Received: 10 September 2021 | Revised: 6 November 2021 | Accepted: 8 November 2021
DOI: 10.1002/jez.b.23111

RESEARCH ARTICLE

JEZ-B MOLECULAR AND DEVELOPMENTAL EVOLUTION WILEY

Comparative morphological study of skeletal muscle weight among the red jungle fowl (*Gallus gallus*) and various fowl breeds (*Gallus domesticus*)

Hideki Endo[1] | **Naoki Tsunekawa**[2] | **Kohei Kudo**[1] | **Tatsuo Oshida**[3] | **Masaharu Motokawa**[4] | **Mitsuru Sonoe**[5] | **Sawai Wanghongsa**[6] | **Chanin Tirawattanawanich**[7] | **Viengsavanh Phimphachanhvongsod**[8] | **Takeshi Sasaki**[9] | **Takahiro Yonezawa**[9] | **Fumihito Akishinonomiya**[1,10]

[1]The University Museum, The University of Tokyo, Tokyo, Japan
[2]Department of Bioscience in Daily Life, College of Bioresource Sciences, Nihon University, Fujisawa, Japan
[3]Laboratory of Wildlife Ecology, Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Japan
[4]The Kyoto University Museum, Kyoto University, Kyoto, Japan
[5]Department of International Development Studies, College of Bioresource Sciences, Nihon University, Fujisawa, Japan
[6]National Parks, Wildlife and Plants Conservation Department, Bangkok, Thailand
[7]Department of Physiology, Faculty of Veterinary Medicine, Kasetsart University, Bangkok, Thailand
[8]Research Management Division, National Agriculture and Forestry Research Institute (NAFRI), Ministry of Agriculture and Forestry, Vientiane, Laos
[9]Faculty of Agriculture, Tokyo University of Agriculture, Atsugi, Japan
[10]Yamashina Institute for Ornithology, Abiko, Japan

Correspondence
Hideki Endo, The University Museum, The University of Tokyo, 7-3-1, Hongo, Bunkyo, Tokyo 113-0033, Japan.
Email: hendo@um.u-tokyo.ac.jp

Funding information
JSPS KAKENHI, Grant/Award Numbers: 17KT0071, 18H03602, 19H00534, 20H01381, 20H01979

Abstract

We examined the weight distribution of skeletal muscles of the red jungle fowl, then compared these values with those of domesticated populations to determine how muscle distribution has changed by selecting breeding. Sonia, Fayoumi, and Rhode Island Red were selected for comparison from livestock breeds, while Japanese Shamo and Thai fighting cocks were selected from cockfighting groups. Principal component analysis was applied using body size-free data. The mass distribution of muscles clearly differed between the wild, livestock, and cockfighting groups, demonstrating that muscle distribution has changed after selecting breeding, coupled with functional demands of each group. The red jungle fowl, which has the ability to fly, could be clearly distinguished from the flightless domesticated populations due to differences in flight pectoral muscle size. The cervical muscles in the wild population were smaller than in the domesticated groups; these do not contribute to flight. The gluteal muscles were larger in the fighting cock group, functionally coupled to their traditionally preferred upright posture. Wild bird populations typically exhibit reduced weight of their hind limbs, associated with flight, but as the red jungle fowl displays largely terrestrial behavior, these muscles are similar in arrangement and relative size to those of the livestock groups. We showed that the mass distribution pattern of skeletal muscles expresses selecting breeding strategy and clearly reflects the specific traits for each group.

KEYWORDS
breeding, chicken, domestication, fighting cock, skeletal muscle

1 | INTRODUCTION

The red jungle fowl (*Gallus gallus*) is the wild ancestor of domesticated fowl, and is widely distributed in southern China, Vietnam, Laos, Cambodia, Thailand, Malaysia, Indonesia, Myanmar, and Bangladesh. The domesticated fowl was bred mainly from the red jungle fowl, whereas the genetic introgression of gray jungle fowl (*Gallus sonneratii*) also contributed to its domestication (Eriksson et al., 2008; Nishibori et al., 2005). Chickens display various morphological characteristics adapted to their use and social needs as livestock that produces meat and eggs, companion animals, external ornament birds, long-crowing birds and game fighting birds, and so forth (Crawford, 1990; Ekarius, 2007; Hahn, 1896; Issac, 1970; Sauer, 1952; Smith & Daniel, 2000; Zeuner, 1963). Studies of morphological variation between domestic and wild populations have a long tradition (Sánchez-Villagra, 2021). Here, we concentrate on postcranial musculature. Because the physical activity and behavior of each chicken breed are functionally determined to a great extent by muscle performance, we expected that the distribution of muscle weights in the fowl body would reflect the breeding based on the requirements brought in by the domestication process. In this study, we investigated two types of domesticated cocks for comparison: the fighting cocks, which included the Japanese Shamo and Thai fighting breeds, and the agricultural livestock breeds (i.e., laying and meat breeds), which included Sonia, Fayoumi, and Rhode Island Red breeds. We compared the muscle mass distribution of wild red jungle fowl with these breeds to examine the functional-adaptational categories of skeletal muscle composition of various fowl breeds.

