ENVIRONMENT, WELL-BEING, AND BEHAVIOR

Behavior differentiation between wild Japanese quail, domestic quail, and their first filial generation

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ABSTRACT The number of wild quail has dramatically reduced in China and reached a state of endangerment with the deterioration of the environment in recent years. In this study, we examined the ecological behaviors of quails in the cage to determine the differentiation level between wild Japanese quail and domestic quail, to detect the relationship between quail behavior and evolutionary differentiation and to analyze the possibility of restoring effective size of wild population. With the on-the-spot observations and measurements, the behaviors of 3 categories of quail, namely wild Japanese quail from the Weishan Lake area in China, domestic quail, and their first filial generation (F_1) were studied. Domestic quail differed from wild Japanese quail in morphological pattern and ecological behaviors, including some indexes of figure type and egg, vocalization, aggression and fighting, and mating, but wild Japanese quail and domestic quail could succeed in mating and reproducing fertile hybrid offspring. There were significant differences between domestic quail and wild Japanese quail in reproductive traits, involved mating times, fertility rate, hatching rate, and hatching rate of fertilized eggs ($P < 0.05$). The first filial generation presented significant difference from the wild Japanese quail in vocalization, aggression and fighting, mating, hatching rate, hatching rate of fertilized eggs, and some egg indexes ($P < 0.05$) and significantly differ from the domestic quail in vocalization, hatching rate, and hatching rate of fertilized eggs ($P < 0.05$). Evolutionary differentiation between wild quail and domestic quail was still at a relatively low level because no reproductive isolation existed. The advantages of the F_1 hybrids in reproductive capacity, fertilization, and hatching recommend that releasing hybrids instead of domestic quails to the wild would be a more effective way to restore the effective size of wild quail population if necessary.

Key words: wild Japanese quail, domestic quail, first filial generation (F_1), behavior, differentiation

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INTRODUCTION

Domestic quail, deriving from wild Japanese quail (*Coturnix japonica*) as laying, meat, and laboratory animals, have produced a flourishing industry (Sano et al., 1995; Chang, 1998). Much research has been reported about the behaviors of domestic quail in the past decades, including sensation and perception, maintenance behavior, development and aging, adult learning, reproductive behavior, parental behavior, and aggressive behavior and dominance (Sefton and Siegel, 1973; Crawford and Akins, 1993; Elizabeth, 1995; Jennifer and Nancy, 2005; Lábaque et al., 2008). Recently, more researchers have focused on reproductive and social behaviors, such as mating, hormonal control and ontogeny of sexual differentiation, male and female sexual behavior, aggressive behavior and dominance, social motivation, and their correlations with the nervous and endocrine system (Erica et al., 1996; Bennett and David, 1998; Galef and White, 1998; Charlier et al., 2005; Formanek et al., 2008). But so far, there is still no research data about behavior differences between wild and domestic quail, and whether these differences correspond with the domestication process remains a question. For example, wild Japanese quail lay 7 to 14 eggs per year, whereas domestic quail can lay about 280 eggs per year under normal feeding conditions (Mandal et al., 1994; Mills et al., 1994). In addition, wild quail are small and have a late sexual maturity, low hatching rate, and survival rate compared with domestic quail. Behavior differentiation is the primary step to systematic divergence in evolution (Price, 2008). Revealing the differentiation of ecological behaviors and hybrid

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fertility between domestic and wild quails can illuminate some changes that happened in the evolutionary process and promote the effective protection and exploitation of the wild quail genetic resources when the population of wild quail has dramatically reduced to an endangered state with deterioration of the environment. To increase the wild quail population, behavior and ecological investigation is the first step. In this paper, we examined the ecological behaviors of quails in the cage involving vocalization, aggression and fighting, mating, and egg-laying, aiming to determine the evolutionary differentiation between wild Japanese quail and domestic quail, the relationship between quail behavior and evolutionary differentiation, and the possibility of restoring effective size of wild population.

