of the hatching date, nested within the production system. The hatching date represented both the generation effect and the hatch effect within a generation. This model was applied to all the variables where the hypothesis of equal variances between the systems was met. For the variables where this was not the case, i.e. NE, DU, LS, and DP, the differences between the production systems were compared with a Student t-test;

– a second analysis was done separately for each system, the model included the fixed effect of the generation number, and the fixed effect of the rank of hatch. In system S1, the rank of hatch was determined according to the hatching date, rank 1 for dates before March 31, rank 2 for dates between April 1 and 15, and rank 3 for dates after April 15. In system S2, only two hatches took place, the first hatch was always before April 25 and the second hatch was after April 25.

Phenotypic correlations between traits were obtained as the residual correlations from the linear model used in the second analysis. Furthermore, the correlations between the estimated generation means of the different variables were calculated according to the COR procedure of SAS® [22] applied to data from system S1, where the number of generations was the highest.

The laying curve corresponds to the trend in the average number of eggs laid each day by 100 geese during a week. A laying goose is defined as a goose which has started to lay an egg and has not yet finished the first cycle of lay. The shape of the laying curve may depend on the number of laying geese, and on the laying intensity of each goose. The laying curve was fitted by 6 different equations, which had been applied already, either to the laying hen or to the goose (Tab. III). The parameters of each equation were estimated by simple linear regression with the GLM procedure of SAS® [22].

3. RESULTS

3.1. The analysis of laying curves and the effect of age on egg characteristics

The average laying curves for systems S1 and S2 are shown in Figure 2. The duration of the laying period differed markedly between systems, being 92 ± 25 days in S1, and 156 ± 35 days in S2. Although they appeared rather different, particularly for the persistency of lay, these curves exhibited some usual characteristics for avian species: a progressive onset of lay, due to a

Table III. Models used to fit the laying curve.

Model number	Equation	Parameters	References
1	$y = a\, t^b \exp(ct)$	a,b,c	Wood [33]; Acs et al.[1]
2	$y = a\, t^b \exp(ct + dt^{1/2})$	a,b,c,d	McNally [13]
3 (Kovalenko 1)	$y = \exp(a + bt + c\, t^2)$	a,b,c	Kovalenko et Tribrat [11]
4 (Kovalenko 2)	$y = \exp(a + bt + c\, t^2 + d\, t^3)$	a,b,c,d	Kovalenko et Tribrat [11]
5 (polynomial 1)	$y = a + bt + c\, t^2 + d\, t^3$	a,b,c,d	–
6 (polynomial 2)	$y = a + bt + c\, t^2 + d\, t^3 + e\, t^4$	a,b,c,d,e	–

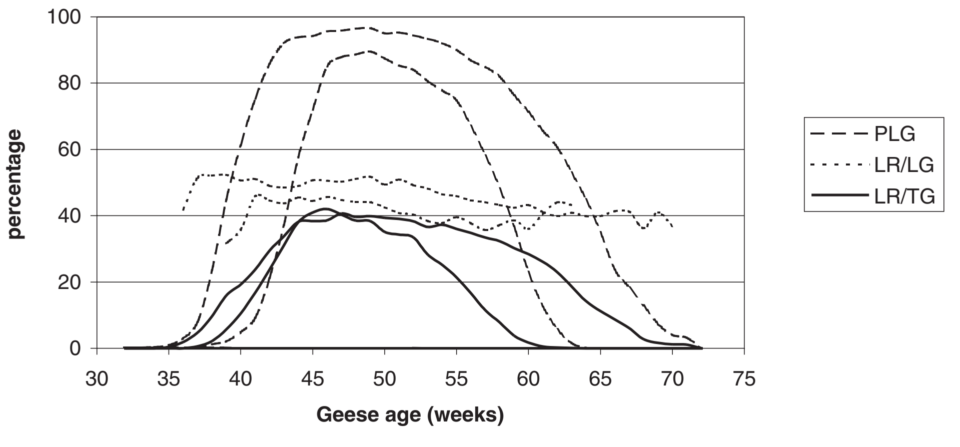

Figure 2. Laying curves (laying rate of total geese -LR/TG) and their components (percentage of laying geese -PLG- and laying rate of laying geese: LR/LG) in both systems (S1 = lower curves, S2 = upper curves).

