



Does maternal social hierarchy affect yolk testosterone deposition in domesticated canaries?

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Dominance is a relative measure that allows asymmetrical relationships between individuals to be quantified. These kinds of relationships often depend on aggressive behaviour and the steroid hormone most frequently associated with aggressiveness is testosterone. Testosterone is present in both sexes and implanting it can provoke a rise of individual aggressiveness leading consequently to an increase of social status. Many researchers have studied the relationship between plasma testosterone and dominance but few have focused on yolk testosterone and social hierarchy. Thus we aimed to study the possible influence of the mother's social status on egg yolk testosterone deposition. Our hypothesis is that dominant females lay eggs containing more testosterone than subordinate females. We recorded the social hierarchy of 24 female domesticated canaries, *Serinus canaria*, and studied the influence of their social status on the concentration of testosterone in their egg yolks and on other egg characteristics. Our results show a significant relationship between a mother's social status and the amount of testosterone deposited in its yolks: the more dominant the females are, the more concentrated in testosterone their eggs are. Our results also show that yolk testosterone increases with laying order, whereas no relationship between mothers' rank number and their clutch size or egg mass was found. We conclude that there is a clear effect of maternal social status on yolk testosterone and discuss dominance inheritance.

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Dominance is a concept commonly associated with social organization. Many definitions have been generated to give sense to such a concept (Drews 1993); most definitions indicate that dominance is a relative concept often used to describe competitive relationships between individuals within a social group (Bernstein 1981; Piper 1997). Dominance relies on repeated asymmetrical agonistic interactions between at least two individuals; the outcome of these interactions leads to a winner (dominant) and a loser (subordinate) (Drews 1993).

The ability of a bird to become dominant can depend on several factors; some of them may be fixed, whereas others are variable (Piper 1997). Among fixed attributes,

we can cite genetic factors: males tend to dominate females (Fugle et al. 1984; Richner 1989). On the other hand, variable attributes such as age can also act on a bird's social rank: for example, the oldest individuals tend to dominate the younger individuals (Richner 1989; Teather & Weatherhead 1995).

Another important factor is the bird's hormonal status; because hormones can have profound influences on behaviour, variation in hormonal concentration can modify the social status of an individual (Archawaranon et al. 1991; Creel 2001; Parker et al. 2002). Testosterone is a steroid hormone frequently associated with aggressive behaviour (Baptista et al. 1987; Wingfield et al. 1990, 2003; Van Duyse et al. 2002; Mazuc et al. 2003; Poisbleau et al. 2005); because aggressiveness plays a key role in dominance interactions (Wilson 1975; Beaugrand 1983), many studies have focused on the relationship between testosterone levels and dominance. In white-throated sparrows, *Zonotrichia albicollis*, testosterone-implanted males show an increase in aggressiveness and social status

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in the presence of unfamiliar opponents (Archwaranon et al. 1991). Similarly, testosterone implants enhance the social rank of female spotless starlings, *Sturnus unicolor* (Veiga et al. 2004). Nevertheless, it is worth noting that, in male and female canaries, *Serinus canaria*, no correlation between natural plasma testosterone levels and social status was found (Parisot et al. 2005).

The previously cited experiments examined the influence of internal testosterone on dominance but testosterone is also a major component of egg yolk and thus could influence the social status of chicks. Schwabl (1993) showed this influence in that chicks hatched from eggs containing high levels of testosterone were more dominant than other chicks, regardless of their sex. Moreover, yolk testosterone concentration can be related to the mothers' aggressiveness (Whittingham & Schwabl 2002; Mazuc et al. 2003). Because yolk testosterone is provided exclusively by the female (Schwabl 1993), the possibility of an indirect transmission of the ability to become dominant through yolk composition can be questioned.

The domesticated canary is a very well studied species in which females can lay eggs in the presence and absence of males. In canaries one important parameter influencing yolk testosterone deposition is male attractiveness (Tanvez et al. 2004; Gil et al. 2004). The ability of unpaired female canaries to lay eggs in the absence of mate stimulation allows us to design an experiment in which male influence can be discarded.