MATERIALS AND METHODS

Subject

Simple random samples of 25 males and 34 females were obtained from wild Japanese quail populations in the Weishan Lake area at the joint boundary of Shandong, Anhui, and the north of Jiangsu Province in China during the migrating seasons in March 2005. Twenty-eight male and 70 female healthy domestic quails were sampled from the local breeding farm. On the last year, the first filial generation (F_1) generation was produced by reciprocal cross between domestic quail and wild Japanese quail also obtained from the Weishan Lake area in 2004. The F_1 from male domestic quail and female wild quail died 2 d after hatching because of weak vitality, and the F_1 in this paper were offsprings of male wild quail and female domestic quail. Twenty-two male and 27 female F_1 quail were also randomly sampled. All of the subject quails were reared under standard cage condition (Lin, 2000).

Housing Conditions and Experiment Design

A metal cage (60 × 44 × 70 cm), made of wire mesh to permit visual access for the experimenter, was located in the main room with 3 chambers. Each quail type took 1 chamber with 3 cages, with 12 quails in each cage as a replication, 3 male and 9 female. Food and water were available ad libitum in each cage. Another 2 wk later after quarantine, all experimental quails were accustomed to the experimental condition. Their behaviors were continuously observed and recorded 12 h a day from 0600 to 1800 h by 3 observers and sound recorders (Sony MZ-R55 Disc Recorder, 20 Hz~20 kHz, Tokyo, Japan) for a total of 122 d, from May 9 to September 7, 2005. Each observer was assigned to each chamber, but they could see themselves and communicate with each other. If necessary, each observer had the capability of taking care of all 3 chambers. A behavior sampling method (Altmann, 1974) was adopted in this study. The behaviors investigated in this study, which included vocalization, aggression and fighting, mating, and egg-laying, were easily observed and typed. To begin the experiment, each observer was trained and did the primitive observation on quail behaviors for 3 d.

Observation and Measurement Items

The behaviors of quails in 1 cage were first recorded as the original data and then statistically analyzed.

Vocalization includes crowing, calling, chirping, tweeting, and singing (Guyomarc'h, 1974). Only those vocalization types that lasted over 1 s were recorded, so the observer could hear the sound easily.

Aggression and fighting between male quails involve threat, followed by pecks and grabs, which are primarily directed at the head, eyes, and neck (Edens et al., 1983). Submissive birds adopt a tilted crouching posture with the head and neck withdrawn and oriented downward. The whole process of aggression and fighting lasts 2 to 30 s.

During mating, the male struts toward the female; stretches himself such that his beak, body, head, and neck are parallel to the ground; and erects his body feathers. The female responds to the strutting of the male by crouching. The male then approaches the female and mounts her, grabs the head or neck feathers of the female in his beak, positions himself on the back of the female, and spreads his wings. The copulatory response sequence results in ejaculation about half of the time. On those occasions, the male arches his back, lowering his cloaca into contact with that of the female. He then displays a rapid shivering movement, which concludes in a few moments of immobility and ejaculation. The male releases his grip on the female and dismounts immediately after ejaculation (Sefton and Siegel, 1973). After dismounting, both the male and the female may ruffle and shake their feathers, and the male may exhibit further strutting and crowing behavior. It should be noted that not all mating we recorded resulted in successful insemination.

Most females lay eggs several hours before dusk (Konishi, 1980). The female preferentially occupies the corner of room and grovels at the position for laying eggs. Female quails made the jubilant sounds after laying.

Weight, beak length, tarsus length, tarsus girth, wing length, body slant length, egg fresh weight, egg length, egg breath, egg volume, and specific gravity of egg were measured, respectively, by electronic balance, vernier caliper, and filament in this study.

The egg index model is as follows:

$$V = 0.51 \times L \times B^2$$

$$D = M/V,$$

where V and L represent the volume of egg (cm^3) and the length of egg (cm), respectively; B is the breadth of egg (cm); M is the fresh weight of egg (g); and D is the specific gravity of egg (g/cm^3).

Figure 1. Wild Japanese quail (left), domestic quail (middle), and first filial generation (F_1; right) (male).

