

The female red jungle fowl (*Gallus gallus gallus*) reproductive investment stimulated by male attractiveness

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Abstract. Lelono A, Riedstra B, Groothuis T. 2024. The female red jungle fowl (*Gallus gallus gallus*) reproductive investment stimulated by male attractiveness. *Biodiversitas* 25: 2931-2936. To maximize their capacity for reproduction, mothers are expected to modify their investment in offspring based on the quality of their mates. A recent study showed that females in female-care only species do so by investing more in egg mass when mated with attractive males rather than in other reproductive traits. In our study, we investigated how red jungle fowl (*Gallus gallus gallus*) mothers invest in clutch production based on the size of the male's comb, a trait signaling attractiveness. We randomly paired 14 females with 14 males of either large or small combs and monitored their egg-laying, clutch completion, and brood rearing. Following the initial clutch, we exchanged male partners and permitted females to establish up second generation. We found that females who were partnered with males who had bigger combs laid down their eggs earlier after pairing compared to those paired with males with smaller combs. However, there were no variations in egg mass or clutch size that we could find. Furthermore, the size of the male's comb influenced the growth and body condition of female chicks, with those sired by males with larger combs being heavier and in better condition at twenty-four weeks old. These data support the premise of the positive Differential Allocation (DA) hypothesis, where maternal investment varies with mate quality, rather than the negative DA, where females more investment in offspring from lower quality mates.

Keywords: Differential allocation hypothesis, female reproductive investment, male attractiveness

Abbreviations: DA: Differential Allocation hypothesis

INTRODUCTION

In line with life history theory, reproductive strategies are expected to evolve to enable individuals to modify their investment in reproduction following predicted fitness returns, particularly in response to variation in partner quality (Kobayashi 2017; Cutting et al. 2021; Laskowski et al. 2021). Females typically face constraints on how many eggs they are able to lay and allocate more resources toward developing zygotes, embryos, and offspring (Křištofik et al. 2014; Watson et al. 2015). This includes a larger investment in the ovum compared to males' investment in spermatozoa, either through gestation or incubation (Křištofik et al. 2014; Carleial et al. 2020a). This holds true even though males in many species invest differently in reproduction through by acquiring and caring for mates and territories (Tan et al. 2017; Carleial et al. 2020a).

With the intention of optimizing both present and future reproductive performance, reproductive strategies entail making decisions about "when to reproduce", "how many offspring to produce", and "how much to invest in the offspring". If females with equal reproductive potential end up mating with male of different quality, a contradiction in reproductive strategies will arise: either she invests more in her present progeny when she mates with high-quality

males because the offspring will likewise be of high-quality (Differential Allocation (DA) hypothesis) (Křištofik et al. 2014; Parker and Pizzari 2015; Watson et al. 2015; Wilson and Burley 2021) or to make up for the offspring's low-quality father, invest more in the present offspring when coupled with low-quality male. (the compensation hypothesis) (Song et al. 2020; Foo et al. 2023). Various factors, including how males and females share the responsibility of raising offspring within a species, can influence the chosen reproductive method (McDonald et al. 2019; Song et al. 2020; Wilson and Burley 2021). Currently, these two theories are considered as a unified continuum, commonly known as positive and negative DA. Positive DA appears to be prevalent among avian species, according to recent research (Haaland et al. 2017; Kindsvater and Alonzo 2014; Laskowski et al. 2021).