variability in the age at sexual maturity, an inflection point for the rate of lay, and a peak of lay. The decreasing phase appeared to be the most specific part of the goose laying curve, with a sigmoidal trend where a linear or logarithmic trend is observed in other birds [8]. The goose is a poor layer as compared to other species, with a 50% rate of lay at the peak of egg production. The peculiar shape of the goose laying curves shown in Figure 2 seemed to be mostly influenced by the variable number of laying geese, rather than the change in laying intensity along the production cycle. The average number of eggs per laying goose decreased slightly, but linearly, with age, as for the laying hen [2, 5, 9, 12]. Bad layers exhibited both a short duration of lay and a low laying intensity, whereas the opposite features were observed for good layers. Among the 6 models tested to fit the goose laying curve (Tab. III), the polynomial models showed the best fit over the entire production period, but could not be adjusted to the progressive onset of laying. Models 1 (Wood) and 2 (McNally) overestimated the production at the peak of laying. None of the models tested could predict accurately enough the total egg production from a partial record at 11 weeks of lay.

Egg characteristics appeared to change along the laying curve. In system S1, egg weight increased in a logarithmic manner at the beginning of the laying period, and quickly reached a plateau at the peak of lay, around a value of 150 g, until the end of the laying period (Fig. 3). The mean egg weight in system S2 did not differ from its value in system S1, probably because egg weight was only recorded at the peak of lay in S2 (Tab. IV). The phenotypic correlations between egg weight and other traits were significantly positive with body weight and age at the first egg in both systems, and slightly, but significantly, negative with egg number, laying duration in system S1, and with laying rate in system S2 (Tab. V).

The frequency of egg abnormalities was also affected by age, with a difference, however, between the two systems (Fig. 4). In system S2, double-yolked eggs or small eggs were rather frequent at the beginning of the laying period, whereas eggs with shell defects, particularly a porous shell, became more frequent at the end of the laying

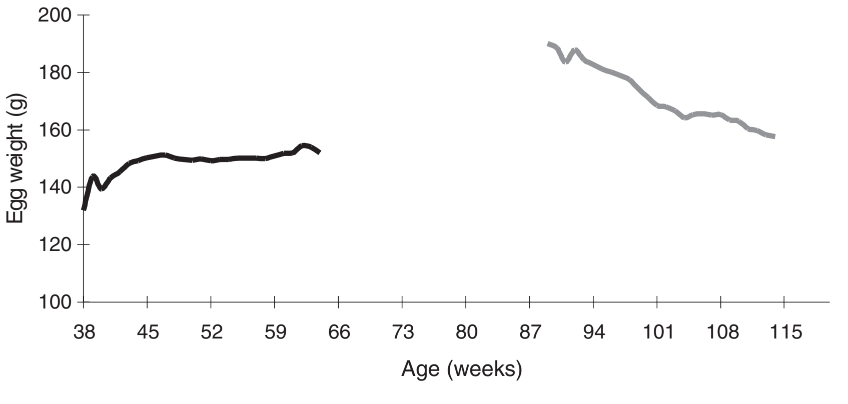

Figure 3. Evolution of the average egg weight according to age in system S1 (1st and 2nd cycles are represented).

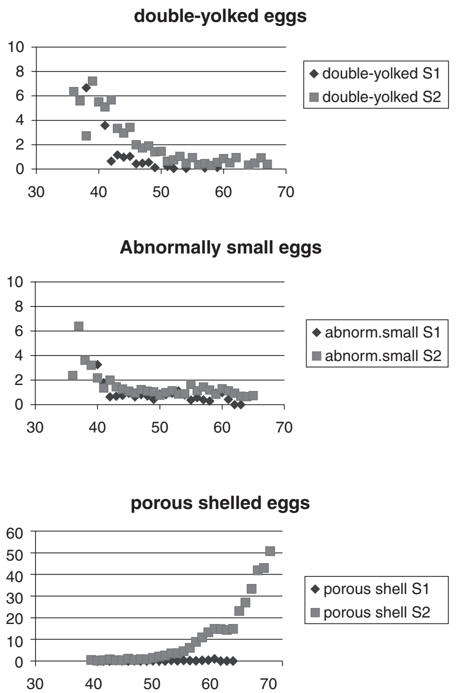

Figure 4. Evolution of some egg abnormalities with age.