2 | MATERIALS AND METHODS

Muscular weights were determined in the 68 male carcasses consisting of red jungle fowl, agricultural breeds (Sonia [Hy-Line Sonia], Fayoumi, Rhode Island Red), and fighting breeds (Japanese Shamo [various Shamo] and Thai fighting cocks [Pra-doo-hang-dam and Leang-hang-kaow]). The red jungle fowl samples used in this study were identified as *G. gallus spadiceus* based on locality and external appearance (Delacour, 1977; Endo et al., 2017; Johnsgard, 1999; Nishida et al., 2000). Fayoumi is a traditional laying breed, whereas Rhode Island Red is a popular dual-purpose breed (Ekarius, 2007). The physiological data of Sonia as commercial layer is available at the Company's website (https://www.hyline.com/literature/sonia). Shamo is one of the tallest ancient breeds from Japan, one that shows aggressive behavior (Ekarius, 2007). Pra-doo-hang-dam and Leang-hang-kaow are also tall breeds for game, with quantified and positively tested a genetic diversity and relationships with the red jungle fowl (Teinlek et al., 2018).

The dead bodies of the domesticated breeds were donated by poultry farms and breeding owners. Red jungle fowl materials had been collected and stored by the National Agriculture and Forestry Research Institute of Laos. The red jungle fowl represented a wild population, Rhode Island Red an agricultural group and Pra-doo-hang-dam a fighting cock (Figure 1). The abbreviations used for the various muscles compared in this study are provided in Table 1. The composition of the individuals of breeds, strains or varieties are shown in Table 2. The body weight range of the red jungle fowl and Thai fighting cocks indicated adult-sized birds, whereas the Sonia, Fayoumi, and Rhode Island Red breeds may have included both adult and subadult individuals. Individuals related to large-sized Shamo (O-Shamo) and middle-sized Shamo (Chu-Shamo) were included in the Japanese Shamo populations and the two typical Thailand breeds of Pra-doo-hang-dam and Leang-hang-kaow were included in the Thai fighting cock population. Only male specimens were compared, however, the data from eight female red jungle fowls were also provided to show the sexual similarities in the charts. The muscles in the trunk, arm, and leg regions were identified by the naked eye. In total, 17 muscles were excised from the carcasses and their weights were determined to the nearest 0.01 g. The muscle weights from the Sonia, Fayoumi, and Rhode Island Red breeds were determined to the nearest 0.1 g.

The weight ratio was calculated as each muscle weight/body weight $\times 10^3$ for functional comparison between the groups. The weight index was defined as the quotient of each muscle weight divided by the geometric mean of all muscle weights in each individual. Principal component analyzes were performed using both weight ratios and indices to reveal any morphological variations in skeletal muscle development among the populations. The results of principal component analysis were visualized to discuss the effect of artificial breeding and domestication of the red jungle fowl in relation to functional demands.

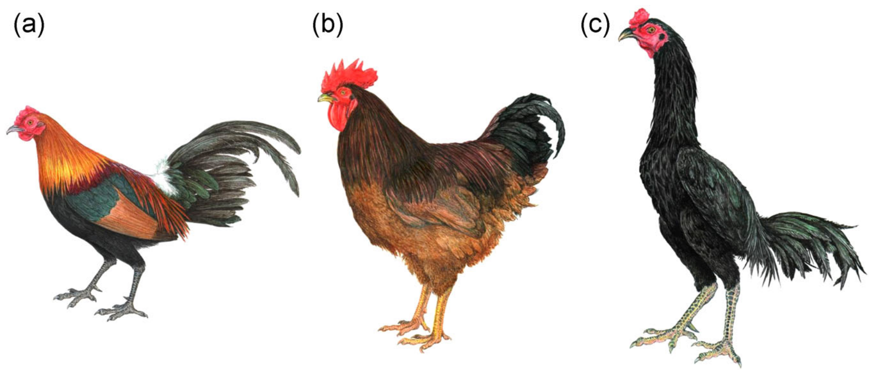

FIGURE 1 Illustrations of the materials used in this study. (a) Red jungle fowl. The wild nondomesticated individual shows a slender body with flight ability. The male exhibits beautiful orange and green feathers. (b) Rhode Island Red. The typical agricultural livestock breed producing meat and egg appears large and heavy. (c) Pra-doo-hang-dam. The fighting breed shows the standing posture with wide chest in the cockfights. Drawn by Takeshi Kitamura

TABLE 1 Weight items examined in this study and their abbreviations

Body weight	BW
Biventer cervicis muscle	BC
Cervical semispinalis muscle	CS
Longus colli muscle	LC
Superficial pectoral muscle	SP
Deep pectoral muscle	DP
External coracobrachial muscle	EC
Internal coracobrachial muscle	IC
Biceps brachii muscle	BB
Biceps femoris muscle	BF
Superficial gluteal muscle (cranial part)	SG
Middle gluteal muscle	MG
Semitendinosus muscle	ST
Semimembranosus muscle	SM
Quadriceps femoris muscle	QF
Adductor muscles	AD
Peroneus longus muscle	PL
Triceps surae muscle	TS

The statistical differences of the weight ratios and weight indices among the three fowl groups were examined using the Kruskal–Wallis test and Mann–Whitney *U* test. Sexual dimorphism was also evaluated in the red jungle fowl by using Mann–Whitney *U* test. The principal component analysis, Kruskal–Wallis test and Mann–Whitney *U* test were carried out by using SPSS software (IBM Japan, Ltd.).

