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Редактор и издатель А.В.Бардин
Кафедра зоологии позвоночных
Биолого-почвенный факультет
Санкт-Петербургский университет
Россия 199034 Санкт-Петербург

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A.V.Bardin, Editor and Publisher
Department of Vertebrate Zoology
St.-Petersburg University
St.-Petersburg 199034 Russia

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Phenetic analysis of skull reveals difference between Hokkaido and Sakhalin populations of the Jungle Crow *Corvus macrorhynchos*

S.Nakamura, A.Kryukov

Sumio Nakamura. Ornithological Society of Japan, Shinjuku, 169-0075 Tokyo, Japan
Alexey Kryukov. Institute of Biology and Soil Science, Far East Branch of the Russian Academy of Sciences, 690022 Vladivostok, Russia

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Introduction

Current content and distribution of biota is highly influenced by climatic oscillations in Pleistocene. These events are still poorly known for East Palearctic, especially for its eastern marginal ecosystems. Such widely distributed species as Jungle Crow *Corvus macrorhynchos* Wagler, 1827 is a convenient model for this kind of study. Jungle Crows prefer a highly concealed nest site in the forest and need a mild climate for breeding (Tamada, Fujimaki 1993, Nakamura 2000), and therefore had to retreat from the northern frontiers during severe glacial periods and were forced to survive in southern refuge located presumably around the East China Sea (Grichuk 1984).

The forest in north-eastern Asia recovered following the last Glacial Maximum (LGM), and Jungle Crows began to recolonize from southern refuge. Two recolonization routes to the north-eastern Asia have been speculated: one via Ussuriland and the other via the Japanese Archipelago (Nechaev 1991). The Jungle Crows originated in the recolonization movement to the Russian Far East up to Amurland and northern Sakhalin is classified as *Corvus macrorhynchos mandshuricus* Buturlin, 1913. The Jungle Crows occurring in the Japanese Main-islands up to the Sakhalin Island originated in the other movement via Japanese Archipelago is classified as *Corvus macrorhynchos japonensis* Bonaparte, 1850. At present Jungle Crows inhabit commonly all around the seacoast of the Japan Sea Rim. It is supposed that a borderline between two subspecies exists there in northern Sakhalin or they co-occur there (Nechaev 1991). The first author collected equal numbers of Jungle Crows in southern, central and northern Sakhalin Island and conducted morphological analysis to confirm the borderline (Nakamura unpubl.). But he could not verify the presence of a contact and/or a hybrid zone, nor a clear geographical cline and/or a gap. Morphological analysis did not offer any strong evidence for ascertaining the coexistence of two subspecies on the Sakhalin Island so this question is still open.

In an earlier genetic study by mitochondrial cytochrome *b* gene Iwasa *et al*. (2002) showed a slight differentiation between northern and southern Sakhalin. However, that time only a few samples were used by partial sequence and clustering was poorly supported. Later Kryukov *et al*. (2012) did not confirm this subdivision within Sakhalin based on much bigger data set and complete sequence of the same gene. They demonstrated low genetic differentiation and high level of gene exchange between the neighboring populations.

In north-eastern Asia there are three main geographical barriers which are supposed to affect the crow's distribution: La Perouse Strait, Tatarsky Strait and Sikhote Alin Mountains in the order of barrier hardness (Fig. 1). La Perouse Strait (Soya Strait) has separated the Sakhalin Island from Hokkaido since the beginning of the Holocene (Ono 1990). This strait is considerably wide (around 42 km) and deep (minimum depth of 60 m). The four Russian areas observed here are separated by two geographic soft barriers: the Tatarsky Strait and the Sikhote-Alin Mountains. The Tatarsky Strait, a long (around 200 km) but narrow (minimum width about 8 km) barrier, has separated the continental seaboard and northern Sakhalin Island since about 7,000 years ago (Nechaev 1991). During the early Holocene period (12,000–7,000 years ago) the Tatarsky Isthmus was present owing to its shallowness (minimum depth 8 m). The Sikhote-Alin Mountains, a very long (around 900 km) and wide (about 200 km) barrier, separate Ussuri-Amurland and the continental seaboard. In the current study, we try to evaluate the significance of these barriers for separation of the populations.