In this observational study, we investigated whether high-ranked female domesticated canaries lay eggs containing more testosterone than subordinate females. We measured the social hierarchy of 24 females in an aviary before and after laying and measured the concentration of testosterone in their eggs. We hypothesize that dominant females, being more aggressive than subordinate females, indirectly transmit this behavioural characteristic to their offspring by laying eggs with higher concentrations of testosterone.

METHODS

Subjects and Housing Conditions

Twenty-four female canaries were selected from a pool of birds reared in our laboratory; their ages varied from 1 to 5 years (mean \pm SE: 2.92 ± 1.5 years). They were fed every day with seeds (mainly canary grass, *Phalaris canariensis*, and rape, *Brassica rapa*) and water ad libitum and twice a week with eggfood (CéDé eggfood: wheat flour, eggs, sugar honey, hemp seed, niger seed, broken hulled oats, poppy seed, vitamins, minerals, amino acids: lysine and methionine, yeast) accompanied with fruits or vegetables.

Before the beginning of the study, individuals were housed in single-sexed groups of five in cages ($1.180 \times 0.475 \times 0.54$ m) mixed with the other 600 birds of both sexes of the laboratory under a short-daylight photoperiod (8:16 h light:dark cycle). One month before the beginning of the observations, to allow the birds to acclimate to their new conditions, the 24 randomly selected females were moved together into an aviary ($4 \times 2 \times 2.5$ m). After this

1-month acclimatization period, the photoperiod was shifted to springtime (12:12 h) and we performed the first session of dominance tests. Two weeks later, the aviary was equipped with 40 nest bowls and nesting material and the photoperiod was changed to long days (16:8 h) allowing the females to lay eggs. After the laying period, we performed the second session of dominance tests.

Domesticated canaries in our laboratory have plumage of various colours (white, bright yellow, grey-brownish, green-melanized, etc...). Thus, it was easy for us to recognize the 24 females; otherwise, when there was a chance of confusing two birds, one bird was lightly marked on the head or tail using nontoxic brown or white paint.

Dominance Tests

Social hierarchy was evaluated in the aviary using a method of competition for access to a food source (Drews 1993; Parisot 2004; Parisot et al. 2004, 2005). Females were food deprived for 1 h and then tested using extra food (fruits or vegetables) as the object of competition. It is worth noting that 1-h food deprivation has no adverse effect on the canaries' health or weight (Parisot et al. 2004) and that, after each test, birds were provided with supplementary food ad libitum. The observations lasted 15 min; during this time all birds were tested simultaneously in the aviary using one type of extra food (apple, boiled egg, cucumber or broccoli at random). During this period, the (1) number of victorious interactions, (2) rank of access, (3) time spent eating and (4) number of accesses to food were recorded for each bird. In cases of severely aggressive interactions, the females had enough space in the aviary to escape. Nevertheless, human intervention was intended if the level of aggressiveness between two individuals became too severe; however, this never occurred. Dominant individuals are defined as the birds obtaining more access to food and winning most interactions over food access (Drews 1993). For each measure, birds were classified from rank 1 to 24, where 1 represents the highest rank (the most victorious bird, the bird that arrived first on food, etc...) and 24 the lowest rank. Then, for each female, we calculated the sum of her ranks, taking the four measures into account: the best possible sum should be 4 (4×1) for a bird who always won and the worst should be 96 (4×24) for a bird who never won. According to these sums, birds were given a dominance rank between 1 and 24; the best possible rank is 1 and the worst is 24.

Social hierarchy was reassessed at the end of the laying period to determine its stability; 40 tests were conducted to evaluate the hierarchies during these two periods.

Egg Sampling

Once the laying period began, the nestboxes were examined daily. When an egg was found, it was individually marked, weighed, frozen and replaced by a dummy egg. Genetic tests performed in our laboratory under similar experimental conditions show that female canaries

do not egg dump (Parisot 2004). Thus, to attribute each egg to the corresponding female we performed daily observations (at least three per day at random hours) to identify which female was brooding in which nest and which egg was laid by the relevant female.