period. These abnormalities were not as frequent in system S1, probably because the laying duration was much shorter.

3.2. Factors affecting total egg number

The production system affected very significantly the average number of eggs, which was much higher in S2 (Tab. IV). The average laying duration was mainly responsible for the difference in egg number, although laying intensity also contributed (41.1% in S1 vs. 45.5% in S2). The age at first egg was also more precocious in S2, by 4 weeks almost (Tab. IV). The age at first egg was significantly affected by the rank of hatch: the geese hatched later in the year entered into lay at a younger age, even under natural lighting conditions. Laying duration tended to be lower for the younger geese, and this was significant in S2. Consequently, the rank of hatch significantly affected the egg number, which was lower in younger geese. Laying intensity, however, did not vary between hatches within generation but varied between generations, in both systems. In agreement with the correlation observed between egg weight and age at first egg, the rank of hatch also affected egg weight, which was lower in younger geese.

3.3. Analysis of laying clutches and laying rhythm

All characteristics differed between the two systems: number of clutches, average clutch length, and maximal clutch length were higher in S2 and the average pause duration was shorter in S2 (Tab. VI). Consequently, the percentage of the productive time was markedly higher in S2. The within-clutch laying intensity was, however, higher in S1, associated to the shorter within-clutch interval between consecutive eggs (Tab. VI): the estimates of t2o corresponded to 41 hours in S1 and 43 hours in S2. In addition, the t2o value was affected by the generation number in S2 but not in S1. In both systems, LS and LSmax were affected by the generation number but the number of clutches was not. The average pause duration was rather stable across generations, it was not affected by generation in S2 and varied because of a single generation in S1.

The rank of hatch did not influence the number of clutches and average clutch length. An effect of hatch was observed on maximal clutch length in S2 only, being shorter in younger geese. In S1 only, the average pause duration was found to be longer for younger geese, which was associated with a lower percentage of productive time.

The correlations calculated in S1 between the estimated generation means of the different variables may indicate the sources of phenotypic variation between

Table IV. Influence of the system (strain-management), generation and rank of hatch on the goose weight and usual laying traits.

	n	Goose weight (g)	Age at 1st egg (d)	Total number of eggs per goose	Laying duration (d)	Laying intensity (%)	Average egg weight (g)
System		**	**	**	**	**	**
System 1							
Lsmeans	852	5950 ± 23	308.9 ± 0.4	37.8 ± 0.6	92.3 ± 1.1	40.7 ± 0.4	149.4 ± 0.4
Root MSE		542	12.6	14.5	24.5	12.9	9.7
Generation[1]		**	ns	**	**	*	ns
Mini-maxi[1]	149-193	5693-6222		35.5-43.9	88.1-99.6	39.2-43.0	
Rank of hatch		ns	**	**	+	ns	**
1	287		322.7 ± 0.8[a]	38.8 ± 0.9[a]	94.1 ± 1.6[a]		151.5 ± 0.6[a]
2	365		310.8 ± 0.7[b]	39.7 ± 0.8[a]	94.2 ± 1.3[a]		150.4 ± 0.5[a]
3	200		295.2 ± 0.9[c]	36.4 ± 1.1[b]	89.5 ± 1.9[b]		147.3 ± 0.7[b]
System 2							
Lsmeans	486	5626 ± 29	281.7 ± 0.5	72.0 ± 0.8	156.2 ± 1.3	45.4 ± 0.5	147.8 ± 0.5
Root MSE		554	10.6	20.8	34.3	8.0	10.2
Generation[1]		**	**	**	**	**	**
Mini-maxi[1]	115-137	5158-5878	267.9-289.7	60.9-86.0	139.2-175.2	43.5-48.9	145.6-150.3
Rank of hatch		ns	**	*	*	ns	**
1	198		290.7 ± 0.8[a]	73.9 ± 1.5[a]	159.5 ± 2.4[a]		150.3 ± 0.9[a]
2	288		272.8 ± 0.6[b]	70.2 ± 1.2[b]	152.9 ± 1.2[b]		145.3 ± 0.7[b]