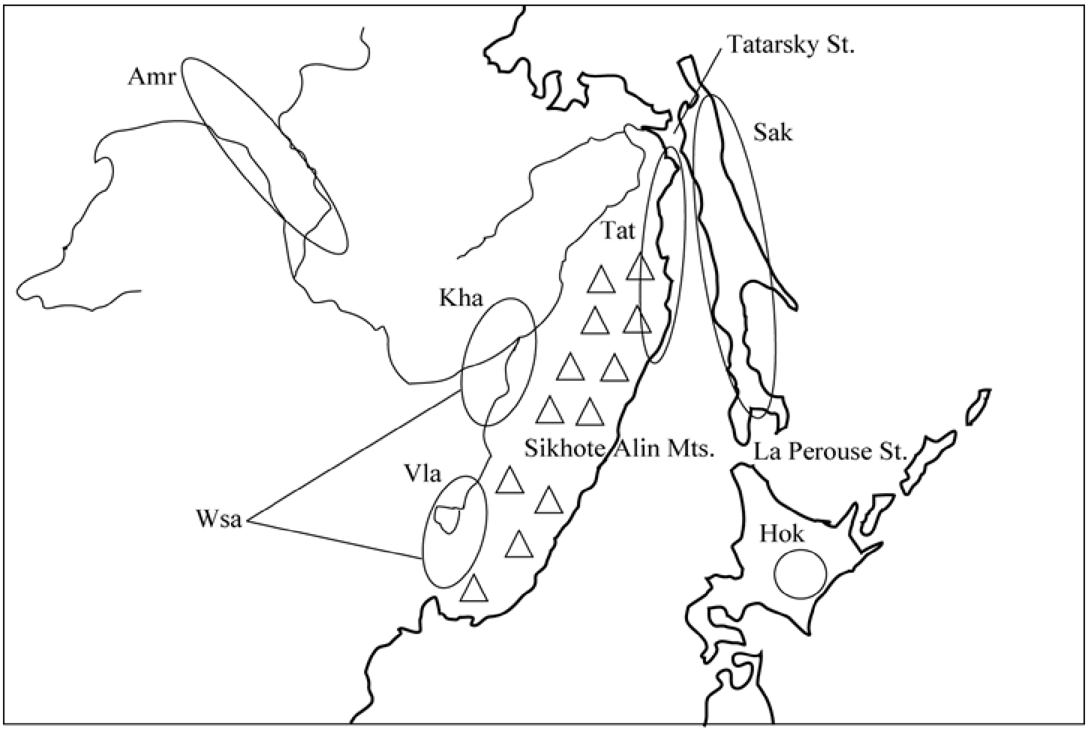

Fig. 1. Map of northeastern Asia. Sampling regions for the five study populations are circled.

Earlier, we identified relationships among five populations from a morphometric approach (Nakamura, Kryukov unpubl). Beside, now we use another nonmetric approach in parallel. In physical anthropology, this approach has proven effective for establishing relationships among human populations. Comparing the incidence patterns of the supraorbital foramen and the hypoglossal canal bridge between 71 populations, Dodo and Sawada (2010) succeeded in depicting the relationships among all major human populations. The results generally coincided with the phylogenetic studies based on mitochondrial DNA (Stringer, McKie 1996, Oppenheimer 2004). Thus, we applied the cranial nonmetric approach in a comparative population study on Jungle Crows. This method was never applied to ornithology before.

In this paper we conducted a nonmetric morphological study on the skull samples collected from five regions in north-eastern Asia. For this, at first we compared incidence frequencies of 10 traits between juvenile and adult sample and found changes accompanying growth of a skull. Then we selected three traits more appropriate for examination of the differences between populations. Finally, we tried to find out any geographic patterns in the incidence frequency between populations for reconstructing the way of the species range settling.

Materials and Methods

Skull samples were collected from five regions (Fig. 1): Hokkaido (northernmost island of the Japanese Archipelago), Sakhalin Island, the continental seaboard (facing the Tatarsky Strait), west and southwest of the Sikhote Alin Mountains (around Khabarovsk and Vladivostok, respectively), and the Upper Amur River. Crow samples from Hokkaido (abbr., Hok) were collected in box traps by the local government in 1989-1990 (Tamada 2004). A list of presumed ages (adult/juvenile) for each specimen was attached to the Hok series. The age estimation was based on inside coloration of upper mandible: adult, black or dark gray without pink; juvenile, largely pink, or a mixture of pink and pale grey (Svensson 1992). This criterion was adapted to crow samples collected in Russian Far East.