Testosterone Assay

Testosterone concentrations in yolks were determined by radioimmunoassay at the Centre d'Etudes Biologiques de Chizé following the extraction and radioimmunoassay method presented in Tanvez et al. (2004) for the same species. The minimal levels of testosterone detected were 15 pg/mg. The mean intra-assay coefficient of variation was 8.0%.

Statistical Analysis

Analyses were computed using SigmaStat version 2.03 (SPSS Inc., Chicago, IL, U.S.A.). Parametric statistics were used to analyse data on egg characteristics (Sokal & Rohlf 1995). Linear regression was used to analyse clutch size according to mothers' rank number and multiple linear regression was used to analyse egg weight and yolk testosterone concentration according to mothers' social status and laying order. *t* Tests were performed to compare the levels of females' aggressiveness and the numbers of interactions before and after laying.

Nonparametric statistics were used on hierarchical data (Sokal & Rohlf 1995). To correlate dominance measures, to analyse hierarchy stability, to study the relation between the females' age and their social status and to examine the relation between clutch size and the variation of mothers' social status we used Spearman rank correlations.

RESULTS

Social Hierarchy

The hierarchy among females was clearly apparent although, as described for canaries and other species, it was not strictly linear (Shoemaker 1939; Barkan et al. 1986): during a few encounters middle-ranked females were defeated by lower ranked females.

Correlations between the four dominance measures

The method used is assumed to be valid if the four measures are positively correlated together: Spearman rank correlations confirmed this assumption (Table 1). It is also worth noting that no age effect on the dominance ranks was found (Spearman rank correlation: $r = 0.223$, $N = 24$, $P = 0.29$).

Hierarchy stability

We evaluated female social hierarchy before and after egg laying. There was a significant correlation between the two hierarchy measurements (Spearman rank correlation: $r = 0.710$, $N = 24$, $P < 0.001$; Fig. 1), indicating that the

Table 1. Spearman rank correlations between the four dominance measures

	Access number	Time spent eating	Number of victorious interactions
Access rank	$R = -0.965^*$	$R = -0.943^*$	$R = -0.940^*$
Access number		$R = 0.950^*$	$R = 0.963^*$
Time spent eating			$R = 0.942^*$

* $P < 0.001$.

social hierarchy was stable throughout the observation period.

Females competed for food throughout the reproductive period. The average number (mean \pm SE) of aggressive encounters per test was 38.3 ± 5.01 before egg laying and 32.3 ± 4.52 after egg laying. There was no significant difference between the level of aggressiveness shown before and after laying (*t* test: $t_{38} = 0.600$, $P = 0.552$). Similarly, the average number (mean \pm SE) of interactions per test remained stable (*t* test: before laying: 77.5 ± 10.5 ; after laying: 70 ± 11 ; $t_{38} = 0.389$, $P = 0.699$). Each female was observed 3.1 ± 0.7 times during each of the 40 tests.

The female ranks used to examine the relationship between dominance and egg characteristics were those obtained from the first hierarchy, this hierarchy was assessed just before the laying period, when the eggs were in formation.

Egg Characteristics

Clutch size and egg mass

The mean \pm SE clutch size was 4.13 ± 0.46 eggs. There was no significant correlation between female rank and number of eggs laid (Spearman rank correlation: $r = 0.015$, $N = 24$, $P = 0.947$). Moreover, no correlation between the clutch size and the variation of the mothers' social status (calculated as the difference of the mothers rank number prior to and after laying) was found (Spearman rank