The muscle weight data of the Sonia, Fayoumi, Rhode Island Red, and Japanese Shamo breeds were also used in a previous study (Endo et al., 2012). We added the muscle weight data of the red jungle fowl and Thai fighting cocks that were genetically controlled as pure-bred Pra-doo-hang-dam and Leang-hang-kaow in this study. Since the QF weight included MV (medial vastus muscle) weight in this study unlike the previous work (Endo et al., 2012), a total of 17 muscle weights were applied in the statistical analyzes.

3 | RESULTS

The raw weight data, weight ratios and weight indices of the 17 skeletal muscles are arranged in the six populations and the red jungle fowl female (Tables 3–5). The results of the principal component analysis using weight ratios (Figure 2a–d) and indices (Figure 2e–h) were drawn as scattergrams. The principal component scores of the red jungle fowl, both including females (Figure 2a,c,e,g) and including only males (Figure 2b,d,f,h) were dotted. The character loading factors and cumulative contribution ratios were arranged on the weight ratios (Table S1) and the weight index (Table S2), respectively.

The separation among the three groups, (red jungle fowls, agricultural breeds, and fighting cock breeds), was confirmed in all charts of the first and second principal components (Figure 2a,b,e,f). The distribution area of the first and second principal component scores were completely separated into the three groups as follows: (1) The fighting cocks: Japanese Shamo and Thai fighting cocks. (2) Agricultural livestock breeds: Sonia, Fayoumi, and Rhode Island Red. (3) The wild population: red jungle fowl (Figure 2a,b,e,f), with only a few dots closely positioned between the agricultural breeds and the fighting cock breeds.

The Kruskal–Wallis test and Mann–Whitney *U* test were applied to these groups, since the principal component analysis showed obvious separation. Most of the ratios and indices were significantly different among the three groups in both weight ratio and index (Table S3). The Kruskal–Wallis test detected significant differences in all measurements except for QF of the weight ratio and PL of the weight index. The sexual

TABLE 2 Numbers, sex, origins, and size range of six populations used in this study

Breed	Strain or variation or locality	Sex	Number	Body weight range (g)
Red jungle fowl	Udomxai and Luang Namutha, North Laos	Male	22	820–1150
		Female	8	500–700
Sonia	Non recorded	Male	25	2373–3067
Fayoumi	PNP/DO	Male	4	1372–1515
Rhode Island Red	RIR-Y8/NU	Male	4	2326–2870
Japanese Shamo	Niigata O-Shamo and	Male	2	4200–6500
	hybrid of Niigata O-Shamo and Okinawa Chu-Shamo			
Thai fighting cocks	6 Pra-doo-hang-dam and 5 Leang-hang-kaow	Male	11	2800–3700
Total			76	

dimorphism showed only in SG and MG of the weight ratios, and in SP and SG of the weight index of the red jungle fowl (Table S4).

Significant differences among the three groups were discerned in all weight ratios and indices by the Kruskal–Wallis test except for two cases, and in most muscles by the *U* test (Table S3). This is consistent with the clear separation of the three groups by the first and second principal component scores. The absolute value of character loading factors of the first principal component was larger in SP, DP, EC, IC, and BB (positive) and BC and CS (negative) (Tables S1 and S2). This indicates that the dots of individuals with larger forelimb muscles were distributed in the positive area, whereas the dots with heavier necks were positioned in the negative area on the PC1 axis. The dots of the red jungle fowl were in the positive region, whereas those of the agricultural breeds were in the negative region. The lighter neck part is consistent with weight saving requirements of flying (Figure 2a,b,e,f). In the second principal component, the character loading factors showed larger values for BF, MG, SM, and TS in the weight indices. SG and PL were also larger in their weight ratios. This shows that the fighting breeds with standing postures and larger extending muscles of the hip joint were concentrated in the positive area (Figure 2a–d).

Morphological sexual dimorphism was clearly displayed in the red jungle fowl, with no overlap body weight ranges between the sexes (Table 2). The *U* test in the weight ratio and index found significant differences only in four cases (Table S4). The results of the principal component analysis omitting the size factor also showed that the male and female dots of the red jungle fowl were intermingled (Figure 2a,e). The scattergrams of the first and second principal component scores including females (Figure 2a,e) and without females (Figure 2b,f) did not seem different in regard to the group separation, since the female dots were fused to the male dot aggregation.

4 | DISCUSSION

The red jungle fowl is a wild avian species with modest flight ability and complex terrestrial social behavior (Delacour, 1977; Johnsgard, 1999). We characterize the domesticated breeds studied here as flightless in contrast to the autonomous flight ability of the wild red jungle fowl.

The SP and DP ratios and indices were the most noteworthy (Tables 4 and 5). Both of these two muscles were larger in the red jungle fowl than in the other domesticated breeds. The SP and DP are the main flight muscles in birds; the larger ratios and indices of the red jungle fowl in contrast to chickens may indicate the preservation of the flight ability in the wild form and the reduction thereof in the domesticated forms. The EC and IC ratios and indices were also much larger in the red jungle fowl compared to the two flightless domesticated populations, because these and other muscles running from coracoid to humerus act as flight and wing oscillation muscles generally in birds like SP and DP (Altshuler et al., 2015; Beaufrère, 2009; Biewener, 1998; Dial et al., 1991; Poore et al., 1997; Tobalske & Biewener, 2008). Various volant birds are generally equipped with pectoral muscles of approximately 17% on average of their total body mass (Greenewalt, 1962). In comparison, only approximately 10% of SP, DP, EC, and IC were measured in this study, thus slightly smaller than average (Table 4), probably due to the fact that red jungle fowl does not often fly. The weight ratio data in various species of Phasianidae, who also display lower flight activity, should be compared in a future study to further elucidate the evolutionary strategy in the flight muscles of this clade.