Crows collected during the migration season (from October to April) were thought to include contamination by crows from Sakhalin Island (Nechaev 1991). Crow samples from Sakhalin Island (Sak) were collected in June 2007 by the first author, and crow samples from the continental seaboard (Tat) and west and southwest of the Sikhote Alin Mountains (Wsa) were collected in June and July 2009, and from Upper Amur (Amr) in June 2012 by the second author. As a result of differences in the collection methods, the Hok sample series contained a large number of juvenile crows but the other sample series contained very few juveniles. While we collected skull samples, except for Hok collection, we gathered DNA samples for molecular study.

To avoid interobserver error, as suggested by Ishida and Dodo (1990), scoring on skull traits was performed by the first author only. Two kinds of needles (diameter 1.0 and 0.1 mm) were used to estimate the diameter of a hole, the depth of a convex, or the height of a gap. Digital calipers, dividers, and a magnifying glass were used. We preferred 10 traits, as follows: spongy front, joint gap, convex seam, long double sulci, thin process os lacrimale, elastic os palatinum, notched ramus mandibulae, supraorbital foramen (abbr., SOF), septum, and pinhole in parasphenoid bone (PPB; Fig. 2-). The presence or absence of each of the 10 traits was judged using the following criteria:

Spongy front: was recorded as being present if a large number of pinholes (diameter ~0.1 mm or less) were observed in the forehead triangle zone (Fig. 2, in triangle; absent).

Joint gap: was recorded as being present if a clear gap was present along the cranio-bill border with a height difference >0.1 mm (Fig. 2, in rectangle; absent).

Convex seam: was recorded as being present if the seam line of cranio-bill border formed a convex curve posteriad >1.0 mm (Fig. 2, in rectangle; absent).

Long double sulci: two parallel sulci start from the cranio-bill border and run toward the bill top; it was recorded as being present if the length of one or both sulci was longer than half of the breadth of the sulci (Fig. 2, in rectangle; absent).

Thin process os lacrimale: was recorded as being present if the thickness of the process on one or both sides at the ends of the os lacrimale was <1 mm (Fig. 2A, in ovals; absent).

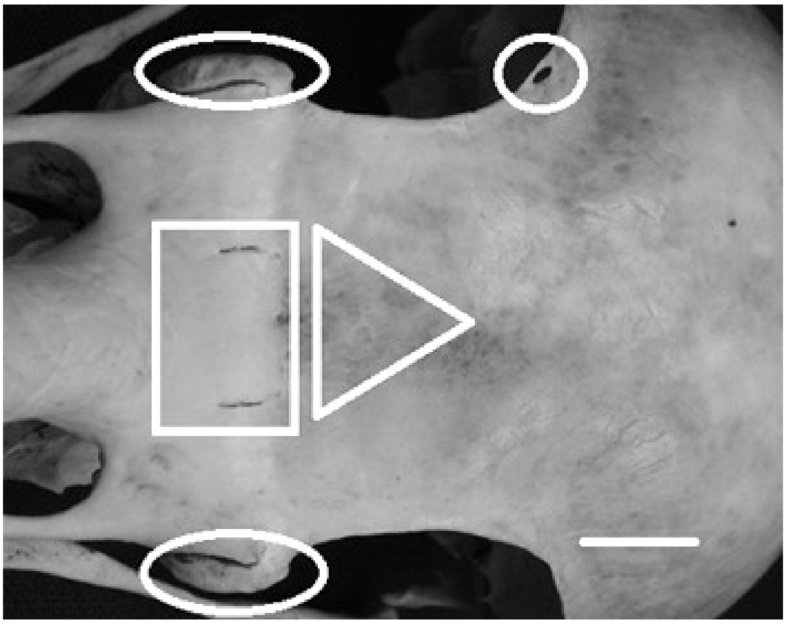

Fig. 2. Plan view focusing on the frontal bone and its neighbors. Process os lascrimale (in oval), supraorbital foramen on the right side of the supraorbital margin (circled), frontal plane (in triangle), and Joint (in rectangle). Double sulci start from the Joint and run toward the bill top (in rectangle). Scale bars equal 5 mm are depicted in each figure.

Elastic os palatinum: the elasticity was estimated as follows: initially holding the skull upright by hand, measuring the length of the os palatinum with the caliper barely making contact, and then holding the skull between the teeth of the caliper with the slightest force and rechecking the length. If the difference between the two measurements was >0.5 mm, it was recorded as being present (Fig. 3, indicated by an arrow).

Notched ramus mandibulae: was recorded as being present if a slit or notch was noted on the inside margin of the ramus mandibulae in the front part of the lower mandible and its depth was >1 mm (Fig. 4, in circle; present).