Fertility rate, hatching rate, and hatching rate of fertile eggs were analyzed according to the following equations (Lin, 2000):

$$\text{Fertility rate\%} = \text{fertilized eggs/hatched ones} \times 100$$

$$\text{Hatching rate} = \text{hatched quails/hatched eggs} \times 100$$

$$\text{Hatching rate of fertile eggs\%} = \text{hatched quails/fertilized eggs} \times 100.$$

Data Analysis

The data were analyzed by SPSS 12.0 software (SPSS Inc., Chicago, IL) using 1-way ANOVA and a nonparametric statistical model (Kruskal-Wallis H test method). Statistical tests are 2-tailed with an α level of 0.05.

RESULTS

Comparison of Biological Features Between Wild and Domestic Quails

The wild Japanese quail (*C. japonica*) is a terrestrial bird that inhabits grassy areas and is indigenous to Japan, China, Korea, and Indochina (Chang, 1995).The wild Japanese quails in the Weishan Lake area in China are more sensitive to the circumstances and more fond of clustering than domestic quails, showing that they are timid and easily scared. They differ from domestic quails in shape, weight, and adaptation (Table 1). Wild quails appear very small and look like a spindle, and they were significantly smaller ($P < 0.05$) in size than the domestic type, but their other traits are similar to domestic quail, such as color of feather stripe, beak shape, chirping, and fear responses (Figure 1). Except the beak length, all of the other indexes of figure type presented significant difference ($P < 0.05$) between wild Japanese quail and the other 2 populations, domestic quail and F_1 (Table 1). Hybrid heterosis existed in F_1 populations in some indexes, such as tarsus length and BW.

Comparison of Behaviors Between Wild and Domestic Quail

Vocalization. During the nonbreeding season, wild Japanese quail vocalized at a higher frequency when feeding at the time from 1000 to 1100 h. But at other times, they hardly vocalized. When stimulated by the outside stimuli, the wild quails created a sharp sound like a duck screech, which lasted 2 to 3 s. In the breeding period, the male quail often quacked at high frequency for courtship, and these sounds were loud, cadenced, and easy on the ear, whereas the female quail rarely vocalized. Crowing patterns of pair-bonded males differed from those of unmated males. Crowing intensity increases as ambient noise level increases. During the whole observation, the vocalization times of domestic quail were the highest all day, whereas those of wild Japanese quail were the lowest except during 1000 to 1100 h. Significant difference were detected ($P < 0.05$) in the vocalization times among the 3 quail populations (Table 2).

Aggression and Fighting. Generally, quail fighting occurs as pecking, and the performance of struggling rarely happens. Under normal circumstances, the dominant male in the cage will stop the mating and eating of other males. The aggression interactions between domestic quails happened at the higher frequencies, whereas wild Japanese quail were at low frequencies. Significant difference ($P < 0.05$) was detected in aggression and fighting times between domestic and wild

Table 1. The index of figure type of domestic quail, wild Japanese quail, and their first filial generation (F_1)

Breed	Sex	Number	BW (g)	Beak length (cm)	Tarsus length (cm)	Tarsus girth (cm)	Wing length (cm)	Body slant length (cm)
Domestic quail	Male	28	106.8 ± 26.6^{a}	1.157 ± 0.067^{a}	3.034 ± 0.395^{a}	1.444 ± 0.188^{a}	14.923 ± 1.145^{a}	9.2 ± 0.5^{a}
	Female	70	134.3 ± 14.3^{a}	1.204 ± 0.157^{a}	3.359 ± 0.285^{a}	1.478 ± 0.188^{a}	15.704 ± 1.991^{a}	10.1 ± 1.4^{a}
Wild quail	Male	25	91.9 ± 5.99^{b}	1.115 ± 0.139^{a}	2.828 ± 0.258^{b}	1.289 ± 0.140^{b}	13.798 ± 1.187^{b}	8.2 ± 0.4^{b}
	Female	34	94.7 ± 18.4^{b}	1.151 ± 0.217^{a}	2.932 ± 0.316^{b}	1.317 ± 0.172^{b}	14.063 ± 1.304^{b}	8.3 ± 0.5^{b}
F_1	Male	22	119.5 ± 14.2^{a}	1.112 ± 0.087^{a}	3.471 ± 0.125^{a}	1.371 ± 0.198^{a}	14.626 ± 0.821^{a}	10.7 ± 0.7^{a}
	Female	27	125.5 ± 28.7^{a}	1.115 ± 0.092^{a}	3.487 ± 0.074^{a}	1.367 ± 0.186^{a}	14.826 ± 0.262^{a}	10.9 ± 1.1^{a}

[a,b]Means within a column lacking a common superscript differ ($P < 0.05$).