ns, +, * and **: non significant, significant at $P < 0.10$, $P < 0.05$ and $P < 0.01$, respectively.
[1] Only minimum and maximum lsmeans of generations are given.

Table V. Phenotypic correlations between laying traits of the geese in both systems (S1 on the1st line and S2 on the 2nd line).

	Age at 1st egg	Laying duration	Laying rate	Av. egg weight	Goose weight	Av. clutch length	Av. pause duration	Number of clutches
Egg number	–0.40** –0.34**	0.78** 0.87**	0.76** 0.66**	–0.10* –0.08	0.03 –0.07	0.52** 0.50**	–0.52** –0.46**	0.37** 0.09
Age at 1st egg		–0.52** –0.37**	–0.13** –0.10*	0.10* 0.23**	0.02 0.06	–0.06 –0.07	0.11* –0.01	–0.34** –0.13*
Laying duration			0.21** 0.24**	–0.10** –0.04	0.01 0.00	0.14** 0.22**	–0.21** –0.16**	0.61** 0.41**
Laying rate				–0.06 –0.11*	0.01 –0.11*	0.67** 0.64**	–0.66** –0.71**	0.00 –0.37**
Av. Egg weight					0.44** 0.23**	–0.02 –0.08	0.03 0.08	–0.07 –0.01
Goose weight						0.03 –0.10	0.02 0.06	–0.02 0.11*
Av. clutch length							–0.17** –0.21**	–0.49** –0.64**
Av. pause duration								–0.38** –0.09

*, **: significantly different from zero at the level 5% and 1%, respectively.

generations. It appeared that the variation between generations in egg number was strongly correlated with the variation between generations in laying duration (r = 0.94) as well as in clutch length (r = 0.94). The variation between generations for the number of clutches and the average pause duration was limited and did not correlate with the variation in egg number.

3.4. Phenotypic correlations between components of egg production

Phenotypic correlations between total egg number and its components appeared remarkably similar across production systems (Tab. V). High positive correlations were found with laying duration and laying rate. A negative correlation was found between egg number and age at first egg, of the same order of magnitude as the correlation observed between the age at the first egg and laying duration. The relationship between age at the first egg and laying duration was even stronger in the natural lighting conditions of system S1.

Regarding the variables related to clutches, both systems exhibited a marked negative correlation between the clutch length and number of clutches, and a low, negative, correlation between the clutch length and pause duration. Correlations between egg number and characteristics of clutches were also similar across systems, except for the number of clutches. Clutch length and egg number were positively correlated (around 0.50), whereas a correlation of a similar magnitude, but of the opposite

Table VI. Influence of the system (strain-management), generation and rank of hatch of the goose on component traits of the laying clutches.