SOF: was recorded as being present if any foramen on the supraorbital margin opened into the orbital cavity (Fig. 2, in circle; present).

Septum: was recorded as being present if an osseous dissepiment existed in the inside orbital cavity between the foramen opticum and the foramen neuro-ophthalmici (Fig. 5, in oval; present).

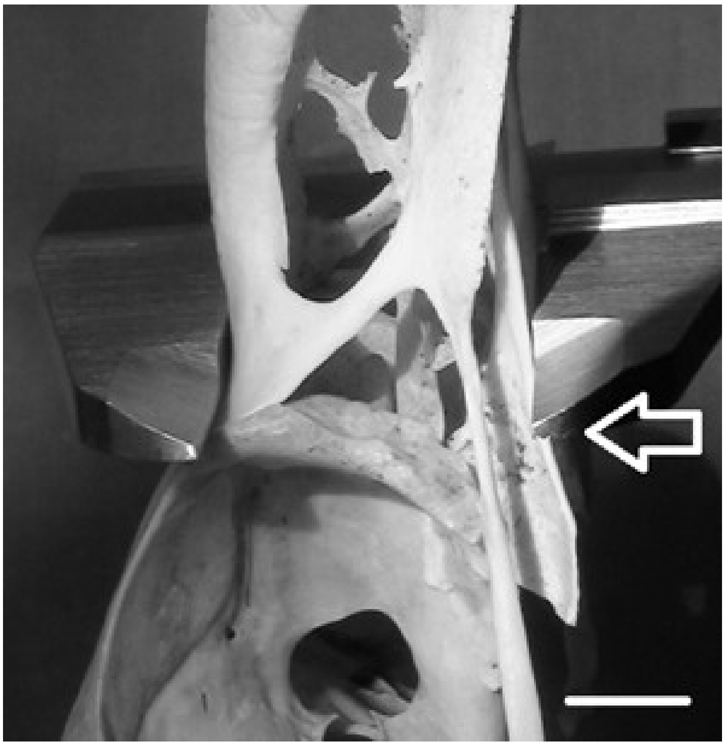

Fig. 3. Right side view, hanging skull with caliper.
Os palatinum (arrow). Scale bars equal 5 mm.

Fig. 4. Plan view of the lower mandible from the upper side.
Bill sheath is taken off. Notch of the ramus mandibulae (circled).
Scale bars equal 5 mm.

PPB: was recorded as being present if there was a pinhole in the parasphenoid bone at the bottom of the cranium near the front end of the lamina parasphenoidalis (Fig. 6, in circle; present). In the cranium of the Jungle Crow, two holes exist on the right and left sides of the parasphenoid bone near the front end of the lamina parasphenoidalis. Each hole is a tuba auditiva (diameter > 1.0 mm). Moreover, some Jungle Crows have a pinhole (nearly 0.1 mm in diameter) on the bottom of the parasphenoid bone, where one tuba auditiva communis is observed instead of two tuba auditivas as in other species (Leliévre 1978; Cracraft 1988; Mayr, Clarke 2003). F.Dzerzhinsky (personal comm.) notes that PPB is not related to the tuba auditiva but represents a rudiment of the embryonic fissura basicranialis anterior, through which a "pocket Ratke" penetrates into the skull and forms adenohypothesis there.

The upper or lower limit of criteria was expedient and set up temporarily. To test for significant differences among populations and sexes, we used the program JMP version 8.0.2.2 (SAS Inc.).

