

The association of social rank with paternity efficiency in competitive mating flocks of Zi goose ganders (*Anser cygnoides* L.)

Jiayue Zhang,^{*,1} Yang Liu,^{*,1} E. Li,^{*} Bolin Ning,^{*} Ying Zhang,^{*} Jinyan Sun,[†] Guojun Liu,[†] and Shengjun Liu^{*,2}

^{*}College of Animal Science and Veterinary Medicine, Heilongjiang Bayi Agricultural University, Daqing 163319, P. R. China; and [†]Heilongjiang Academy of Agricultural Sciences, Animal Husbandry Research Institute, Harbin 150086, P. R. China

ABSTRACT The purpose of this study was to investigate the influence of social rank (**SR**) on paternity efficiency (**PE**) in competitive mating flocks of geese. Thirty ganders and 150 geese (Zi geese, *Anser cygnoides* L.) aged approximately one, were divided into 3 groups. Flock 1 included 10 ganders and 50 female geese, flock 2 included 11 ganders and 55 female geese, and flock 3 included 9 ganders and 45 female geese. The frequency of the agonistic behavioral interactions (**ABI**) of the ganders and mating activity (**MA**) were video recorded in each flock. The SR of each gander was determined by the frequency of ABI with a score of 1 to 3 (1 being the dominant and 3 the most subordinate). To clarify the difference between being dominant and submissive, we collapsed rank 2 and rank 3 into a “subordinate” category. In total, 280 eggs

were collected, and 219 goslings were hatched. Parent–offspring relationships among 399 individuals from the 2 generations were identified via 20 micro-satellite markers, and the PE of each gander was calculated. There was no significant difference in individual body weight and semen quality factor among the different SR groups (dominant and subordinate), and the SR of the ganders was significantly correlated to PE for the 3 flocks. Goslings of high-ranking ganders contributed 48.68% in flock 1, 37.50% in flock 2, and 47.62% in flock 3. Approximately 45% of all goslings were sired by the 7 dominant ganders of the 30 total ganders across the 3 flocks. As SR has been shown to be heritable in geese, the selection of high-ranking ganders might be an effective way to improve reproductive efficiency in commercial geese flocks.

Key words: Zi goose, social rank, paternity efficiency, mating activity

2021 Poultry Science 100:101415

<https://doi.org/10.1016/j.psj.2021.101415>

INTRODUCTION

Geese have lower reproductive efficiency than that of other poultry species such as chickens and ducks (Jerysz and Łukaszewicz, 2013) owing to the physiological characteristics of the species itself and a continuous selection for growth rate (Łukaszewicz, 2010). Selecting ganders with higher breeding potential in goose production is necessary for improving geese reproductive efficiency (Gumułka and Rozenboim, 2015a). The correlation between animal behavior and fertility has

been an important consideration in poultry rearing (Gumułka and Rozenboim, 2016); thus, if some observable behavioral or phenotypic characteristics can be linked to fertility in ganders, individuals can be retained or eliminated from breeding flocks.

There is a clear hierarchy in social bird species (Ode et al., 2015; Shimmura et al., 2015); the frequency of agonistic behavioral interactions (**ABI**) is generally used to determine the rank of birds within that hierarchy (social rank; **SR**) (Gumułka and Rozenboim, 2016; Kim and Zuk, 2000). Many aspects of animals' lives, including their health, reproduction, physiology, body weight (**BW**) gain, and genetic expression, could be affected by SR (Chase and Seitz, 2011). In red jungle birds, individuals that initiate aggressive interactions (fighting, pecking, and displacement) usually receive the most dominant ranking in their group (Kim and Zuk, 2000). Generally, female fowl are more willing to copulate with high-ranking males within the hierarchy (Pizzari and Birkhead, 2000). Weiß and Foerster (2012)

© 2021 The Authors. Published by Elsevier Inc. on behalf of Poultry Science Association Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Received March 8, 2021.

Accepted July 20, 2021.

¹These authors contributed equally to this work and are considered equal first authors.

²Corresponding author: lsj4396@163.com

verified that significant heritability was not only found for aggression rate, but also for dominance rank in graylag geese. Therefore, it is sensible to screen ganders with high social ranking for breeding.

Mating activity (**MA**) can be described by courtship displays, copulation attempts, successful copulation (**SCOP**), and interaction disrupted with agonistic behavior (Gumułka and Rozenboim, 2016). This behavior is composed of a series of consecutive actions in sequence and not only is it related to the reproductive performance of the population, but also related to the survival of the race (Gumułka and Rozenboim, 2015b). The frequency of mating behaviors in multimale populations, which may be caused by courtship stimulation and male mating competition in female geese, are higher than that in single-male populations (Gumułka and Rozenboim, 2016).