To investigate whether female investment in current reproduction varies based on mate quality, this study aims to provide novel insights. Various characteristics, including behavioral traits like food provisioning and vigilance, may serve as indicators of male quality (Cerit and Avanus 2007; Alvarez-Fernandez et al. 2019; Carleial et al. 2020a) along with morphological traits such as comb size. Jungle fowl (*Gallus gallus gallus*) exhibit comb size, which positively influences female mate choice (Carleial et al. 2020a). Additionally, comb size is inherited and associated with

social dominance (Desta 2019; Carleial et al. 2020a). Furthermore, a smaller comb is linked to a lower level of immune-competence, suggesting that only high-quality males can afford the cost of reduced immune competence (Łukaszewicz et al. 2017; Lelono et al. 2019c; Foo et al. 2023). These correlations suggest a relationship between attractiveness and phenotypic quality, where males with larger combs are considered of higher quality due to their dominance and lower levels of circulating lymphocytes (Carleial et al. 2020a; 2020b) rendering them more appealing to females than those with smaller combs. To assess whether rooster quality influences investment in female reproduction in the clutch, we initially paired hens randomly with either large-combed or small-combed roosters and allowed them to produce a clutch.

MATERIALS AND METHODS

Animals model

In this study, we employed 14 pairs of sexually inexperienced red jungle fowl (*Gallus gallus gallus*), which were bred in captivity and obtained from our own breeding stock at the University of Groningen, The Netherlands. All hens and 10 of the roosters were aged between two and three years, while the remaining 4 roosters were one year old. Male combs typically mature at one year old, with subsequent alterations in size influenced by environmental factors. Prior to the commencement of the experiment, roosters and hens were separated into two distinct groups based on sex and housed in separate outdoor aviaries.

Experimental design

To assess male quality and ensure balanced distribution of hens across the experimental groups, we conducted two rounds of biometric measurements on all parent birds at the outset of the pairing process. We measured body weight to the nearest gram and comb dimensions, specifically comb length and comb area. To determine the dimensions of the combs, we attached a circular sticker with a diameter of 0.8 cm to each male's comb. We then took photographs of all the combs using a digital camera (Canon SX 500 IS: focal length 4.3-129.0 mm), focusing specifically on the left side of the rooster heads. Afterwards, we imported these images into GIMP 4.8, where we manually outlined the combs and

calculated the number of pixels within the outlined area. By comparing this pixel count with that of the sticker, which had a known surface area and was captured in the same photograph, we determined the size of the combs. Furthermore, we evaluated the coloration of the combs using a spectrophotometer.

The roosters were subsequently ranked based on comb size, serving as the primary indicator of quality. The 7 birds with the largest combs were categorized as "large combed" roosters, while the remaining 7 with smaller comb sizes were designated as "small combed" roosters. Details of male phenotypic traits are provided in Table 1. In the first round of reproductive attempt, we paired 7 large comb size males with 7 randomly selected females and 7 small comb size males with another 7 randomly selected females. In the second round of mating, we used the same method, where 7 large comb size males were paired with 7 females that had previously mated with small comb size males. The pairings were chosen randomly to avoid any bias from the assessor.

To maintain consistency in the two categories of females' average body mass, reference Table 2. These pairs were then accommodated together in one of 14 identical aviaries, each measuring 1.5×3×2.5 m (length×width×height). Inside these aviaries, the pairs had continuous access to water and standard chicken pellets as their diet, along with facilities such as a dust bathing area, perch, and nest site. Daily inspections were carried out to monitor egg production, and upon laying, eggs were weighed, marked with a non-toxic felt-tipped pen for identification, and placed back in the nest for incubation, hatching and raising their chicks. Once their chicks reached one month of age, they were removed and placed in separate cages. The female and male parents were then separated to allow for recovery. Once the birds had recovered, we reversed the procedure to eliminate the impact of the initial pairing: females that were initially paired with a male with a large comb were now paired with a small comb male, and vice versa. This adjustment was made after the first clutch was produced and removed. Following this change, we repeated the same process to measure the biometric characteristics of the males once again. Because females initially paired with males with large combs began laying eggs a week earlier than those paired with males with small combs, they had an extra week to recuperate from their initial reproductive effort.