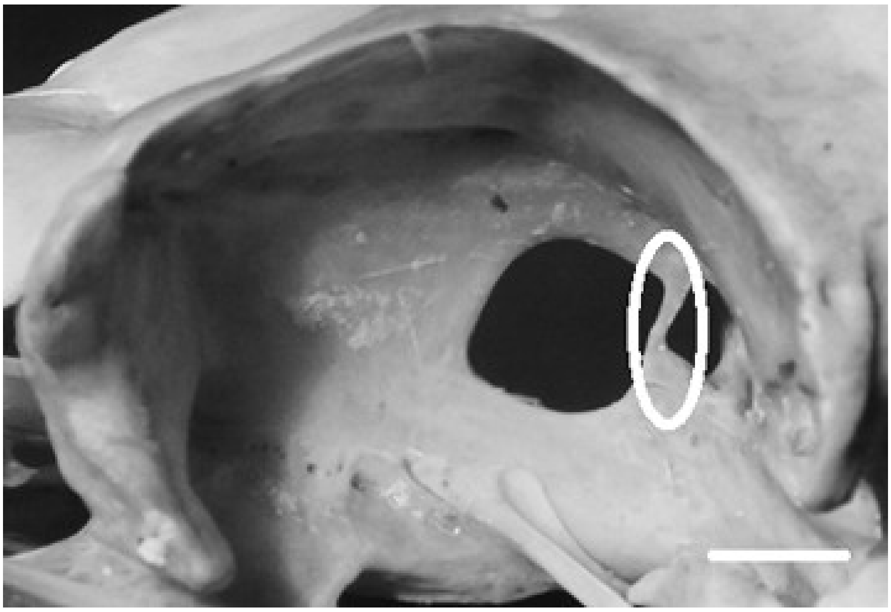

Fig. 5. Left side view of the orbital cavity. Septum (in oval). Osseus dis-sepiments separate from the foramen opticum (left side hole) and the foramen neuro-ophthalmici (right side hole). Scale bars equal 5 mm.

Fig. 6. Dorsal view, Pinhole in the parasphenoid bone (circled). Scale bars equal 5 mm.

Results

Initially we needed to find any appropriate traits for distinguishing juvenile skulls from adult ones and accurate comparisons among populations. In physical anthropology the traits that were observed solely in juvenile skulls were excluded. We compared the juvenile and adult samples of Hok series, because only Hok series contained many juvenile samples. We only examined samples collected in breeding season that were expected to be free from a contamination of migrating Sakhalin crows.

Table 1 presents a summary of the comparison between adult and juvenile skulls for both sexes separately. No significant differences in frequencies were noted between the sexes in either age category. According to their growth patterns, the 10 traits were classified into three groups. The first group included such traits as spongy front, joint gap, convex seam, long double sulci, thin process os lacrimale, elastic os palatinum, and notched ramus mandibulae. The frequencies of these seven traits decreased and reached zero by the adult stage. The second group included SOF and septum, the frequencies of which increased with growth. The third group was PPB. Its frequency did not change from the juvenile to adult stages. In all traits, except for PPB, there were significant differences between adult and juvenile samples (Fisher's exact test, $P < 0.05$).

Table 1. A summary of the comparison between adult and juvenile skulls that were collected in breeding season in Hokkaido.
P: number of crania showing trait (present); **O**: number of crania actually observed.
In a few samples, some traits were not recorded because of damage during cleaning.
F: frequency of occurrence for the trait, in %. In all traits, except for pinhole in parasphenoid bone (PPB), there were significant differences between adult and juvenile samples: Fisher's exact test, $P < 0.05$

Traits	Hok-male				Hok-female			
	Juvenile (n = 18)		Adult (n = 9)		Juvenile (n = 26)		Adult (n = 16)	
	P/O	F	P/O	F	P/O	F	P/O	F
Spongy front	14/18	78	0/9	0	19/26	73	0/16	0
Joint gap	14/18	78	0/9	0	18/25	72	0/16	0
Convex seam	12/18	67	0/9	0	12/25	48	0/16	0
Long double sulci	12/18	67	1/9	11	18/25	72	0/16	0
Thin process os lacrimale	9/18	50	0/9	0	23/26	88	0/16	0
Elastic os palatinum	4/18	22	0/9	0	7/26	37	0/16	0
Notched ramus mandibulae*	2/8	25	0/4	0	4/11	36	0/7	0
Supraorbital foramen	3/18	17	6/9	67	5/26	19	10/16	63
Septum	4/18	22	6/9	67	4/24	17	11/15	73
Pinhole in parasphenoid bone	1/18	6	0/9	0	1/26	4	0/16	0

* Because of bill sheath was not taken off in the Hok specimens, "notched ramus mandibulae" could not be observed clearly in many samples.

All the trait of the first group was vanished according to a progress of ossification. The second group showed different feature. SOF: in some juvenile samples we found a hole in a thin transparent film (periosteum) which jutted out from orbital cavity margin. A frontal diploic vein passed through this hole in human skull (Dodo 1987).This hole would become

SOF when this thin film is ossified. Septum: in the process of ossification, an open window in the boundary of orbitas dwindles and there a stalactite and stalagmite like structure comes out in the upper and under side of the window frame. In some matured samples, dwindling windows were divided by an osseous dissepiment, column like structure. The third group, PPB showed no difference between juvenile and adult skull on appearance.

A comparison among the five crow populations was performed using all of the adult samples that were collected during the breeding season. Among the 10 traits studied, we choose SOF, septum, and PBB because the seven traits in the first group were not observed in adult specimens. Table 2 presents a summary of the comparison of five populations for both sexes separately.