The weight ratios and indices for BC, CS, and LC of the neck region were larger in the domesticated breeds than in the red jungle fowl (Tables 4 and 5). Birds have evolved centralized body mass to concentrate powerful flight muscles to the thoracic region (Marek et al., 2021; Proctor & Lynch, 1993). The neck represents a small portion of the weight in flying birds, since birds are constrained by selective pressure for weight reduction for flight. Although the neck is not generally consumed as food in the domesticated meat breeds, humans have bred the domesticated populations to increase their total body weight, resulting in relatively larger weight ratios including the cervical region. The larger ratios in the BC and CS of the Japanese Shamo breed (Table 4) may reflect that the action of elevating the head and neck to attack opponent are important in cock games. Conversely, the red jungle fowl with flying ability is restrained from increasing body weight, resulting in lighter neck muscles.

TABLE 3 Weights (g) of the muscles in various breeds including red jungle fowl

	Body weight	BC	CS	LC	SP	DP	EC	IC	BB	BF	SG	MG	ST	SM	QF	AD	PL	TS
Red jungle fowl (male)	946.82	0.42	1.89	1.64	71.80	20.77	2.51	1.92	2.64	12.50	0.96	5.18	4.77	7.83	9.84	3.55	4.98	14.00
	105.35	0.08	0.38	0.26	10.73	4.04	0.37	0.51	0.42	1.96	0.21	0.81	1.22	1.41	2.10	0.73	0.92	2.18
Sonia	2648.08	1.60	8.06	7.12	114.52	39.86	5.42	3.96	5.87	29.32	2.79	14.02	16.06	19.69	29.31	10.67	12.91	35.88
	175.22	0.28	0.69	0.90	14.07	3.64	0.50	0.43	0.59	3.32	0.32	1.51	1.96	2.66	2.62	1.23	1.58	3.01
Fayoumi	1445.25	0.65	4.18	3.54	64.40	27.50	2.65	2.13	2.65	16.05	1.23	7.08	6.18	11.80	13.98	5.85	7.25	18.58
	71.27	0.13	0.46	0.35	6.28	1.15	0.10	0.10	0.17	1.01	0.10	0.50	0.15	0.67	0.94	0.34	0.21	1.45
Rhode Island Red	2616.25	1.56	7.53	4.80	88.62	36.37	5.73	4.31	5.56	25.88	2.48	12.56	15.15	17.57	25.83	9.79	13.88	35.92
	224.47	0.35	2.16	1.13	8.38	4.29	0.77	0.46	0.69	3.38	0.65	1.19	2.58	1.33	3.60	2.38	2.11	3.96
Japanese Shamo	5350.00	3.23	16.89	10.95	230.17	103.18	10.09	6.50	14.00	64.77	6.71	36.30	33.26	47.44	58.46	22.32	33.23	88.06
	1626.35	0.78	7.56	4.63	27.08	27.47	1.70	0.47	3.68	16.09	2.21	7.37	5.00	11.71	5.17	6.54	2.01	23.39
Thai fighting cocks	3109.09	1.75	7.14	5.98	137.92	51.26	6.13	4.41	7.76	42.48	3.48	18.05	20.42	29.18	33.40	14.44	17.71	55.86
	320.01	0.33	2.14	1.28	20.57	8.51	1.20	0.76	0.91	9.31	0.49	1.87	2.35	4.53	4.41	1.53	3.36	7.98
Red jungle fowl (female)	616.25	0.28	1.12	0.98	47.89	13.67	1.65	1.21	1.61	7.89	0.52	2.98	2.92	4.84	5.75	2.20	3.05	8.56
	70.09	0.05	0.28	0.18	6.42	2.79	0.45	0.22	0.23	1.69	0.11	0.39	0.56	0.64	0.88	0.76	0.86	1.81

Note: Mean values are arranged in upper row, whereas standard deviation in lower row.

TABLE 4 The weight ratios of each muscle in various breeds including the red jungle fowl