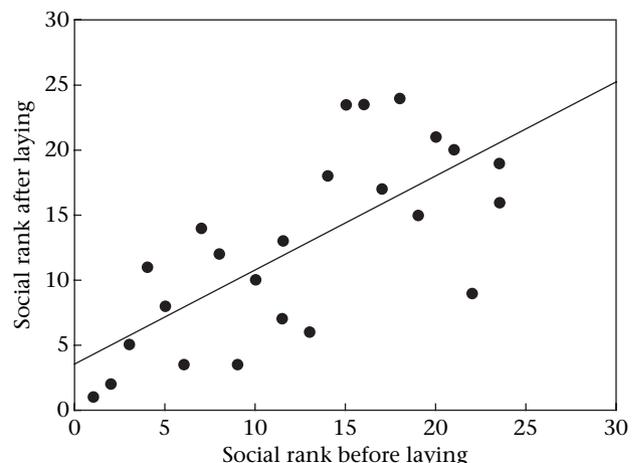


Figure 1. Correlation between the social ranks of the females before and after laying (Spearman rank correlation: $R = 0.710$, $P < 0.001$).

correlation: $r = 0.288$, $N = 24$, $P = 0.17$). Thus, in our study, mother social status did not influence clutch size.

For egg mass, a multiple linear regression analysis showed no relation between this value and the two independent variables: mother rank number ($P = 0.541$) and laying order ($F_{2,70} = 0.189$, $P = 0.999$).

Yolk testosterone concentration

When we examined the relationship between yolk testosterone concentration and female social status we took into consideration the laying order as an independent variable because previous studies showed a positive relationship between yolk testosterone and laying sequence in canaries (Gil et al. 2004; Tanvez et al. 2004). Thus, we performed a multiple linear regression analysis with yolk testosterone concentration as a dependent variable and mother rank number and laying order as independent variables.

The analysis showed a relation between dependent and independent variables: the dependent yolk testosterone concentration can be predicted from a linear combination of the two independent variables: mother rank number ($P = 0.023$) and laying order ($P = 0.006$).

Yolk testosterone concentration = $49.508 - (1.167 \times \text{mother rank number}) + (9.357 \times \text{laying order})$ with $N = 73$, $R = 0.395$, $R^2 = 0.156$ and $\text{adj}R^2 = 0.132$.

The ANOVA indicates a significant regression: $F_{2,70} = 6.46$, $P = 0.003$. Thus, yolk testosterone was higher when the mothers were more dominant (with a rank tending towards 1) and its level increases with laying order (Fig. 2).

DISCUSSION

The social hierarchy based on food competition allowed us to classify the females according to their behaviour: the more dominant females come sooner and more often,

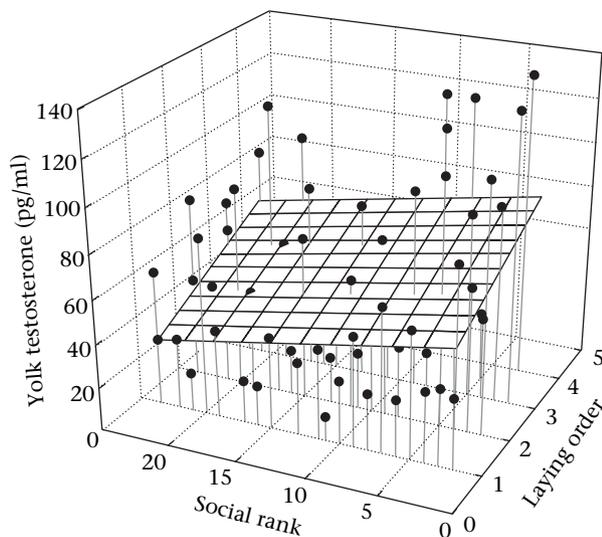


Figure 2. Three-dimensional scatter showing yolk testosterone concentration according to female social rank and laying order. Individual data and regression plane are shown.

spend more time on extra food and win more interactions than the more subordinate females which manifest opposite behaviour. The social status of individuals was consistent across the reproductive period because dominance ranks measured before and after laying were significantly correlated. Our observations on laying order corroborate previous studies showing that testosterone concentration increases as eggs are laid (Schwabl 1993; Gil et al. 2004; Tanvez et al. 2004). Moreover, we show an absence of an effect of maternal social hierarchy on egg weight but a clear significant effect of this status on yolk testosterone deposition; dominant females lay eggs with greater amounts of testosterone than subordinate females. Müller et al. (2002) showed an effect of maternal social rank on yolk testosterone deposition in chickens, *Gallus gallus domesticus*, but this effect depended on the future sex of the chick; indeed, high-ranked mothers lay male eggs with a higher testosterone concentration whereas low-ranked mothers lay female eggs with a greater amount of testosterone. In our study, we could not take into account the sex ratio of the clutch because no male was present in the aviary and thus the eggs were not fertilized.