Table 2. Frequencies of three nonmetric cranial traits of adult crows collected from five populations. All of the crows were collected during the breeding season. Between neighboring populations, significant differences were detected using Fisher's exact test. Only four cases were significant. Abbreviations and symbols are the same as in Table 1

Traits	Hok		Hok/Sak	Sak		Tat		Wsa		Amr	
	P/O	F	*P*	P/O	F	P/O	F	P/O	F	P/O	F
Males	(*n* = 9)			(*n* = 34)		(*n* = 19)		(*n* = 16)		(*n* = 18)	
Supraorbital foramen	6/9	67	ns	24/33	73	9/18	50	10/16	63	8/18	44
Septum	6/9	67	*	7/34	21	7/19	37	4/14	29	10/17	59
Pinhole in the parasphenoid bone	0/9	0	***	30/31	97	17/17	100	16/16	100	18/18	100
Females	(*n* = 16)			(*n* = 30)		(*n* = 17)		(*n* = 22)		(*n* = 16)	
Supraorbital foramen	10/16	63	ns	23/30	77	7/16	44	13/20	65	8/15	53
Septum	11/15	73	***	6/29	21	6/17	35	7/22	32	10/16	63
Pinhole in the parasphenoid bone	0/16	0	***	29/29	100	17/17	100	22/22	100	16/16	100

* – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$.

Significant differences between neighboring populations were detected using Fisher's exact test. The populations of Hok, Sak, Tat, Wsa, and Amr are scattered in serial order; therefore, pairings in the tests were Hok/Sak, Sak/Tat, Tat/Wsa, and Wsa/Amr (Fig. 1). None of the tests found significant differences except for four cases in the Hok/Sak pairing (Table 2). The frequency of SOF showed a random and homogeneous distribution among the five populations. The frequency of septum demonstrated a clear difference between Hok and Sak, but no differences existed among the four Russian populations. The frequency of PPB demonstrated a more discrete gap between Hok and the four Russian series than that of the septum. All of the Hok samples were scored as absent regarding PPB and all of the other samples (Sak, Tat, Wsa, and Amr) were scored as present, except for one adult male sample from Sak, which was collected in June in southern Sakhalin (310 km north of the La Perouse Strait). In every population no significant differences were observed in the frequencies between sexes.

We tried to find out any sign of gene exchange between Sakhalin and Hokkaido. To compare the frequency of PPB among all of the Hok samples, we classified them into eight groups by three categories: male and female, juvenile and adult, breeding season and nonbreeding season (Table 3). In every group, no significant differences in frequency were detected between the sexes. During the breeding season, two PPB-present samples were observed among the juveniles: one from 18 males and one from 26 females that were trapped in August in central Hokkaido (290 km south of the La Perouse Strait). During the nonbreeding season, additional PPB-present samples were found in every group.

Table 3. Comparison of the frequency of a pinhole in the parasphenoid bone (PPB) between birds collected during the breeding season and nonbreeding season in the Hokkaido series.
Abbreviations and symbols are the same as in Table 1

Period of the year	Hok-male				Hok-female			
	Juvenile (*n* = 34)		Adult (*n* = 22)		Juvenile (*n* = 38)		Adult (*n* = 35)	
	P/O	F	P/O	F	P/O	F	P/O	F
Breeding season	1/18	6	0/9	0	1/26	4	0/16	0
Nonbreeding season	2/16	13	4/13	31	2/12	17	3/19	16

In addition, we examined 20 juvenile skulls collected in Russia for PPB and we verified the presence of PPB in every juvenile skull. In the four Russian populations, both adult and juvenile Jungle Crows possessed the PPB trait. No significant differences were observed in the frequencies between sexes.

Discussion

Comparison among five crow populations

In physical anthropology, SOF is classified in the hyperostotic category on the basis of its developmental nature and is considered closely related to genetic background (Dodo 1987). The incidence frequency of SOF is relatively independent of environmental conditions, such as diet (Dodo, Ishida 1990, Ossenberg *et al.* 2006). In ornithology, SOF, septum, and PPB have not been studied before and their functions are not known. The four Russian regions in this study (Amr, Wsa, Tat, and Sak) are distributed in an approximately longitudinal direction and their climate types change steadily from a severe continental climate to a mild oceanic one (Fig. 1).