Fertility and hatchability are important economic factors that represent major components of reproductive performance (Salamon, 2020). Paternity efficiency (**PE**), as a manifestation of fertility, refers to the percentage of chicks produced by a sire in relation to the total number of chicks produced in a flock (Donoghue et al., 1999; Ely et al., 2017). To determine PE, molecular markers such as microsatellite markers are often used to identify the optimal parent-offspring pairing using likelihood or exclusion methods with statistical software (Ojeda et al., 2016). Donoghue et al. (1999) analyzed the PE of different cocks at genomic DNA fingerprints and reported that there was a significantly skewed distribution in the number of offspring sired by males. Birkhead et al. (1999) and King et al. (2000) found that in domestic chickens and turkeys, respectively, a disproportionately higher number of progeny are sired by males with high sperm mobility. Bilcik and Estevez (2005) found that in broiler breeders, mating behavior cannot be solely used as a reliable indicator of male reproductive success, and that sperm competition mechanisms seem to be in place in multiple male groups.

The aim of this study was to explore the correlation between SR and PE using Zi geese, simultaneously to investigate the influence of SR on MA in geese.

MATERIALS AND METHODS

This study protocol was approved by the Ethics Committee for the Use and Care of Animals at Heilongjiang Bayi Agricultural University (Daqing, China).

Animals and Experimental Design

The experiments were conducted at the Yuanfang goose breeding company in Daqing, Heilongjiang Province, China (latitude: 46°52'; longitude: 124°27'; altitude: 145 m). The subjects were Zi geese (a small-type breed, *Anser cygnoides* L.) that were approximately one year in age. The Zi goose is native to North-East China and is noted for its high egg production (Ji et al., 2020). The experiment consisted of 3 flocks. Birds in flock 1

and flock 2 were aged 12-mo-old, while birds in flock 3 were aged 10-mo-old at the start of the study.

The geese were kept in a poultry house with windows combined with access to an outside yard; the windows of the poultry house were painted dark. During the experiment, there were 12 to 15 h of natural light and a temperature of 15°C to 28°C. The hours of light can be controlled by letting geese out only for a period required of natural light from 6:00 am to 6:00 pm and keeping them inside for the period of darkness. Each goose is provided with one square meter in the house and 2 square meters in the yard. Rice husks were used as the mattresses in the nests, and they were large enough (96 cm × 85 cm) to comfortably hold several standing geese and also allowed for the geese to turn around easily in the house.

All geese were provided with the same ingredients and nutrient composition in the experimental diets (corn 52%, soybean meal 18%, alfalfa meal 5%, rice hull 10%, barley 10%, vitamin, and trace mineral mix 5%; nutrient composition: AME 11.16 MJ/kg, CP 15.65%, Lysine 0.77%, Metione 0.29%, crude fiber 5.02%, calcium 1.18%, total phosphorus 0.64%). Free access to limestone was provided to geese in the yard to supplement their calcium intake. The birds had free access to both food and water at all times.

The geese were all healthy and the BW of the geese was measured using an electronic balance (Sartorius AZ212, Gottingen, Germany; precision of 0.1 g). All ganders were screened according to semen quality testing to determine semen quality factor (**SQF**) as follows:

Semen quality factor

= ejaculate volume (mL)

× sperm concentration ($\times 10^6$ /mL)

× live and morphologically normal spermatozoa (%)

Individuals with SQF values greater than 20 were treated as normal and were selected for the experiment.

Three flocks of geese were established by dividing the studied individuals into groups based on BW. Flock 1 included 10 ganders and 50 female geese, flock 2 included 11 ganders and 55 female geese, and flock 3 included 9 ganders, and 45 female geese (1:5 ratio of male: female) (Yang et al., 2017). Each flock was raised in a separate house with yard. All female geese which had healthy fertility were subject to being chosen randomly to form the experimental population.

Flock 1 and flock 2 experiments were conducted from May 1st to July 1st, 2018, and flock 3 experiments were conducted from May 1st to July 1st, 2019.

Social Rank and Recording of Behaviors

A video camera (720p, Haikang Weishi, Jiangsu, China) recording system was set up at each of the 4 corners of each experimental pen. The frequency of the ganders' ABI and MA was recorded during daily

observation periods (6:00 am to 6:00 pm) in the reproductive season (May 1st to June 15th).

Different paint colors were utilized to mark the necks and backs of the ganders to distinguish and observe individual behaviors. Using different paints, the ganders were numbered as follows: ganders of flock 1 were numbered as A1 to A10, ganders of flock 2 were numbered as B1 to B11, and ganders of flock 3 were numbered as C1 to C9. The frequency of ABI between ganders was observed to determine the SR (Kim and Zuk, 2000). Ganders were ranked from 1 to 3 based on at least 10 ABI per pair, with 1 being the most dominant and 3 the most subordinate. Two individuals (A7 and A9) in flock 1, 3 individuals (B5, B8, and B10) in flock 2, and 2 individuals (C6 and C9) in flock 3 were placed in the most dominant group (Rank 1). Five individuals (A1, A3, A4, A5, and A6) in flock 1, 5 individuals (B1, B3, B4, B6, and B7) in flock 2, and 2 individuals (C3 and C5) in flock 3 were placed in the middle level group (Rank 2). Three individuals (A2, A8, and A10) in flock 1, 3 individuals (B2, B9, and B11) in flock 2, and 5 individuals (C1, C2, C4, C7, and C8) in flock 3 were placed in the most subordinate group (Rank 3).