	BC	CS	LC	SP	DP	EC	IC	BB	BF	SG	MG	ST	SM	QF	AD	PL	TS
Red jungle fowl (male)	0.442	1.998	1.737	75.703	21.837	2.658	2.010	2.779	13.343	1.014	5.461	5.127	8.271	10.349	3.753	5.245	14.835
	0.068	0.347	0.234	5.812	2.488	0.299	0.373	0.265	2.411	0.169	0.520	1.387	1.191	1.511	0.607	0.674	2.071
Sonia	0.603	3.050	2.686	43.200	15.066	2.051	1.497	2.219	11.065	1.056	5.293	6.062	7.426	11.075	4.031	4.874	13.561
	0.100	0.263	0.285	4.071	1.201	0.177	0.148	0.205	0.887	0.112	0.425	0.606	0.779	0.776	0.392	0.489	0.931
Fayoumi	0.451	2.884	2.447	44.626	19.047	1.839	1.474	1.834	11.127	0.850	4.903	4.282	8.171	9.690	4.052	5.027	12.884
	0.092	0.219	0.198	4.745	0.865	0.144	0.111	0.104	0.894	0.083	0.400	0.266	0.431	0.850	0.247	0.312	1.275
Rhode Island Red	0.591	2.839	1.825	33.989	13.912	2.188	1.649	2.122	9.889	0.944	4.825	5.776	6.722	9.854	3.754	5.288	13.769
	0.092	0.610	0.330	3.467	1.182	0.197	0.124	0.151	0.892	0.193	0.583	0.702	0.215	0.781	0.917	0.521	1.530
Japanese Shamo	0.609	3.086	2.008	44.299	19.402	1.927	1.259	2.633	12.213	1.249	6.894	6.369	8.948	11.303	4.178	6.452	16.561
	0.040	0.474	0.254	8.405	0.763	0.268	0.295	0.112	0.706	0.033	0.717	1.002	0.531	2.469	0.047	1.585	0.662
Thai fighting cocks	0.579	2.379	1.985	45.956	17.058	2.026	1.481	2.593	14.112	1.163	6.025	6.827	9.742	11.098	4.811	5.877	18.565
	0.084	0.686	0.359	7.368	2.898	0.292	0.327	0.396	2.996	0.192	0.832	1.077	1.772	1.259	0.538	0.999	2.573
Red jungle fowl (female)	0.444	1.811	1.595	77.741	22.198	2.691	1.970	2.628	12.739	0.844	4.869	4.730	7.856	9.357	3.547	4.898	13.852
	0.037	0.337	0.280	6.341	3.751	0.714	0.341	0.351	2.020	0.155	0.650	0.810	0.587	1.364	1.119	1.069	1.956

Note: Mean values are arranged in upper row, whereas standard deviation in lower row.

TABLE 5 The weight indices of each muscle in various breeds including the red jungle fowl

	BC	CS	LC	SP	DP	EC	IC	BB	BF	SG	MG	ST	SM	QF	AD	PL	TS
Red jungle fowl (male)	0.093	0.421	0.368	16.036	4.628	0.561	0.427	0.588	2.809	0.214	1.156	1.080	1.744	2.187	0.793	1.109	3.127
	0.011	0.064	0.052	1.306	0.557	0.050	0.087	0.053	0.412	0.031	0.108	0.273	0.190	0.286	0.125	0.136	0.315
Sonia	0.131	0.667	0.588	9.448	3.296	0.449	0.327	0.485	2.419	0.231	1.157	1.326	1.623	2.422	0.882	1.065	2.964
	0.019	0.052	0.067	0.869	0.263	0.038	0.032	0.037	0.178	0.024	0.081	0.130	0.149	0.157	0.090	0.099	0.157
Fayoumi	0.101	0.649	0.574	10.014	4.279	0.413	0.331	0.412	2.498	0.191	1.101	0.961	1.835	2.176	0.910	1.128	2.890
	0.021	0.062	0.060	0.842	0.127	0.021	0.013	0.021	0.146	0.015	0.083	0.031	0.076	0.161	0.053	0.030	0.212
Rhode Island Red	0.133	0.641	0.433	7.689	3.147	0.495	0.373	0.480	2.243	0.213	1.093	1.302	1.525	2.226	0.845	1.196	3.114
	0.016	0.129	0.091	0.731	0.222	0.044	0.020	0.012	0.251	0.036	0.129	0.083	0.113	0.055	0.171	0.098	0.286
Japanese Shamo	0.124	0.632	0.411	8.952	3.943	0.390	0.254	0.535	2.481	0.254	1.398	1.289	1.817	2.282	0.850	1.301	3.366
	0.001	0.145	0.083	1.019	0.148	0.024	0.040	0.018	0.047	0.026	0.038	0.104	0.032	0.326	0.056	0.222	0.124
Thai fighting cocks	0.118	0.485	0.408	9.353	3.476	0.414	0.303	0.527	2.866	0.237	1.227	1.390	1.984	2.270	0.985	1.199	3.787
	0.014	0.134	0.080	1.008	0.479	0.054	0.069	0.037	0.451	0.025	0.075	0.125	0.258	0.215	0.109	0.166	0.342
Red jungle fowl (female)	0.100	0.404	0.357	17.403	4.957	0.595	0.441	0.588	2.844	0.188	1.087	1.056	1.770	2.092	0.786	1.096	3.114
	0.012	0.058	0.058	0.458	0.665	0.097	0.071	0.063	0.326	0.023	0.077	0.142	0.216	0.233	0.218	0.226	0.476

Note: Mean values are arranged in upper row, whereas standard deviation in lower row.