The measurements in a cranial metric study showed a longitudinal cline (our unpubl. data). However, the frequency distributions of SOF, septum, and PPB did not show any clines, but randomness or constancy instead (Table 2). This difference suggests that in Jungle Crows, these three traits serve a little adaptive function if any.

Table 2 shows that almost all of the statistical tests found no significant differences, except between the Hok and Sak populations. For these populations, significant differences were noted in septum and PPB in both sexes simultaneously. If the manifestation of septum and PPB is related to genetic background, then do these clear differences indicate that the Hokkaido and Russian populations belong to different lineages? Despite the absence of a significant difference in SOF between Hok and Sak, we suggest that they do. Among the five populations, the incidence frequencies of three traits demonstrated different patterns: SOF was homogeneous to some degree, septum was highly variable, and PPB was the same among all of the Russian populations, which were clearly different from the populations in Hokkaido. We consider that the degree of gene expansion is responsible for these differences: the appearance of SOF reflects an old event and this trait is now widely distributed; otherwise it may represent the ancestral state of this feature. In contrast, the appearance or disappearance of PPB was the most recent event and at present, this trait is found only in limited regions or one region. The geographic patterns in the incidence frequencies for septum and PPB do not support drawing a border between two recolonization movements around central Sakhalin or across the Tatarsky Strait but implies such a border across the La Perouse Strait. A craniometric study that we conducted reached the same conclusion (our unpubl. data).

Seasonal change in PPB in Hokkaido population

The frequency of PBB did not change from the juvenile to adult stages. It seems likely that this trait is completed in early stages of growth, i.e. pre-fledgling stage.

Winter migrations from Sakhalin Island to Hokkaido were suggested by Nechaev (1991) and observed by Ueta (2008). In view of the considerable number of Sakhalin crows that migrate to Hokkaido during the non-breeding season, the influx of PPB-present crows from Sakhalin Island probably has caused an increase in the frequency of PPB (Table 3).

During the breeding season, the existence of three unusual samples (two PPB-present Hok juveniles, Table 1, and one PPB-absent Sak adult male, Table 2) cannot be ignored. The two PPB-present juveniles from Hokkaido were collected in August, and they were therefore 2-3 months old. Even though they bore the PPB trait, it is unlikely that they were born in Sakhalin Island and flew across the La Perouse Strait (width

42 km). We hypothesize that they were born in Hokkaido from a PPB-bearing parent or parents. The PPB-absent adult on Sakhalin was collected during the breeding season; consequently, it had a chance to breed there. These observations may be considered as an evidence of introgression between the two island populations in both directions.

Discordance between nonmetric craniological and phylogenetic approach

Our nonmetric craniological approach presumes the existence of two distinct groups: Russian group and Japanese group both face each other across the La Perouse Strait. But our molecular phylogenetic approach (Kryukov *et al.* 2012) demonstrates another feature: Jungle Crows show a low level of differentiation throughout its range. Almost all mitochondrial sequences are united in one phylogenetic group without major substructuring with only one exception concerning the population of the Cheju Island. All haplotypes are weakly divided into two groups – mainland and island groups. Within Sakhalin we found no pronounced genetic differentiation, neither between Sakhalin and Hokkaido.

We consider that this discordance is induced by two factors, a difference in nature of approaches and a peculiar situation of Jungle Crows under climatic oscillation in Pleistocene.

In general, morphological traits are overlaid with the newest modifications upon the old ones which are eliminated entirely. Any trait conserves the latest reconstructions. Morphological presumption is effective only about the Holocene event, but would not be a powerful tool to assume an event of pre-LGM period. On the contrary in genetic approach, any mutation is conserved cumulatively and equally in mtDNA: there is no discrimination between the newest mutations and the old one. Present geographical distribution of haplotypes reflects all the changes of spatial distribution and gene exchange that happened in the past, not only in the Holocene but also including the Pleistocene.