The frequency of MA, including the frequency of courtship displays, copulation attempts, and SCOP were recorded (Table 1).

Paternal Test

We collected eggs daily and stored them at 15.5°C at a relative humidity of 69%. Then, we hatched the eggs every 7 d. We collected 100, 100, and 80 eggs for hatching in flocks 1, 2, and 3, respectively, resulting in 76, 80, and 63 goslings being born into flocks 1, 2, and 3, respectively.

Blood samples were collected from all parents and goslings from the 3 flocks. The blood samples of the parents were marked as their individual number (IN) and the

blood samples of the goslings were marked in their order of birth. The blood samples were treated for DNA sample extraction (DP348, Tiangen, Beijing, China) to determine PE value. DNA samples were marked to match the blood samples. To 8 μL loading buffer (RT201, Tiangen, Beijing, China), 2 μL of each DNA sample was mixed. The samples were analyzed spectrophotometrically using a NanoDrop 2000 (Thermo Fisher Scientific, Rochester, NY), and considered pure when the O.D. 260/280 ratio was 1.8 to 2.0. Ten μL of the DNA sample was then diluted with double distilled water (ddH₂O) to obtain a concentration of 25 ng/ μL for amplification. Twenty microsatellites that have previously been applied to geese paternity testing (B. L. Ning, unpublished data) were used to process the DNA samples via PCR (T100, Bio-Rad Laboratories Inc., Hercules, CA). Details of the microsatellite markers and primers are given in Table 2. The PCR amplification systems (25 μL) included 12.5 μL 2 \times ES Taq Master-Mix, 1 μL Forward Primer (10 μM), 1 μL Reverse Primer (10 μM), 1 μL Template DNA, and 9.5 μL ddH₂O. The PCR reaction procedures were as follows: predenaturation (94°C) for 5 min, denaturation for 35 cycles (denaturation [94°C] for 30 sec, annealing [52.7 to about 64°C] for 30 sec, and extension [72°C] for 30 sec), final extension (72°C) 10 min, and storage at 4°C for no more than 2 d prior to sequencing (B. L. Ning, unpublished data). The PCR products were sent to Shanghai Sangon Company, Ltd. for sequencing by a DNA automatic sequencer (ABI3730, Applied Biosystems Inc, Woolston, United Kingdom).

The Gene Marker V1.91 Software (Beijing Huasheng Hengye Technology Co. Ltd., Beijing, China) was utilized to determine the microsatellite marker genotype of each sample. DNA sample genotype results were determined by Servus 3.0.7 (Amirian et al., 2019). The number of alleles per locus varied from 5 to 13 with a mean value of 7.05. The expected heterozygosity ranged from 0.437 to 0.803 (mean 0.612), and the total exclusion probability of 20 microsatellite loci was 0.9958. The number of goslings for each gander was used to calculate the PE. PE was calculated as the percentage of goslings produced by a gander divided by the total number of goslings produced in a flock.

Statistical Methods

Data were collected for the BW, ABI, MA, SQF, and PE of each gander. All results were presented as means with standard error of the mean (df = 27). To clarify the difference between a gander as dominant or submissive, we collapsed rank 2 and rank 3 into a “subordinate” category. Using a Mann-Whitney test ($\alpha = 0.05$), we tested the differences in BW, MA, SQF, ABI and PE in the dominant and subordinate group. Because the data on males in each group were not independent, we ran a Pearson partial correlation analysis to determine potential relationships among SR, BW, ABI, MA, SQF, and PE. All statistical analyses were performed using SPSS

Table 1. Description of criteria for the behavior of mating activity and agonistic behavioral interactions.

Behavior	Definition
Courtship displays ^a	The gander exhibits exaggerated walking, approaching the female and then lightly preening her neck or back feathers; the gander and goose chase each other during the encounter
Copulation attempts ^a	The gander approaches a crouched female from the front of her body or forces her down and places a foot on her back
Successful copulation ^a	Calculation of total matings, including successful matings and unsuccessful matings
Agonistic behavioral Interactions ^b	The number of observed occurrences of aggressive approaches, including active attacks (fighting, pecking, and displacements), initiated attacks, and creating a threat

^aAdapted from Zhang et al. (2019).

^bAdapted from Gumufka and Rozenboim (2016).

Table 2. Microsatellite markers and primers used to identify parent-offspring relationships and calculate paternity efficiency in Zi geese.