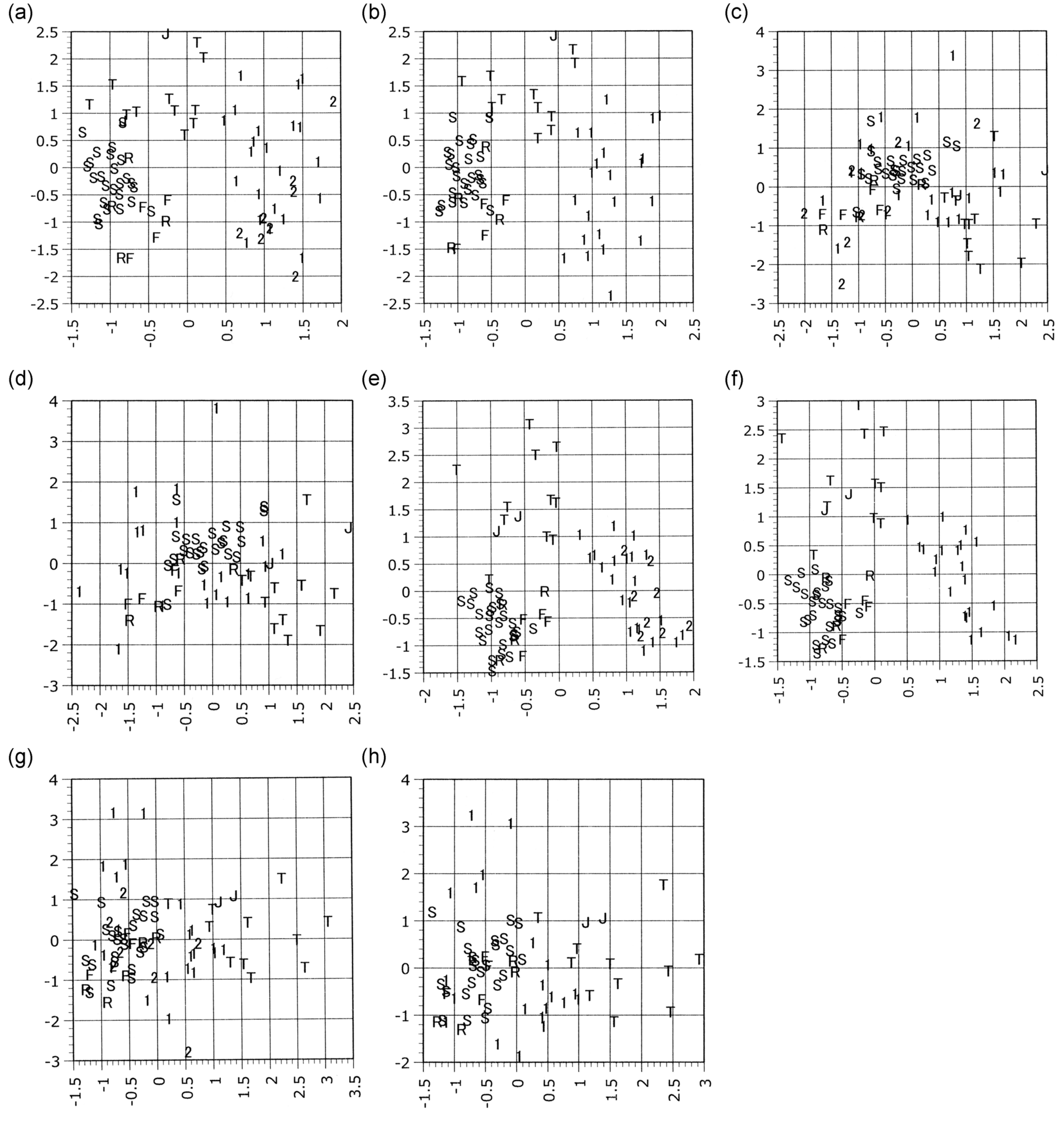

FIGURE 2 Scattergrams showing the principal component scores from all muscle weight ratios (a–d) and indices (e–h). The horizontal axis indicates the first principal component and the vertical axis shows the second principal component (a, b, e, f). The second principal components are shown on the horizontal axis and the third principal component on the vertical axis (c, d, g, h). The data either include the females of the red jungle fowl (a, c, e, g), or not (b, d, f, h). Symbols of the breeds are as follows: 1, red jungle fowl (male); 2, red jungle fowl (female); S, Sonia; F, Fayoumi; R, Rhode Island Red; J, Japanese Shamo; T, Thai fighting cocks

The BB ratio and index were larger in the fighting cock groups than in the livestock groups consisting of Sonia, Fayoumi, and Rhode Island Red. The BB ratio of the male red jungle fowl was larger than fighting cock groups, whereas the BB index of the red jungle fowl was larger in both males and females. These results suggest that BB related to the wing movement may be larger in the flight populations than in flightless populations. Although fighting cocks cannot fly, we hypothesize that their much larger total body size may induce a partial weight gain in the upper arm and elbow regions. In addition, the active flapping and strong attacks using the forearm region of the wing in the fowl game may also require larger BB in the fighting cock breeds.

The fighting cocks were equipped with heavier SG and MG ratios and indices (Tables 4 and 5). The two muscles function as an extender of the hip joint. The large fighting cocks (Japanese Shamo and Thai fighting cock breeds) are grouped into the standing type (Endo et al., 2012); the vertical extension of the body trunk by these muscles is the preferred posture in the cock fight. We suggest that the standing posture showing wide chest is also ornamental (Kudo et al., 2017).

The weight ratios of BF, ST, SM, QF, AD, PL, and TS, and the weight indices of SM, PL, and TS were largest in the fighting cock groups (Tables 4 and 5). These muscles are related to hindlimb and foot movements, this their larger size makes functional sense as high jumping and running performance are generally required in cock fights (Chakraborty, 2018; Chakraborty & Chakraborty, 2016; Dundes, 1994). The ST, QF, AD, and PL in the red jungle fowl also showed ratios that were as large as the three other agricultural breeds bred for the development of muscles as chicken production. The heavy muscles in the hindlimb hinder flight performance, however, the larger ST, QF, AD, and PL are functionally important for the long-distance walking lifestyle of the red jungle fowl. The TS acts as a motor of the planter flexion of the foot joint and the flexion of the thigh joint (König & Liebich, 2014; Proctor & Lynch, 1993). The larger TS may contribute to the specialized running behavior in the fighting breeds.