Table 1. Phenotypic characteristics (mean and s.e.m. in brackets) of large - (N=7) and small combed roosters (N=7)

Male comb size	First clutch				Second clutch			
	Large	Small	t	p	Large	Small	t	p
male body mass (gr)	1232.3 (68.5)	1043.3 (42.0)	5.06	0.046	1131.0 (61.6)	1005.2 (27.3)	0.137	0.084
comb size (cm ²)	18.9 (0.98)	10.5 (1.09)	32.00.	<0.001	19.0 (0.89)	10.0 (1.20)	37.04	<0.001
brightness	9.4 (0.71)	9.3 (0.93)	00.02	0,614	9.3 (0.52)	11.2 (1.61)	01.45	0.175
Chroma (dimensionless)	1.29 (0.14)	1.41 (0.16)	00.32	0,402	1.32 (0.08)	1.36 (0.21)	0.03	0.596
Hue (nanomeers)	624.6 (3.41)	611.9 (8.83)	02.01	0,127	612.6 (5.93)	597.7 (14.02)	1.11	0.215
female body mass (gr)	874.1(29.2)	828.8(36.9)	0.066	0.243	833.4 (19.5)	859.3 (20.0)	0.059	0.256

Note: Body mass is measured in grams, comb size in cm², brightness as a percentage of reflectance, chroma is dimensionless, and hue is expressed in nanometers

Table 2. Reproductive performance (values \pm standard error of the mean, sample size indicated in parenthesis) of females initially paired with large-combed roosters and subsequently with small-combed roosters, or vice versa, is reported

Male comb size	First clutch		Second clutch	
	Large	Small	Small	Large
CIT (days)	10.1 \pm 2.2 (7)	17.6 \pm 1.6 (5)	15.7 \pm 3.5 (7)	8.2 \pm 2.01 (4)
clutch size (numbers)	6.0 \pm 0.6 (7)	6.6 \pm 1.2 (5)	5.7 \pm 0.7 (7)	6.0 \pm 0.4 (4)
average egg mass (g)	30.8 \pm 1.2 (7)	31.8 \pm 0.8 (5)	32.4 \pm 1.2 (7)	33.5 \pm 0.6 (4)
hatching success (%)	63.6 \pm 10.9 (5)	71.1 \pm 8.5 (5)	64.7 \pm 10.3 (5)	50.0 \pm 9.5 (4)
hatching mass (g)	23.3 \pm 1.2 (22)	24.0 \pm 0.8 (22)	21.0 \pm 1.1 (16)	22.8 \pm 0.5 (12)

Note: Mass is measured in grams, hatching success is measured in percentage, clutch size is measured by numbers, while CIT (clutch initiation time) is recorded in days

Chick rearing and development

On the day the chicks hatched, each was weighed and marked with a unique color using flexible rubber leg bands. They were then kept in the home cage with both parents for five weeks. This setup was chosen because male physical traits could influence the hens' reproductive decisions during incubation and chick rearing. Although female red jungle fowl and feral chickens (*Gallus gallus domesticus*) usually raise their chicks alone in the wild, they may encounter males or other brooding females while foraging due to overlapping territories. Males have been observed to occasionally feed chicks, a behavior we also noted occasionally. Informal observations indicated that the males in our study generally kept their distance from the brooding hen and her chicks, showing minimal interaction.

For permanent identification, three weeks later, metal wing tags with numbers were used in place of the rubber leg bands. All of the first clutch's offspring were housed in a single, when they were five weeks old, and the second clutch's offspring were housed in a separate, identical aviary. The male and female chicks from the first clutch were divided and placed in two aviaries when they were three months old. To prevent aggressiveness between males from different clutches, the males from the second clutch were kept in a separate aviary while the females from the clutch were merged with the first clutch. At 24 weeks old (approximately five and a half months), we measured the body mass and tarsus length of all offspring using sliding calipers.