Marker	Primer sequence (5'-3')	Ta (°C)	Fragment (size/bp)
ans 2	F:TTCTGTGCAGGGGCGAGTT R:AGGGAACCGATCACGACATG	58	215
ckw 11	F:CTGAGTTGAACCTGATGCAGAC R:AACACCAAAGGAGAGCAGAGAC	59	186
ckw 12	F:CATAAGTTCTCCCAAACAAGAGTG R:AGAAAGGGACACACAGCTAACC	55	204
ckw 21	F:CAAGGTAGTCATAAAACCCAGAAC R:AACAAAACTAATGGCAGGAAA	54	351
ckw 49	F:TGAACACACATGCAGACTGG R:TTTGGGAGACAGAGCCTTTT	60.5	204
zaas 001	F:TCTTTCATGGTCTTTGGCAGA R:TTTTTCGAGATTGTGTGGAG	53.7	172
zaas 006	F:GACACACTGCTGCCACTTTC R:TCCAGTGCCTAAGTGTCTGTT	52.7	197
zaas 033	F:GTTTGTGCCCCTGCATTTGTA R:GGTGGGAGGTTTTGGAGAGT	54.6	202
zaas 036	F:TCCCAGCTTCACTCCTTTTC R:GTGGTGTCTTTCGCGGTGTAG	54.6	199
zaas 054	F:CCCCACACCCCAAAAATA R:AAGGCTAGTTTGCCACAGGA	60.3	176
zaas 060	F:GAATACAGCCCTGCATTGAAA R:TCTCCCACAGTCTCTGTT	52.7	197
zaas 061	F:CTCCACAGCAGCAAGGTAGC R:CGTTAGCATCTCCACATTG	54.6	168
zaas 071	F:TGTAAGTCCCATCCCAAACA R:AGGGAGTGACAGTGTAGGTGGT	56.5	198
zaas 144	F:GGCCACATTCACCTCTTTT R:TAGCACCTCGGAGGGTCA	58.4	199
zaas 154	F:CGTGTTCATGCTCAAAAAGGAG R:TGCTTCTCATGGAAAACAACG	56.5	215
zaas 169	F:CGTGTTCATGCTCAAAAAGGAG R:TGCTTCTCATGGAAAACAACG	64	200
zaas 175	F:TGAGTAGTGGGGTCCCTGAA R:CCCATCTGCTAGTCCAGCTT	58.4	203
zaas 177	F:GAAAGCTCCCTGATGCTGTT R:CCTCCATGGGAATGTTTTCT	58.4	206
zaas 178	F:GTCATATGGCCTGCACTGTC R:TGGTCACTGTGCTTGACTTTG	57.5	208
zaas 181	F:CAGAACAGGGAAGGGATGTG R:TTCACATCTGCAGGTTTCAGG	58.4	180

11.0 (SPSS Inc., Chicago, IL) for Windows, and significance was accepted at $P < 0.05$.

RESULTS

Body Weight and Social Rank

Details of the 3 SR gander groups are shown in [Table 3](#). The subordinate gander group exhibited a lower frequency of ABI (2.94 ± 0.46 /times/12 h) than that of the dominant group (10.71 ± 0.94 /times/12 h) ($P = 0.061$; $N = 30$). Social rank was not correlated with BW ($r = 0.133$; $P = 0.490$) ([Table 4](#)).

Social Rank and Mating Activity

The frequency of MA in the 3 SRs of the 3 flocks is shown in [Figure 1](#). For dominant ganders, the frequency of courtship displays (6.35 ± 1.77 /times/12 h) was not significantly different to that of the subordinate SRs (4.23 ± 0.32 /times/12 h) ($P = 0.386$; $N = 30$).

The dominant gander group exhibited a higher frequency of copulation attempts (7.48 ± 1.43 /times/12 h)

and SCOP (3.92 ± 0.69 /times/12 h) than the frequency of copulation attempts (4.57 ± 0.64 /times/12 h) ($P = 0.010$; $N = 30$) and SCOP (0.99 ± 0.19 /times/12 h) ($P < 0.001$; $N = 30$) for the subordinate groups in the 3 flocks.

No significant relationship was found between SR and courtship displays ($r = -0.243$; $P = 0.204$) or copulation attempts ($r = -0.008$; $P = 0.966$), but SR correlated significantly with SCOP ($r = -0.583$; $P = 0.001$) ([Table 4](#)).

Social Rank and Semen Quality Factor

The SQF values of the ganders in 3 flocks are shown in [Table 3](#). For dominant ganders, SQF was not significantly different than that of the subordinate ganders ($P = 0.700$; $N = 30$). SR was not correlated with SQF in all 3 flocks ($r = -0.750$; $P = 0.144$) ([Table 4](#)).

Social Rank and Paternity Efficiency

Following incubation, the number of offspring was 76 in flock 1, 80 in flock 2, and 63 in flock 3. There were differences in PE among the gander groups of different SR.

Table 3. Mean (\pm standard error of the mean) social rank, body weight, agonistic behavioral interactions, number of goslings, and paternity efficiency of the 2 levels of social rank in the 3 flocks of Zi geese.