Table 2. Statistical analysis on behaviors of domestic quail, wild Japanese quail, and their first filial generation (F_1)

Behaviors	Domestic quail	Wild Japanese quail	F_1
Number/days	36/122	36/122	36/122
Vocalization	91.6 ± 22.39[a]	2.80 ± 0.936[b]	13.0 ± 2.148[c]
Aggression and fighting	9.7 ± 0.841[a]	0.17 ± 0.121[b]	8.1 ± 0.861[a]
Mating	20.6 ± 5.801[a]	1.6 ± 0.458[b]	20.7 ± 8.631[a]

[a–c]Means within a row lacking a common superscript differ ($P < 0.05$).

quails. The F_1 showed no significant difference ($P > 0.05$) from domestic quails but presented significant difference ($P < 0.05$) from wild quails (Table 2).

Mating. Sexually mature domestic males have the most successful copulations in the early afternoon but make few mating attempts in the late afternoon. Domestic quails and F_1 hybrids were not different ($P > 0.05$) in mating frequency, but they each had much more mating frequency than the wild quails (Table 2). Wild quails copulated less frequently, only during 0900 to 1000 h and during 1100 to 1200 h, which was significantly different ($P < 0.05$) from either of the other 2 populations.

Egg-Laying. Domestic quail and F_1 often lay eggs in the afternoon, mostly after 1530 h. No egg-laying behaviors were observed in wild quail at daytime with a harvest of 30 eggs, indicating that they lay eggs at night. The eggs of F_1 and domestic quail had an elliptical shape, beautiful eggshell color, smooth surface, and random black pigment distribution, whereas wild Japanese quail eggs showed an awl-like shape, dull eggshell color, and rough surface. Eggs of F_1 were close to domestic quail eggs in fresh weight and specific gravity and exceeded the latter in length, breath, and volume with no significant differences ($P > 0.05$). Except the specific quality, all egg indexes of wild Japanese quail were significantly lower than that of domestic quail and the F_1 generation ($P < 0.05$; Table 3), inferring that the corresponding traits of egg indexes belong to dominant heredity.

Reproductive Performance. In this study, eggs were collected consecutively and divided into 4 batches to incubate. The means of fertility eggs and hatched quails during incubation were calculated. No significant difference ($P > 0.05$) was found in fertilization rate between F_1 and domestic quail or wild Japanese quail, whereas significant difference ($P < 0.05$) was found between domestic quail and wild quail (Table 4). The 3 quail populations showed significant differences ($P < 0.05$) in hatching rate and hatching rate of fertilized eggs among one another.

DISCUSSION

The Behavior Differentiation of Quail

Vocalization, aggression and fighting, mating, and egg-laying are the key behavioral characteristics of quails (White and Galef, 1999). Generally, these behavioral types presented significant difference between domestic quail and wild Japanese quail in this study. Only during 1000 to 1200 h in the whole observation period did wild quails have more activity, and at other times they were immobile, which obviously differs from domestic quails. Birds usually vocalize in a state of fear, fighting, and mating (Erica et al., 1996). Although the sound of domestic quail and wild Japanese quail is similar, the vocalization frequency of wild quail is significantly lower than that of domestic quail, except the feeding time. This may reflect the nature of wild quail because they rarely vocalize in the wild except for courtship to avoid danger, whereas domestic quail never worry about it. The expression of aggression and fighting behavior in quail can be influenced by nutritional, environmental, and hormonal factors (Kuo, 1960). Sachs (1966) has suggested that the expression of aggression is, to a large extent, a reflection of the fact that in the wild males are polygamous and territorial and sexual dimorphism is limited. The artificial condition in this study did not bring crucial problems to wild quails; they had a relatively free life, but their aggression and fighting behavior was statistically the lowest among the 3 quail populations, as well as vocalization. The big difference between them could be developed from the domestication process because wild quails are in nature nocturnal birds, not diurnal birds.