Data analysis

We used parametric tests of all statistical analyses based on the normal distribution of raw data and model residuals. First, we assessed whether our grouping of males into large and small combed categories resulted in two groups with significantly different comb sizes (surface area), and whether other phenotypic traits such as comb color and body mass varied between these groups using independent t-tests (Table 1). Similarly, we analyzed whether female body mass differed between the two treatments at the beginning of both the first and second reproductive attempts using multivariate tests (Table 1).

To examine female reproductive performance, including Clutch Initiation Time (CIT), clutch size, and average egg mass, we conducted a multivariate test comparing these variables between reproductive attempts with large combed males and those with small combed

males is using a general linear model. Additionally, we assessed differences in hatching success (as our primary interest lay in CIT, clutch size, and average egg mass) using a one-sample T-test. It's worth noting that two females—one initially paired with a small combed male and the other with a large combed male—failed to reproduce in both conditions and were consequently excluded from all analyses on reproductive investment due to lack of data beyond clutch size (which was zero).

Chick body mass at hatching and 24 weeks post-hatching was assessed through generalized linear mixed models, where body mass was averaged per mother for same-sex siblings. Mother was considered a random factor, while male quality, offspring sex, and the interaction between male quality and offspring sex were regarded as fixed variables. Furthermore, we conducted two post-hoc tests (one-sample T-test) first within female chicks and two within male chicks, owing to the notable interaction effect on growth (body mass and condition) between offspring sex and male quality.

RESULTS AND DISCUSSION

Phenotypic differences between males and females

Our analysis of comb size revealed substantial disparities between the two male groups (Table 1). Specifically, large combed males exhibited comb surface areas approximately twice as large as those of small combed males. Moreover, during the initial reproductive attempt, large combed males were notably heavier than their small combed counterparts, with a similar trend observed in the subsequent attempt. Notably, there were no discernible variations in comb color characteristics between the groups (Table 1). Additionally, neither treatment nor reproductive stage (first or second clutch) exerted any noticeable effect on female body mass (Table 1, first row).

Female investment in reproduction

Male comb size did not influence clutch size ($F_{1,11}=0.02$, $P=0.91$) or egg mass ($F_{1,11}=0.15$, $P=0.71$). However, hens began laying eggs approximately one week earlier when paired with a large-combed rooster compared to a small-combed one (Figure 1; multivariate GLM: $F_{1,11}=5.05$, $P=0.05$). Hatching success did not vary significantly (one-sample T-test $T=0.583$, $P=0.576$). Refer to Table 2 for details on reproductive variables.

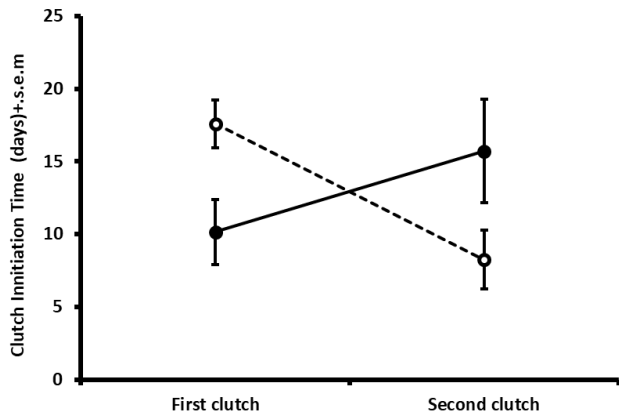


Figure 1. The average clutch initiation time (in days, presented as mean \pm standard error of the mean) for hens initially paired with a large combed male followed by a small combed male is depicted by closed dots. Conversely, the reverse treatment is illustrated by open dots