Flock	SR	N	BW (g)	SQF	ABI (times/12 h)	NG	PE (%)
1	Dominant	2	4983.1 \pm 531.8 ^a	58.9 \pm 23.9 ^a	11.25 \pm 1.12 ^a	18.50 \pm 0.50	24.34 \pm 0.66 ^a
	Subordinate	8	4779.1 \pm 134.4 ^a	65.6 \pm 24.1 ^a	3.42 \pm 0.95 ^b	4.88 \pm 1.43	6.41 \pm 1.88 ^b
2	Dominant	3	5516.6 \pm 417.7 ^a	80.6 \pm 39.3 ^a	12.28 \pm 0.87 ^a	10.00 \pm 1.00	12.08 \pm 1.50 ^a
	Subordinate	8	4608.8 \pm 141.9 ^b	66.8 \pm 23.4 ^a	3.00 \pm 0.85 ^b	6.25 \pm 0.73	7.97 \pm 0.97 ^a
3	Dominant	2	4146.4 \pm 426.1 ^a	98.1 \pm 39.3 ^a	7.82 \pm 1.57 ^a	15.00 \pm 4.00	23.81 \pm 6.35 ^a
	Subordinate	7	3781.8 \pm 162.8 ^a	76.9 \pm 55.7 ^b	2.32 \pm 0.53 ^b	4.71 \pm 1.13	7.48 \pm 1.79 ^b

^{a,b}The means following the same lower-case letters in the column of the same flock do not differ ($P > 0.05$) using the Mann-Whitney test. Dominant: Rank 1, subordinate: Rank 2+ Rank 3. Geese in flock 1 were 10-mo-old, and geese in flock 2, and flock 3 were 12-mo-old at the start of the study. Abbreviations: ABI, average agonistic behavioral interactions (times/12 h); BW, average body weight (g); N, number of ganders in a social rank; NG, number of goslings; PE, average paternity efficiency (%); SQF, average semen quality factor; SR, social rank.

Table 4. Pearson partial correlation results for social rank, body weight, mating activity, semen quality factor, and paternity efficiency.

Correlated traits		r	P
SR	BW	0.133	0.490
SR	Courtship displays	-0.243	0.204
SR	Copulation attempts	-0.008	0.966
SR	SCOP	-0.583	0.001
SR	PE	-0.658	0.000
SR	SQF	-0.750	0.144
PE	SQF	0.260	0.673
PE	SCOP	0.308	0.104

Abbreviations: BW, body weight (g); PE, paternity efficiency (%); SCOP, successful copulation; SQF, semen quality factor for ganders; SR, social rank (dominant and subordinate).

Goslings of ganders with a high social ranking contributed 48.68% of the total goslings in flock 1, 37.50% in flock 2, and 47.62% in flock 3; all significantly exceeded 30% of the total goslings ($P < 0.001$; $N = 30$). Therefore,

SR was significantly correlated with PE ($r = -0.658$; $P < 0.001$) (Table 4).

DISCUSSION

In China, domestic geese are generally reared in large groups on the floor and allowed to mate naturally (Lin et al., 2020a). The breeding efficiency of males has always been a concern for goose breeders (Jerysz and Lukaszewicz, 2013), and there are seldom reports concerning the relationship between SR and PE in geese because of the inability to distinguish and observe individual ganders' MA and trace the genetic relationship between parent and offspring in large breeding populations (McDonald et al., 2017). With the use of 20 microsatellite markers, we can effectively solve the problem of paternity testing in

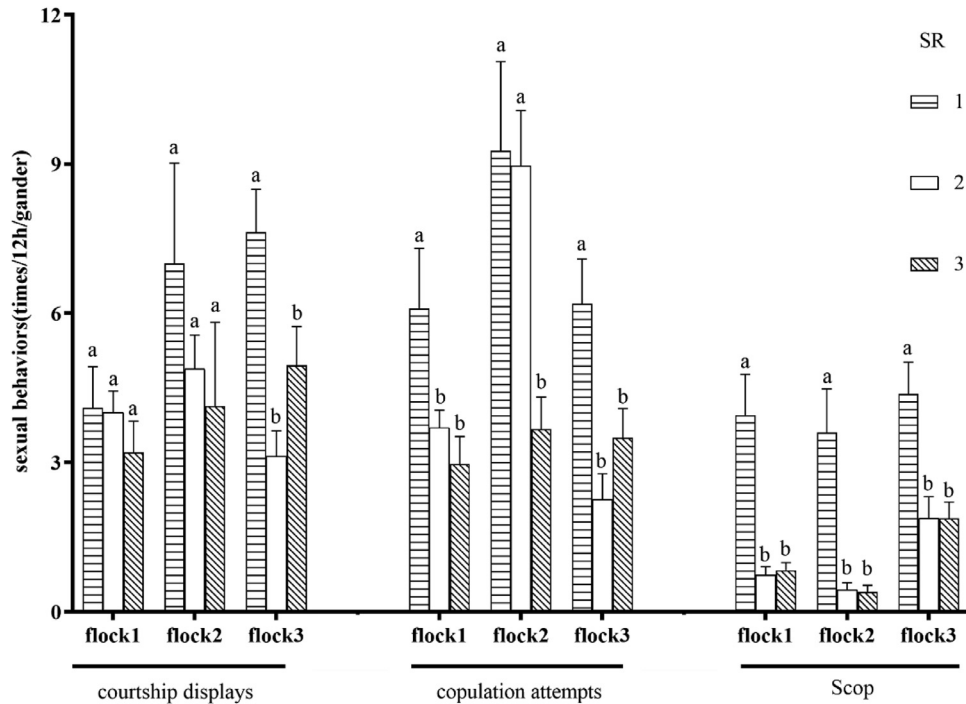


Figure 1. The frequency of mating activity in different social hierarchies in the 3 flocks of Zi geese.