	n	Average clutch length (eggs)	Maximum clutch length (eggs)	Number of clutches	Average pause duration (days)	Percent productive duration	Within clutch laying intensity (%)	Within clutch interval between consecutive eggs (days)
System	1222	**	**	**	**	**	**	**
System 1								
Lsmeans	852	4.4 ± 0.1	12.1 ± 0.4	9.0 ± 0.1	6.5 ± 0.2	0.51 ± 0.01	0.91 ± 0.02	1.71 ± 0.01
Root MSE		2.1	6.7	3.4	5.1	0.18	0.56	0.17
Generation[1]		**	**	ns	**	**	**	ns
Mini-maxi	149-193	4.1-5.3	11.1-14.3		5.9-8.1	0.47-0.57	0.82-1.04	
Rank of hatch		ns	ns	ns	*	*	ns	ns
1	287				5.9 ± 0.3[b]	0.51 ± 0.01[a]		
2	365				6.2 ± 0.3[b]	0.53 ± 0.01[a]		
3	200				7.2 ± 0.4[a]	0.49 ± 0.01[b]		
System 2								
Lsmeans	370	7.7 ± 0.2	26.6 ± 0.5	11.3 ± 0.2	4.8 ± 0.2	0.69 ± 0.01	0.71 ± 0.02	1.78 ± 0.01
Root MSE		4.4	14.4	4.5	2.4	0.16	0.20	0.09
Generation[1]		**	**	ns	ns	**	*	**
Mini-maxi	115-137	6.55-9.24	24.5-31.3			0.64-0.74	0.67-0.74	1.75-1.81
Rank of hatch		ns	+	ns	ns	ns	ns	ns
1	147		28.1 ± 1.2[a]					
2	223		25.5 ± 1.0[b]					

ns, +, * and **: non significant, significant at $P < 0.10$, $P < 0.05$ and $P < 0.01$, respectively.
[1] Only minimum and maximum lsmeans of generations are given.

sign, was found between the pause duration and egg number. In the S1 system, the number of clutches was positively correlated to the egg number and independent from the laying rate, whereas the number of clutches was negatively correlated to the laying rate and independent from the egg number in the S2 system. Also, the correlation between the number of clutches and pause duration differed between the systems, and was significantly negative only in S1. Interestingly, the average clutch length was independent from the age at the first egg in both systems.

Correlations involving egg weight were rather similar across systems. They were slightly negative with laying duration, laying rate and egg number, but positive with age at the first egg, late-maturing geese laying larger eggs.

Whatever the system, body weight at the onset of lay was weakly, and generally not significantly, correlated with age at the first egg, and subsequent laying traits. A trend for a lower laying rate in heavier geese was indicated in the S2 system only. Body weight was significantly correlated with egg weight.

4. DISCUSSION

4.1. Factors affecting laying performance

The differences between the two systems were obvious for all traits investigated, with dramatic effects on the total number of eggs, the laying duration, the average clutch length and the percent of productive time. These differences may have arisen from a combination of effects of the breed and management system, which cannot be separated. The control of photoperiodism, however, is likely to explain the major part of this difference. Laying duration has been shown to be strongly affected by lighting conditions [26, 27]. The limitation of day length, as done in the S2 system, allows for a longer laying period which results in an increased number of eggs. Furthermore, the housing of geese in individual cages, as done in the S2 system, has been shown to prevent the onset of broodiness, a behaviour which is very detrimental to laying persistency [10]. Thus, both lighting and housing conditions may have contributed to the higher laying performance of geese placed in the S2 system. Within the S2 system, lighting conditions showed some variation between generations, which could not be related to an obvious trend of the generation means. The best performance was observed in generation 3 where day length was increased rapidly from 8 h to 10 h 30 between weeks 2 and 4 of the year. Earlier and more progressive photostimulation, or a longer day length (11 h or 11 h 30) were not associated to better laying performance, but selection was going on at the same time on the number of goslings, a trait not analysed in the present study.

The hatch effect, within generation, influenced a number of traits in a similar way in both systems: age at first egg, egg production, laying duration, average egg weight, average duration of pauses. The first egg was laid at the same time whatever the day of hatch, so that the age at the first egg was lower for geese born later. These results were in agreement with those of Borisov [4] indicating that geese born later, in July vs. February, began to lay younger, at the age of 42 weeks vs. 52 weeks. Sexual maturity is less a matter of age than of lighting conditions, which act as a synchroniser in a wide range of ages, from 20 to 40 weeks.