When a female lays eggs with high androgen concentrations, its chicks will undergo the effects of these steroids. In black-headed gull, *Larus ridibundus*, eggs injected with androgens (testosterone and androstenedione) hatch sooner (Eising et al. 2003). Chicks hatching from these eggs are more active and respond more quickly to the approach of their parents (Eising & Groothuis 2003); they also beg more and grow faster (Eising et al. 2001). Moreover, in experiments relying on a testosterone treatment (instead of mixed androgens), survival is enhanced in European starling chicks, *Sturnus vulgaris* (Pilz et al. 2004), whereas in domesticated canaries chicks beg more often (Schwabl 1996a), are more aggressive (Schwabl 1993) and grow faster (Schwabl 1996a). Nevertheless, yolk testosterone can also have a negative effect on chicks' immunity as in the Chinese painted quail, *Coturnix chinensis* (Andersson et al. 2004), and in the common lizard *Lacerta vivipara* (Uller & Olsson 2003), and can decrease survival and growth as in yellow-legged gull chicks, *Larus michahellis* (Rubolini et al. 2006). Similarly, yolk androgen injection (testosterone and androstenedione) can reduce offspring survival (Sockman & Schwabl 2000).

In his first study on yolk steroids, Schwabl (1993) demonstrated that the social status of canary chicks (males or females) was positively correlated with their yolk testosterone levels; the more the egg from which they hatched contained testosterone, the more dominant they were later (from day 43 until day 131). In the present study we show that dominant female canaries lay eggs containing more testosterone than subordinate females. Taking into account these two studies, we can hypothesize that dominant females' chicks could thus become more dominant later because of the higher concentration of testosterone in their yolks.

Dominance heritability is a very controversial subject; however, the concept of dominance per se does not allow heritability because it is a relative concept taking into account only a particular social group or dyad and thus cannot be genetically inherited (Piper 1997). Social rank

can vary according to the social group: Nol et al. (1996) showed in Japanese quails, *Coturnix japonica*, that juvenile and adult social ranks were not correlated and suggested that this absence of correlation could be due to a modification of social conditions between the two periods. In contrast, it has been shown that personality traits can be genetically transmitted, as is the case for exploratory behaviour (Drent et al. 2003) or foraging strategies which are also known to be associated with individual social status (Parisot et al. 2004).

If a female can transmit its dominance ability through yolk composition the mechanisms leading to this differential allocation of testosterone should be investigated. Indeed, we show here that dominant females lay eggs with higher testosterone concentrations, whereas a previous study on the same pool of birds showed no relation between social status and plasma testosterone concentration (Parisot et al. 2005); so, the females laying eggs with a higher amount of testosterone are not necessarily the females with a higher plasma testosterone concentration. The origin of yolk testosterone is controversial; some studies show a direct link between the concentrations of female internal testosterone and yolk testosterone (Schwabl 1996b; Clotfelter et al. 2004), whereas other studies show no direct relation between plasma and yolk testosterone concentration (Doi et al. 1980; Hammond et al. 1980; Hackl et al. 2003). These studies suggest that, with regard to testosterone, the follicle has a higher influence on yolk composition than the plasma; our results tend to support this suggestion.

Studies have shown that when females lay eggs with higher amounts of testosterone their chicks benefit from this increase in various ways (see earlier cited references). The results presented here allow us to elaborate on this because they suggest that there is a transfer of testosterone by the dominant female and this could be a mechanism leading chicks to be more aggressive and dominant later; however, chicks' future social conditions cannot be neglected. A longitudinal study examining the development of the social status of chicks hatching from dominant or subordinate female eggs depending on social conditions would be of interest.

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