^{a,b}Values marked with different letters on the bars are significantly different ($P < 0.05$).

SR: The ganders were ranked from 1 to 3 based on at least 10 ABI per pair, with 1 being the most dominant and 3 the most subordinate (Kim and Zuk, 2000)

Abbreviation: SCOP, successful copulations.

geese, but the observation of behavior is still limited by population size. Fowl populations are made up of several small groups, and each group consists of several families or pairs (Ottinger and Mench, 1989). Limited by the inability to distinguish and observe ganders' MA in large groups, we set up 3 small experimental groups to investigate SR effects on ganders' MA and PE. Our results may also be applicable to large goose breeding populations.

Social Rank and Individual Body Weight

Many factors, such as sexual/social experience, reproductive hormones, BW, and age, determine the outcome of ABI and, thus, determine an individual's SR in a flock. Francis et al. (2018) reported that differences in body mass may result in between-species dominance hierarchies that place the heaviest species in the greatest control of supplementary feeding sites. Furthermore, Kim and Zuk (2000) discovered that larger individuals of both sexes tend to be dominant in the social hierarchy; however, body size is rarely the sole determining factor in SR for birds. Similarly, we found no correlation between the gander's BW and SR. Ganders from each flock came from the same species with the same age, and the coefficients of variation of BW were 8.87%, 11.38%, and 11.88% in flock 1, flock 2, and flock 3, respectively. When body differences among different ganders are relatively small, other individuals' characteristics, such as prior social experience (winning or losing), may have an effect on a gander's SR in a flock (Chase and Seitz, 2011).

Social Rank and Mating Activity

There were many interactions between individuals (male vs. male, male vs. female, female vs. female) within each flock. Three factors are likely to be of significance in influencing the frequency of MA: direct interference by dominant animals, female choice of mates, and logical suppression of reproduction resulting from social stress (Creel, 2005). High-ranking ganders compete with other ganders, pecking them or interrupting their MA, thereby competing for mating opportunities with females. Geese are usually polygamous, and females are more willing to choose to mate with high-ranking males. Thus, in this context, because high-ranking ganders have more opportunities to copulate successfully, SR was significantly correlated ($P < 0.05$) with SCOP in this study. The SCOP for each gander can be assumed to be a combined result of flock social interactions, reflecting the comprehensive reproductive ability of males in a natural mating population (Gumuřka and Rozenboim, 2015b). SCOP can provide clear and easily quantifiable markers of the reproductive ability of individuals. Such markers could be utilized not only in the selection of geese males for breeding but could also serve as criteria for recognizing ganders with disease problems.

Domestic geese share typical traits with wild species in which fixed pair bonds are common (Gumuřka and

Rozenboim, 2016; Hirschenhauser et al., 2000; Poisbleau et al., 2006). This characteristic may have 2 effects on flock reproduction. First, from our records of paternity, we observed that one individual female mated with only one to 2 ganders in a flock (J. Y. Zhang, unpublished data). Second, a high-ranking gander mated with 5 to 10 females in the breeding season; however, most ganders, especially low-ranking ones, mated with only one or 2 regular females. This finding differs from that of chickens, which do not exhibit any fixed mating with hens (Lin et al., 2020b). An infertile gander that only mates with its fixed female may lead to low levels of fertility in the next generation of goslings.

Bilcik and Estevez (2005) compared the effect of male-male competition and harem systems on MA in broiler breeders and found that the level of male-male competition had a significant effect on the reduction of the frequency of MA, and increased male-male competition did not increase the number of forced copulations. From the above points, there does not seem to be an overmating problem if higher SR males are selected in natural mating flocks. Therefore, it is worthwhile to select high-ranking and high-quality semen males as geese breeders.

Effect of Semen Quality and Successful Copulation on Paternity Efficiency

Semen quality affects fertilization success and directly affects the number of offspring for birds that have been artificial inseminated (Liu et al., 2008; Sun et al., 2019) or are in a harem mating system (Farooq et al., 2018; Gumuřka and Rozenboim, 2015a).

However, in a competitive mating system, we found no direct correlation between semen quality and PE. This result is consistent with Bilcik et al. (2005). Lower fertility in males as compared to that of other individuals in a flock is not due to differences in the fertilization capacity of their semen, but due to their failure to mate with as many females. The frequency of SCOP and reliable semen quality are 2 necessary factors for higher quality reproductive males in naturally mating flocks. There was no correlation between SR and SQF or SQF and PE in this study, indicating that SCOP is the prerequisite and semen quality is a secondary factor, which may be the main reason behind the nonsignificant correlation between SQF and PE.

Social Rank and Paternity Efficiency

In this study, there was a significant correlation between SR and PE. This was in agreement with the results of a previous study on chicken which demonstrated that SR significantly affected fertility (Lhamon, 2015).