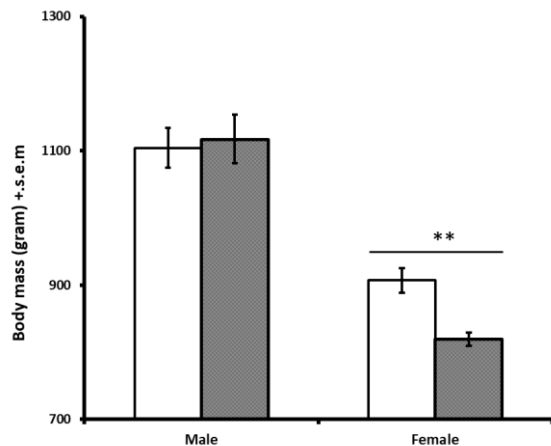


Figure 2. Average body mass (in gram \pm s.e.m.) of males and females chicks sired by large - (open bars) or small combed roosters (dark bars) 24 weeks after hatching

Chick growth

There were no effects observed for male comb size ($F_{1,16}=0.384$, $p=0.538$), offspring sex ($F_{1,16}=0.544$, $p=0.463$), or their interaction on body mass at hatching (GLMM: $F_{1,16}=1.44$, $p=0.706$). However, by twenty-four weeks after hatching, male chicks had surpassed female chicks in body size (GLM, $F_{1,16}=37.3$, $p<0.001$). While there was no direct impact on male comb size ($F_{1,15}=0.29$, $p=0.599$), there was an association in body mass between the sex of the offspring and the size of the male comb. ($F_{1,15}=5.29$, $p=0.036$).

Male chicks from large-combed males did not significantly differ from male chicks from small-combed males ($N=13$ vs. $N=19$; Figure 2; GLMM; $F_{1,24}=6.66$, $p=0.101$). However, female chicks from large-combed males ($N=13$) outweighed female chicks from small-combed males ($N=14$; $F_{1,11}=11.82$, $p=0.006$; Figure 2).

Furthermore, physical condition was affected by a relationship between male comb size and offspring sex (body mass/tarsus length; $N=59$, $F_{1,15.4}=7.98$, $p<0.013$): female chicks of small-combed fathers exhibited lower condition scores compared to female chicks of large-combed fathers (12.3 ± 0.19 vs. 14.1 ± 0.47 ; $N=27$, $F_{1,11}=13.82$, $p=0.003$), while no difference was observed in male chicks (13.9 ± 0.78 vs. 13.3 ± 0.47 ; $N=32$, $F_{1,3.6}=0.881$, $p=0.406$).

Discussion

In this study, we assessed if red jungle fowl roosters' comb sizes have an impact on female reproductive investment and the development of their offspring. Comb size serves as a proxy for male quality, as it is a proven indicator of male attractiveness, correlates with social dominance, reduces immune competence (a cost only high-quality individuals can bear), and is heritable (Carleial et al. 2020a; 2020b; Song et al. 2020). In our population, roosters with larger combs (both in maximum length and size) were heavier but did not differ in comb color from those with smaller combs (indicative of lower quality). Based on the assumption that birds frequently demonstrate positive differential allocation (Khwaja et al. 2018; Wilson and Burley 2021) and that when paired with attractive males, females of species that only care by herself invest in egg size or large quantities (Lelono et al. 2019b), the reasoning makes it reasonable that females that mated with large-combed males would lay larger eggs. We did not see this influence on clutch size or egg mass, though. Indeed, we discovered that hens matched with large-combed males began laying eggs earlier, which is typically preferable in areas with varying seasons (Laskowski et al. 2021; Węgrzyn et al. 2023).

Our findings align with both a) the parental quality hypothesis, which suggests that the earliest breeders may be of the highest quality (Watson et al. 2015; Węgrzyn et al. 2023), and b) the positive differential allocation hypothesis, which proposes that partner attractiveness stimulates reproductive investment (Laskowski et al. 2021; Watson et al. 2015; Węgrzyn et al. 2023). Despite potential behavioral differences between males with varying comb sizes (Tan et al. 2017; Carleial et al. 2020a), the females in the two treatment groups did not invest in egg mass or clutch size differently, and there were not any noticeable morphological variations between them. As a result, we can presume that these behaviors varied randomly among our treatments, which could have influenced the accuracy of our findings. However, the main factor affecting clutch initiation time appears to have been assessed male quality (comb size).