The change in egg weight along the production cycle was also studied by Shalev and Pasternak [28], using weekly means from two breeds, the White goose in Israel and the Grey goose from Toulouse. Their data showed a sharp increase in egg weight from 36 weeks of age to 50 weeks of age, thereafter egg weight appeared to reach a plateau around 155 g for Grey geese, until 60 weeks of age. Details on the management system of geese were not available in their study. Shalev and Pasternak [28] concluded that a similar equation could be used to predict the change in egg weight across poultry species, provided that the data were expressed in terms of percentage of mean egg weight and percentage of maximum age. In the present study, the weight of the first eggs laid by the geese of the S1 system was around 130 g, rather similar to the initial values found by Shalev and Pasternak [28] in Grey geese, and the subsequent trend was very similar.

In the S1 system, data were also obtained on egg weight during the second production cycle [8]. On average, egg weight was larger in the second cycle (Fig. 3), which was in agreement with previous results [15, 20], but a regular decrease in egg weight was observed all along the second cycle, which could be due to the fact that geese were losing weight.

4.2. Detailed analysis of the laying rhythm

The definition of the laying clutch was expected to provide further insight into the difference in egg production patterns between the two production systems. The mean interval between two neighbouring ovipositions within one clutch was estimated to be 41.0 h in S1 and 42.7 h in S2. These values were higher than those found by Stasko et al. [30], who obtained values close to 36 h, using the same definition of a clutch as in the present paper. The present estimates were close to the duration between successive ovipositions obtained by Chun Xiang and He Guang [7] in the White Roman geese (45.7 h), and lower than the duration of 46 to 48 h observed by Celebi and Guven [6]. Thus, a variation can be found between breeds and between management systems for an interval between ovipositions. Within each goose, on average for both systems, the proportion of 1 day-intervals within consecutive eggs of the same clutch was found to be about 35%. This does not mean that 35% of the intervals were 24 hours. In the case of a goose laying one egg every 36 hours, and with egg collection twice a day (at 9 a.m. and 4 p.m. for instance), it can be shown by simple simulation [8] that 50% of the intervals will appear as 1 day and 50% as 2 days. Indeed, the sequence of days, where + and – indicate a day with and without an egg collected, respectively, will be +–++–++–. In the case of a goose laying one egg every 48 h, 100% intervals will be 2 day-intervals. Our situation (41–43 h between ovipositions and a proportion of 2 day-intervals at 65%) is intermediate and can therefore be accounted for by the discrepancy between laying rhythm and daily rhythm. Of course, intervals between consecutive eggs certainly vary from the average, leading possibly to further irregularities. For instance, the occurrence of 3, 4 or 5 eggs in a row exist in the strain studied, although rarely, and need further investigation.

The interval between neighbouring ovipositions is the sum of the time required for egg formation, and of the time lag between oviposition and the next ovulation. Within a clutch, the time between an oviposition and the ovulation of the following egg is expected to be slightly positive. The possibility of a negative value, however, cannot be ruled out, but this has not been documented in geese. Such a case may occur in the chicken, for instance in the laying hen with a high ovulation rate [24] and, with a different mechanism, in broiler strains where it is often associated with the laying of abnormal eggs [16]. Thus, both time components (egg formation, time lag) could be variable. This suggests the interest of investigating the variability existing between and within breeds, and the possibility of selecting this trait to improve egg production, as already quoted by Stasko et al. [30] and Schneider [25].

Quite interestingly, the S2 production system with the highest laying rate and highest egg number did show a slightly longer interval between ovipositions. In the laying hen, the highest laying rate and the longest clutches are found when the mean interval between ovipositions becomes close to 24 hours [31]. In the extreme situation where the interval is exactly 24 hours, the clutches would not be observed any longer, because the hen would lay an egg every day. In fact, the existence of laying clutches can be seen as the consequence of a lack of synchronisation between the endogenous rhythm of follicular maturation on the ovary, on the one hand, and the external lighting rhythm affecting the neuro-endocrinological control on ovulation, on the other hand. In the goose, this lack of synchronisation reaches extreme values, because the internal rhythm appears to vary between 36 and 48 hours, whereas the external rhythm is limited to a 24 h nycthemeral cycle. Ahemeral light-dark cycles have been tested in the laying hen, in order to further investigate the laying rhythm, in situations of short, long, or even continuous light, but this would be very difficult to try in the goose, because of its high sensitivity to light duration.