As high-ranking ganders compete with other ganders, females are more willing to mate with high-ranking males (Kralj-Fiřer et al., 2010). Different from chickens, Denk et al. (2005) suggest that in waterfowl males, a penis-like copulatory organ may allow for more

behavioral control of females as sperm ejection may be less possible. It can be assumed that dominant ganders are likely to transfer relatively more semen volume into individual females' reproductive tract because of higher copulatory frequencies, indicating that SR is the main factor that determines whether a gander has finished mating successfully and whether females retain a male's sperm in a competitive social mating structure. This may explain the significant correlation between ganders' SR and PE in our study.

CONCLUSION

Selection of high-ranking ganders is important in competitive mating flocks, as it has shown great promise as a method for improving the reproductive efficiency in geese. In addition, the use of SCOP in the selection of breeding males could assist in slowing the trend of declining reproductive potential with rapid growth selection. Ultimately, this could result in the selection of more genetically sound stock for reproduction.

ACKNOWLEDGMENTS

The authors thank Professor Zhiquan Wang of the University of Alberta, Canada, for his suggestions on the language of the manuscript.

Funding: The work was supported by the Natural Science Foundation of Heilongjiang province [grant number JJ2019LH0985], Heilongjiang Provincial Scientific and Technological Achievements Transformation and Promotion Project (2019), and the Science Research Project of Heilongjiang Bayi Agricultural Reclamation University [grant number ZRCPY201809].

DISCLOSURES

The authors declare no conflicts of interest.

SUPPLEMENTARY MATERIALS

Supplementary material associated with this article can be found in the online version at [doi:10.1016/j.psj.2021.101415](https://doi.org/10.1016/j.psj.2021.101415).

REFERENCES

- Amirian, A., Z. Zafari, Z. Sharifi, A. Kordafshari, M. Karimipoor, and S. Zeinali. 2019. Characterization and haplotype study of 6 novel STR markers related to the KCNQ1 gene in heterogeneous cardiovascular disorders in the Iranian population. *Turk. J. Med. Sci.* 49:453–457.
- Bilcik, B., and I. Estevez. 2005. Impact of male-male competition and morphological traits on mating strategies and reproductive success in broiler breeders. *Appl. Anim. Behav. Sci.* 92:307–323.
- Bilcik, B., I. Estevez, and E. Russek-Cohen. 2005. Reproductive success of broiler breeders in natural mating systems: the effect of male-male competition, sperm quality, and morphological characteristics. *Poult. Sci.* 84:1453–1462.
- Birkhead, T. R., J. G. Martínez, T. Burke, and D. P. Froman. 1999. Sperm mobility determines the outcome of sperm competition in the domestic fowl. *Proc. Biol. Sci.* 266:1759–1764.
- Chase, I. D., and K. Seitz. 2011. Self-structuring properties of dominance hierarchies: a new perspective. *Adv. Genet.* 75:51–81.
- Creel, S. 2005. Dominance, aggression, and glucocorticoid levels in social carnivores. *J. Mammal.* 86:255–264.
- Denk, A. G., A. Holzmann, A. Peters, E. L. Vermeirssen, and B. Kempnaers. 2005. Paternity in mallards: effects of sperm quality and female sperm selection for inbreeding avoidance. *Behav. Ecol.* 16:825–833.
- Donoghue, A. M., M. R. Bakst, P. Drummond, S. Haqqe, E. J. Smith, and D. J. Donoghue. 1999. Paternity efficiency in turkey differs extensively after heterospermic insemination. *J. Appl. Poult. Res.* 8:214–221.
- Ely, C. R., R. E. Wilson, and S. L. Talbot. 2017. Genetic structure among greater white-fronted goose populations of the Pacific flyway. *Ecol. Evol.* 7:2956–2968.
- Farooq, U., I. A. Malecki, M. Mahmood, and G. B. Martin. 2018. Correlation between objective semen analysis and fertility in Japanese quail. *Theriogenology* 115:23–29.
- Francis, M. L., K. E. Plummer, B. A. Lythgoe, C. Macallan, T. E. Currie, and J. D. Blount. 2018. Effects of supplementary feeding on interspecific dominance hierarchies in garden birds. *PLoS ONE* 13:1–13.
- Gumułka, M., and I. Rozenboim. 2015a. Breeding period-associated changes in semen quality, concentrations of LH, PRL, gonadal steroid and thyroid hormones in domestic goose ganders (*Anser anser f. domesticus*). *Anim. Reprod. Sci.* 154:166–175.
- Gumułka, M., and I. Rozenboim. 2015b. Mating activity and sperm penetration assay in prediction of the reproduction potential of domestic goose ganders in a harem system. *Anim. Reprod. Sci.* 161:138–145.
- Gumułka, M., and I. Rozenboim. 2016. Effect of the age of ganders on reproductive behavior and fertility in a competitive mating structure. *Ann. Anim. Sci.* 17:733–746.
- Hirschenhauser, K., E. Möstl, B. Wallner, J. Dittami, and K. Kotrschal. 2000. Endocrine and behavioural responses of male Greylag geese (*Anseranser*) to pairbond challenges during the reproductive season. *Ethology* 106:63–77.
- Jerysz, A., and E. Łukaszewicz. 2013. Effect of dietary selenium and vitamin E on ganders' response to semen collection and ejaculate characteristics. *Biol. Trace Elem. Res.* 153:196–204.
- Ji, H., W. Guo, C. Niu, Y. Li, S. Lian, X. Zhan, J. Guo, L. Zhen, H. Yang, and S. Li. 2020. Metabonomics analysis of Zi goose follicular granulosa cells using ENO1 gene expression interference. *J. Anim. Physiol. Anim. Nutr.* 104:838–846.
- Kim, T., and M. Zuk. 2000. The effects of age and previous experience on social rank in female red junglefowl, *Gallus gallus spadiceus*. *Anim. Behav.* 60:239–244.
- King, L., T. S. Sonstegard, E. J. Smith, D. W. Burt, S. P. Lerner, and A. M. Donoghue. 2000. Sperm mobility is predictive of paternity efficiency in turkeys as determined by microsatellite genotype identification of potential sires. *Br. Poult. Sci.* 41:13–14.
- Kralj-Fišer, S., B. M. Weiß, and K. Kotrschal. 2010. Behavioural and physiological correlates of personality in greylag geese (*Anser anser*). *J. Ethol.* 28:363–370.
- Lhamon, E. K. 2015. Broiler breeder mating behavior and the effects of pre-incubation embryo integrity modifications on broiler performance. MS Thesis. Univ. Arkansas, Fayetteville.
- Lin, M. J., S. C. Chang, T. J. Chen, W. C. Lin, S. Y. Peng, and T. T. Lee. 2020a. Effect of line and floor type on growth performance and feather characterization during the growth period of White Roman geese. *Asian-Australas. J. Anim. Sci.* 33:1455–1462.
- Lin, X. T., F. R. Lan, J. Y. Li, N. Yang, and C. J. Sun. 2020b. Study on genetic contribution of roosters and their behaviors in colony cages. *China Poultry* 42:9–11.
- Liu, S. J., J. X. Zheng, and N. Yang. 2008. Semen quality factor as an indicator of fertilizing ability for geese. *Poult. Sci.* 87:155–159.
- Łukaszewicz, E. 2010. Artificial insemination in geese. *Worlds Poult. Sci. J.* 66:647–658.
- McDonald, G. C., L. G. Spurgin, E. A. Fairfield, D. S. Richardson, and T. Pizzari. 2017. Pre- and postcopulatory sexual selection favor aggressive, young males in polyandrous groups of red junglefowl. *Evolution* 71:1653–1669.