This study aimed to investigate the influence of red jungle fowl roosters' comb size on female reproduction investment and the offspring development. Comb size is a well-established proxy for male quality, indicating male attractiveness, correlating with social dominance, and impacting immune competence (Parker and Pizzari 2015; McDonald et al. 2019; Carleial et al. 2020a). Larger comb roosters in our population were heavier than smaller comb roosters, but their comb colors were the same. Based on the

theory that birds often demonstrate positive differential allocation (Kindsvater and Alonzo 2014; Wilson and Burley 2021) and that, when paired with attractive males, females of species with female-only care is provided more in egg size or mass. (Lelono et al. 2019b), it's reasonable that females that mated with large-combed males would lay larger eggs. However, we did not observe this effect on egg mass, nor did we find an effect on clutch size. However, we identified that hens that were paired with large-combed males began laying eggs earlier. In seasonal conditions, early breeding generally generates greater outcomes (Węgrzyn et al. 2023).

Our findings support both a) the parental quality hypothesis, which posits that the earliest breeders are often of higher quality (Senécal et al. 2021; Węgrzyn et al. 2023), and b) the positive differential allocation hypothesis, which suggests that partner attractiveness stimulates reproductive investment (Watson et al. 2015; Song et al. 2020; Senécal et al. 2021). We did not find any phenotypic variations between females in the two treatment categories, nor did they invest differently in egg mass or clutch size, despite possible behavioral differences between males with differing comb sizes. Nonetheless, perceived male quality (comb size) appears to be the primary factor influencing clutch initiation time. Additionally, females paired with large-combed males produced female chicks with greater weight and higher condition scores; although no parallel effects were observed in male chicks. The lack of effects in male chicks was surprising, suggested that paternal genetics might contribute to developmental differences but couldn't exclude non-genetic paternal effects.

The study proposed that such non-genetic paternal effects might be transmitted through the chemical compounds present (such as various steroid hormones in the roosters' ejaculates (Alvarez-Fernandez et al. 2019; Lelono et al. 2019a), while the oviduct of hens has steroid receptors. (Hrabia and Le 2014) and also deposit androgens to the eggs (Hsu et al. 2022). Recent research suggests that testosterone concentrations in the ejaculate differ between large and small combed males (Lelono et al. 2019a). There's a possibility that testosterone from the ejaculate penetrates the egg when fertilization occurs, potentially impacting chick development. However, this influence would likely be sex-specific, considering the typical behavior of maternal hormones (Groothuis et al. 2019). Males status also reflected on their testosterone hormone both in ejaculate and circulation (Lelono et al. 2019a, 2019b).

Our experimental setup did not differentiate between the paternal effects and maternal responses. Consequently, maternal factors which includes the quantity of testosterone deposited in the yolk according to sex, could explain our results a) This is supported by evidence that testosterone enhances early growth (Groothuis et al. 2019), b) there is a difference in hormone deposition based on paternal quality in avian species (Hsu et al. 2022), b) that depending on the sex of the embryo, avian mothers can add testosterone to the yolk (Lelono et al. 2019b). This provides the intriguing theory that maternal hormone deposition is important, and may be influenced by cryptic paternal characteristic like the

hormone composition of the father's ejaculate (Borziak et al. 2016; Lelono et al. 2019a).

In conclusion, our research confirms other studies that indicate female reproductive investment and offspring development in red jungle fowl are influenced by the father's attractiveness. Currently, we are investigating whether this effect is solely based on the way that females interpret a male comb physically or involves chemical substances in male ejaculates. We found no evidence that females of red jungle fowl, a species that has only female care, invest more in egg mass, even though our results support the positive differential allocation hypothesis, as evidenced by the fact that females mated with large-combed males laid eggs earlier than those mated with small-combed males. These results provide validity to the hypothesis that, in female-care-only species, when partnered with attractive male, females invest more in egg mass.

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