The difference in total egg number between S1 and S2 production systems appeared to be due to a difference in clutch length rather than to a difference in the number of clutches. Longer clutches are expected to be observed when the interval between ovipositions is regular in the same female, and has reached an equilibrium state relative to the light-dark cycle. The identification of an optimum value for the interval between ovipositions in a given environment would be quite desirable, keeping in mind that any modification in the time required for egg formation might affect egg weight, and even more importantly, egg shell quality. Indeed, a decrease in egg shell quality was observed with age in S2, which may prevent many eggs from being incubated. This could be due to a change with age in the oviposition rhythm, but also to nutritional deficiencies in the ageing goose. It is quite important to investigate further the reasons for this trend in egg quality, otherwise, it may become a limiting factor of gosling production. Furthermore, the male reproductive ability may decrease with age and could also become a limiting factor of reproduction, in spite of an increased length of laying period in S2.

4.3. Correlations between traits

The two systems showed a great similarity in the pattern of phenotypic correlations between component traits of total egg production. The high correlations found in both systems between egg number (NE) on the one hand, and laying duration or laying rate, on the other hand, confirmed those found by Schneider [25] on Italian Geese and Stasko et al. [29] on various genetic types. Likewise, the positive correlations between NE and laying precocity ($r = 0.40$ and 0.34 in S1 and S2 respectively) ranked within the range of values found previously: $r = 0.47$ [15], $r = 0.23$ [25]. These correlations, as well as the relationship between laying precocity and egg weight, are totally consistent with the results known in the laying hen. The low negative correlation between NE and egg weight conformed to the results of Wezik and Sochocka [31], as did the quasi null correlation between NE and goose body weight with the value of 0.13 found by Meritt [14].

It must be noticed, however, that egg number was more strongly correlated with laying duration than with laying intensity in S2, as compared to S1, where both correlations were almost identical. Furthermore, the correlations involving the number of clutches (NS) and other components of egg production (number of eggs, laying intensity or pause duration) also showed differences between the systems.

In S2, the clutches were longer and also more variable (lsmeans ± residual standard deviation at 7.7 ± 4.4 eggs) than in S1 (4.4 ± 2.1 eggs). Consequently, clutch length was a much better predictor of total egg number than the number of clutches, which was poorly correlated with NE (0.09). In S1, the clutches were shorter but less variable, consequently the number of clutches could partially predict the total egg number, and the correlation between NE and NS was higher (0.37). When variability in clutch length is limited, pause duration is affected by the number of clutches, as found in S1, with a negative correlation of –0.39 between DP and NS. When clutch length is more variable, as it is in S2, the number of clutches is not significantly correlated with pause duration (–0.09 in S2).

Finally, the correlation between NS and overall laying intensity differed also between systems, because the within-clutch laying intensity is a better predictor of overall laying intensity when clutches are long and not numerous, as in S2. Consequently, the more clutches in S2, the lower was the overall laying intensity, I, of the goose (–0.37), whereas there was no relationship between NS and I in the S1 system.

5. CONCLUSIONS

Except for the laying curve, which differed markedly from the reference curve known in the laying hen, it appeared that variability in, and covariances between, egg number, sexual maturity, egg weight and body weight, exhibited several features which are consistent with the situation known in the hen. One exception may be the hatch effect found on the age at first egg, which is due to the seasonality of the goose. The detailed analysis of laying rhythm provided a description of egg production which could be interpreted on the basis of the knowledge in the laying hen, taking into account that the duration of egg formation in a goose is not compatible with a 24 h nycthemeral light-dark cycle, and that the goose is a very photosensitive bird. Further studies are now needed, regarding the genetic part of the phenotypic variability examined here, as well as the correlations with the production of goslings, which is the most important economic objective for goose production.

ACKNOWLEDGEMENTS

The authors are grateful to the staff of technicians at the ‘Unité Expérimentale sur les Palmipèdes à Foie Gras’ (INRA) and at the “Gourmaud Sélection S.A.” company, for performance recording and management of animals.

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