- Ode, M., A. Asaba, E. Miyazawa, K. Mogi, T. Kikusui, and E. I. Izawa. 2015. Sex-reversed correlation between stress levels and dominance rank in a captive non-breeder flock of crows. *Horm. Behav.* 73:131–134.
- Ojeda, G. N., P. S. Amavet, E. C. Rueda, P. A. Siroski, and A. Larrera. 2016. Mating system of Caiman yacare (Reptilia: Alligatoridae) described from microsatellite genotypes. *J. Hered.* 108:135–141.
- Ottinger, M. A., and J. A. Mench. 1989. Reproductive behaviour in poultry: implications for artificial insemination technology. *Br. Poult. Sci.* 30:431–442.
- Pizzari, T., and T. R. Birkhead. 2000. Female feral fowl eject sperm of subdominant males. *Nature* 405:787–789.
- Poisbleau, M., H. Fritz, M. Valeix, P. Y. Perroi, S. Dalloyau, and M. M. Lambrechts. 2006. Social dominance correlates and family status in wintering dark-bellied brent geese, *Branta bernicla bernicla*. *Anim. Behav.* 71:1351–1358.
- Salamon, A. 2020. Fertility and hatchability in goose eggs: a review. *Int. J. Poult. Sci.* 19:51–65.
- Shimmura, T., S. Ohashi, and T. Yoshimura. 2015. The highest-ranking rooster has priority to announce the break of dawn. *Sci. Rep.* 5:1–9.
- Sun, Y., F. Xue, Y. Li, L. Fu, H. Bai, H. Ma, S. Xu, and J. Chen. 2019. Differences in semen quality, testicular histomorphology, fertility, reproductive hormone levels, and expression of candidate genes according to sperm motility in Beijing-You chickens. *Poult. Sci.* 98:4182–4189.
- Weik, B., and K. Foerster. 2012. Age and sex affect quantitative genetic parameters for dominance rank and aggression in free-living greylag geese. *J. Evol. Biol.* 26:299–310.
- Yang, H. M., Y. Wang, Z. Y. Wang, and X. X. Wang. 2017. Seasonal and photoperiodic regulation of reproductive hormones and related genes in Yangzhou geese. *Poult. Sci.* 96:486–490.
- Zhang, Y., Y. Yao, M. M. Wang, Y. Z. Yang, T. T. Gu, Z. F. Cao, L. Lu, C. An, J. W. Wang, G. H. Chen, Q. Xu, and W. M. Zhao. 2019. Comparisons in geese of the courtship, mating behaviors and fertility of the Carlos and Sichuan breeds and the breed crosses. *Anim. Reprod. Sci.* 204:86–94.