The dot fusion between sexes in the red jungle fowl (Figure 2a,e) suggests that the terrestrial and short-distance flying behaviors may not influence sexual dimorphism in muscle mass distribution in the wild population. Although the walking behavior and territory or home range size are obviously different between males and females (Wanghongsa & Hayashi, 2010; Wanghongsa et al., 2018), the body size-free analysis could not clearly detect sexual dimorphism in the skeletal muscle distribution in this species.

Since it is a quantity independent of body weight, we suggest that the weight index (Figure 2e,f) can be used to reveal the muscle weight distribution of the three functional groups more clearly than the weight ratios can (Figure 2a,b), since weight ratio is directly affected by body weight. The trends in the cumulative contribution ratios were not more clearly so different among the four principal component analyzes (Tables S1 and S2). These results indicate that the first and second principal components totally contained almost 50–55 of the shape information. The third principal component explains only approximately 8%–10%, and could not separate the breeds in this analysis (Figure 2c,d,g,h). The dots of the red jungle fowl were distributed widely in the entire range of the third principal component. The agricultural breeds and fighting cock breeds were dotted in a similar range for the third principal component.

Sonia, Fayoumi, Rhode Island Red, Japanese Shamo, and two Thailand game cocks were independently established with long breeding histories, indicating that various genetically independent fighting and agricultural breeds are equipped with similar muscle weight distribution in convergence-like selecting breeding. In the case of game cocks, humans of different cultural backgrounds (e.g., Japan and Thailand) converge on a preference for similar attitudes and actions from the fowls. The cockfight has been continued not only for gambling purposes, but also as a deeply spiritual relationship between humans and cocks (Chakraborty, 2018; Chakraborty & Chakraborty, 2016; Dundes, 1994). The breeder demands that fighting cocks have physiological function capable of winning the game. The traditional breeders also believe that in the spiritual world, the appearance of their chicken can be given a fantasy image of aggressiveness, masculinity, and dignity to fascinate cockfighting viewers, although these ambiguous aims of selection are not objective. Because these complicated needs determined the distribution of muscle mass in fighting cocks (Kudo et al., 2017), their body size and shape are morphologically distinguished from those of the meat and layer breeds as confirmed by the results of this study.

The Fayoumi is one of the most traditional breeds from ancient Egypt and shows a higher performance as egg layers (Ekarius, 2007). The population is now maintained also as an experimental animal. The Sonia is also one of the high-spec layers. The three agricultural breeds, Fayoumi, Sonia, and Rhode Island Red, do not belong to the standing type, and show usual proportions of muscle mass distribution as agricultural-production fowl.

The present analyzes demonstrated a much higher variation in muscle weight distribution in chicken breeds than in red jungle fowl and how functional groups can be differentiated based on muscle mass distribution.

ACKNOWLEDGMENTS

This study was financially supported by JSPS KAKENHI Grant Numbers 17KT0071, 18H03602, 19H00534, 20H01381, and 20H01979 from Japan Society for the Promotion of Science (JSPS).

CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

AUTHOR CONTRIBUTIONS

Naoki Tsunekawa, Sawai Wanghongsa, and Chanin Tirawattanawanich conceived the project and designed experiments. Mitsuru Sonoe, Viengsavanh Phimphachanhvongsod, Tatsuo Oshida, and Masaharu Motokawa conducted experiments. Kohei Kudo, Takeshi Sasaki, and Takahiro Yonezawa analyzed the results. Hideki Endo and Fumihito Akishinonomiya wrote and edited the manuscript. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information to this article.

ORCID

Hideki Endo http://orcid.org/0000-0003-4779-0399
Tatsuo Oshida https://orcid.org/0000-0003-0863-9530
Masaharu Motokawa https://orcid.org/0000-0002-5359-0070
Takeshi Sasaki https://orcid.org/0000-0003-4210-5022
Takahiro Yonezawa https://orcid.org/0000-0002-0012-1887

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/jez.b.23111

REFERENCES

Altshuler, D. L., Bahlman, J. W., Dakin, R., Gaede, A. H., Goller, B., Lentink, D., Segre, P. S., & Skandalis, D. A. (2015). The biophysics of bird flight: Functional relationships integrate aerodynamics, morphology, kinematics, muscles, and sensors. *Canadian Journal of Zoology*, *93*(12), 961–975.

Beaufrère, H. (2009). A review of biomechanic and aerodynamic considerations of the avian thoracic limb. *Journal of Avian Medicine and Surgery*, *23*(3), 173–185.

Biewener, A. A. (1998). Muscle function in vivo: A comparison of muscles used for elastic energy savings versus muscles used to generate mechanical power. *American Zoologist*, *38*(4), 703–717.

Chakraborty, P. (2018). Social Impact of cock fight: The study among the Santals. *Research Journal of Humanities and Social Science*, *9*(4), 754–758.

Chakraborty, P., & Chakraborty, F. (2016). Social-cultural aspects of cock fight: A study among the Santals of Foringdanga, Paschim Medinipur, West Bengal, India. *Imperial Journal of Interdisciplinary Research*, *2*(10), 2116–2120.

Crawford, R. D. (1990). *Poultry breeding and genetics*. Elsevier.

Delacour, J. (1977). *The pheasants of the world* (2nd ed.). Country Life.

Dial, K. P., Goslow, G. E., & Jenkins, F. A. (1991). The functional anatomy of the shoulder in the European starling (*Sturnus vulgaris*). *Journal of Morphology*, *207*(3), 327–344.