Table 3. Statistical analysis on egg indexes of domestic quail, wild Japanese quail, and their first filial generation (F_1)

Egg indexes	Domestic quail	Wild Japanese quail	F_1
Number	60	30	50
Fresh weight (g)	10.94 ± 0.91[a]	6.93 ± 0.80[b]	10.89 ± 0.89[a]
Length (mm)	3.18 ± 0.14[a]	2.78 ± 0.09[b]	3.19 ± 0.11[a]
Breadth (mm)	2.50 ± 0.06[a]	2.16 ± 0.08[b]	2.52 ± 0.08[a]
Volume (mm^3)	10.14 ± 0.08[a]	6.61 ± 0.08[b]	10.33 ± 0.07[a]
Specific gravity (g/mm^3)	1.08 ± 0.46[a]	1.05 ± 0.34[a]	1.05 ± 0.42[a]

[a,b]Means within a row lacking a common superscript differ ($P < 0.05$).

Table 4. The fertility, hatchability, and hatching rate of fertilized eggs of domestic quail, wild Japanese quail, and their first filial generation (F_1)

Indexes	Domestic quail	Wild Japanese quail	F_1
Hatching times	4	4	4
Hatching eggs/time	14, 15, 14, 17	7, 8, 5, 10	11, 12, 17, 10
Fertility rate	0.87 ± 0.01^{a}	0.42 ± 0.10^{b}	0.61 ± 0.12^{ab}
Hatching rate	0.77 ± 0.07^{a}	0.22 ± 0.07^{b}	0.40 ± 0.03^{c}
Hatching rate of fertilized eggs	0.88 ± 0.08^{a}	0.53 ± 0.01^{b}	0.67 ± 0.11^{c}

[a–c]Means within a row lacking a common superscript differ ($P < 0.05$).

Wild Japanese quails are seasonal breeding birds, and they usually copulate from May to October every year, whereas domestic quails lay eggs all year around. The low frequency of mating in wild quail reflects its nature in the wild, causing a low fertility rate, hatching rate, and hatching rate of fertilized eggs in wild quail.

The Evolutionary Differentiation of Quail in China

According to Chinese literature, the history of quail domestication can go back to at least 1500 yr ago (Chang et al., 2001, 2005). In Japan, quail has been domesticated since at least the 12th century AD, when it was kept as a song bird (Kovach, 1974; Kimura, 1996). The difference in size and shape between the domestic and the wild quail reflects the effect of the domestication. No reproduction isolation was observed in this study between wild and domestic quails, which indicated a close relationship between them during and after their independent evolutionary process. However, ethological isolation in vocalization, aggression and fighting, and mating behaviors to a certain degree observed in this study has formed during the evolutionary process, indicating a relatively large evolutionary differentiation. In addition, the lowest reproductive capacity of wild Japanese quail among the 3 quail species and the fact that F_1 from male domestic quail and female wild quail failed survival also demonstrated a large evolutionary differentiation to a certain degree. From the above conflict evidence, we made a comprehensive conclusion that quail populations in China had a relatively low evolutionary differentiation among them.

A Way to Restore Wild Quail Population

Wild quail and domestic quail can exchange genes and produce a fertile hybrid offspring. Due to the sharp decrease of the wild quail population and the deterioration of the ecological environment in recent years, the wild quail in China has become endangered and many researchers advocate restoring wild quail populations through releasing domestic quails to the wild (Schmid and Wecsler, 1997, 1998; Chang et al., 2006). The advantages of the F_1 hybrids in reproductive capacity, fertilization, and hatching recommend the F_1 hybrids as a good candidate to be released to the wild, which can increase the wild population more quickly and more authentically. In total, the findings in this study, on the one hand, provide a new way to improve domestic quail through the introduction of a wild gene bank to breed new commercial strains with better performance, like large-type and large weight quail. On the other hand, we prefer releasing hybrids to the wild instead of domestic quails to restore the wild quail population if necessary.

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