Dundes, A. (1994). *The cockfight. A casebook*. The University of Wisconsin Press.

Ekarius, C. (2007). *Storey's illustrated guide to poultry breeds*. Storey Publishing.

Endo, H., Mori, K., Hosojima, M., Mekwichai, W., Ogawa, H., Tsunekawa, N., Yamasaki, T., Hayashi, Y., & Akishinonomiya, F. (2012). Functional-morphological characteristics in the musculoskeletal system of standing-type cocks including some game breeds. *Japanese Journal of Zoo Wildlife Medicine*, *17*(3), 131–138.

Endo, H., Tsunekawa, N., Sonoe, M., Sasaki, T., Ogawa, H., Amano, T., Son, N. T., Pimphachanhvongsod, V., Kudo, K., Yonezawa, T., & Akishinonomiya, F. (2017). Geographical variation in the skeletal morphology of red jungle fowl. *British Poultry Science*, *58*(4), 348–357.

Eriksson, J., Larson, G., Gunnarsson, U., Bed'hom, B., Tixier-Boichard, M., Strömstedt, L., Wright, D., Jungerius, A., Vereijken, A., Randi, E., Jensen, P., & Andersson, L. (2008). Identification of the *Yellow Skin* gene reveals a hybrid origin of the domestic chicken. *PLoS Genetics*, *4*, e1000010.

Greenewalt, C. H. (1962). Dimensional relationships for flying animals. *Smithsonian Miscellaneous Collections*, *144*(2), 1–46.

Hahn, E. (1896). *Die Haustiere und ihre Beziehunbgen zur Wirtschaft des Menschen*. Duncker & Humblot.

Issac, E. (1970). *Geography of domestication*. Prentice-Hall.

Johnsgard, P. A. (1999). *The pheasants of the world, biology and natural history* (2nd ed.). Smithsonian Institution Press.

König, H. E., & Liebich, H.-G. (2014). *Veterinary anatomy of domestic mammals. Textbook and colour atlas* (6th ed.). Schattauer.

Kudo, K., Tsunekawa, N., Ogawa, H., & Endo, H. (2017). Comparative functional morphology of the skeletal forelimb, pectoral girdle, and sternum in Japanese native domestic fowls. *Journal of Poultry Science*, *54*(1), 47–56.

Marek, R. D., Falkingham, P. L., Benson, R. B. J., Gardiner, J. D., Maddox, T. W., & Bates, K. T. (2021). Evolutionary versatility of the avian neck. *Proceedings of the Royal Society B*, *288*, 20203150.

Nishibori, M., Shimogiri, T., Hayashi, T., & Yasue, H. (2005). Molecular evidence of hybridization of species in the Genus *Gallus* except for *Gallus varius*. *Animal Genetics*, *36*(5), 367–375.

Nishida, T., Rerkamnuaychoke, W., Tung, D. G., Saignaleus, S., Okamoto, S., Kawamoto, Y., Kimura, J., Kawabe, K., Tsunekawa, N., Otaka, H., & Hayashi, Y. (2000). Morphological identification and ecology of the red jungle fowl in Thailand, Laos and Vietnam. *Animal Science Journal*, *71*(5), 470–480.

Poore, S. A., Ashcroft, A., Sánchez-Haiman, A., & Goslow, G. E. (1997). The contractile properties of the M. supracoracoideus in the pigeon and starling: A case for long-axis rotation of the humerus. *The Journal of Experimental Biology*, *200*(23), 2987–3002.

Proctor, N. S., & Lynch, P. J. (1993). *Manual of ornithology. Avian structure & function*. Yale University Press.

Sánchez-Villagra, M. R. (2021). *The process of animal domestication*. Princeton University Press.

Sauer, C. O. (1952). *Agricultural origins and dispersals*. The American Geographic Society.

Smith, P., & Daniel, C. (2000). *The chicken book*. The University of Georgia Press.

Teinlek, P., Siripattarapravat, K., & Tirawattanawanich, C. (2018). Genetic diversity analysis of Thai indigenous chickens based on complete sequences of mitochondrial DNA D-loop region. *Asian-Australasian Journal of Animal Sciences*, *31*(6), 804–811.

Tobalske, B. W., & Biewener, A. A. (2008). Contractile properties of the pigeon supracoracoideus during different modes of flight. *The Journal of Experimental Biology*, *211*(2), 170–179.

Wanghongsa, S., Endo, H., & Hayashi, Y. (2018). Roosting territory of white ear-lobed red jungle fowl (*Gallus gallus gallus*). *Journal of Life Sciences*, *12*, 75–82.

Wanghongsa, S., & Hayashi, Y. (2010). Activity and density of red jungle fowl (*Gallus gallus*) in a dry evergreen forest in Thailand. *Journal of Yamashina Institution for Ornithology*, *41*(2), 141–152.

Zeuner, E. F. (1963). *A history of domesticated animals*. Harper and Row.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Endo, H., Tsunekawa, N., Kudo, K., Oshida, T., Motokawa, M., Sonoe, M., Wanghongsa, S., Tirawattanawanich, C., Phimphachanhvongsod, V., Sasaki, T., Yonezawa, T., & Akishinonomiya, F. (2022). Comparative morphological study of skeletal muscle weight among the red jungle fowl (*Gallus gallus*) and various fowl breeds (*Gallus domesticus*). *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 338, 542–551. https://doi.org/10.1002/jez.b.23111