Ecological demands for breeding of Jungle Crows and geographical character of refuge area is another factor. In repeated glacial periods of the Pleistocene, Jungle Crows had to retreat from the northern frontiers and were forced to survive in southern refuges. Compared to related species Carrion Crows *Corvus corone*, Jungle Crows prefer a highly concealed nest site in the forest and need a milder climate because their just hatching nestling is stark naked (Nechaev 1991, Miyazaki 2009). In the case of Carrion Crows it can nest in sparse forest, even in isolated deciduous low tree in open land and their just hatching chicken is covered with down. In every region the hatching of Jungle Crows occurs later than that of Carrion Crows, ca.2 weeks in the North (Nechaev 1991) and ca. 4 weeks in the South (Tamada, Fujimaki 1993, Nakamura 2000). As a result, Carrion crow could reach as far to the North in its distribution as Chukotka peninsula at present. Therefore, it seems likely, the refuge of Carrion Crow would include relatively more cold and dry habitat than that of Jungle Crows. During ice age a vast plain emerged from the continental shelf of East China Sea owing to a descent of sea level. Korean-Tsushima Strait changed to a narrow stream/isthmus and lost its role of geographical barrier. As a result there appeared one united refuge: southern Korea, East China land and southern Japan (Ohshima 1990). Optimum habitats for Jungle Crows spread along the seacoast of Southern Japan and East China land (Ray, Adams 2001). This geographical configuration made possible to exchange gene between mainland and island group. When the ice age ended, the East China land and the isthmus disappeared. Then the two groups were isolated and the expansion of distribution range began. And when the next ice age started, the gene reshuffling process was repeated. It seems likely that this scenario could explain the phylogeographic special feature of Jungle Crows: a low level of variation and differentiation due to ancestral polymorphism supported by gene flow between populations.

Conclusions

The powerful high and large bill of Jungle Crow is well adopted to use different kinds of hard food such as nuts and seeds, braking tree branches in agonistic behavior, etc. So the most of the features under our study should be related to such adaptations. However our approach was concentrated on revealing geographic variation along limited set of populations. Our finding of the difference between Hokkaido and Sakhalin crow populations by such tiny cranial features as shape of septum and pinhole in parasphenoid bone, even though the adaptive functions of these traits are unknown at present, implies a border of two recolonization waves in Holocene periods. Further complex morphological, ecological and genetic studies are needed to better understanding such processes.

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Summary

Jungle Crow *Corvus macrorhynchos* Wagler, 1827 is widely distributed in East Asia, but no so far to the North. It requires dense forest and rather mild climate for breeding, therefore during the ice ages they vacated around the Japan Sea Rim in favor of southern refuge located around the East China Sea. After the Last Glacial Maximum, Jungle Crows began to recolonize the north-eastern Asia presumably via two routes: one via the Japanese Archipelago, and the other via Ussuriland (Nechaev, 1971). This might lead to appearance of two subspecies: *C. m. mandshuricus* and *C. m. japonensis*. We attempted to find out any new features in purpose to reveal a place where these two recolonization movements have encountered. Detailed analysis

of delicate differences in the skulls of five populations of Jungle Crow from Primorsky, Khabarovsky, Amur regions, Sakhalin and Hokkaido islands was conducted. Based on 197 cleaned skulls, 88 from females and 109 from males, we determined incidence frequencies for 10 characters which provide adaptations of the species' strong bill. 7 features were revealed in juveniles only, frequency of the two others change during the life, and for the remaining stay stable. No difference between males and females was found. For frequencies of pinhole in parasphenoid and septum shape in orbital cavity, we found a significant difference between Hokkaido and Sakhalin populations, while for all other characters studied and between other populations, differences were not significant. The results obtained do not correspond neither to subspecies subdivision for *C. m. mandshuricus* and *C. m. japonensis*, nor to previous genetic data by mitochondrial cytochrome B gene which revealed an island and mainland groups of haplotypes (Kryukov *et al.* 2012). In the same time, as a result of using the phenetic (nonmetric morphological) study on the skull, we show that two movements encountered at the La Perouse Strait. Furthermore we found an indirect evidence for current introgression between Sakhalin and Hokkaido populations.

Фенетический анализ черепа выявляет различие популяций большеклювой вороны *Corvus macrorhynchos* Хоккайдо и Сахалина

С.Накамура, А.П.Крюков

Большеклювая ворона *Corvus macrorhynchos* Wagler, 1827 широко распространена в восточной Азии, но не заходит далеко на север. Для гнездования ей необходима древесная растительность, и под воздействием ледников из-за деградации лесов она была оттеснена предположительно в бассейн Восточно-Китайского моря. После максимума последнего оледенения она расселилась на север предположительно двумя путями: вдоль материка и через Японские острова (Нечаев 1971). С этим связано наличие двух подвидов: *C. m. mandshuricus* и *C. m. japonensis*. В попытке найти новые признаки, чтобы определить место встречи этих волн расселения, проведён анализ тонких различий в строении костей черепа у пяти популяций большеклювой вороны из Приморского и Хабаровского краев, Амурской области, Сахалина и Хоккайдо. На отпрепарированных 197 черепах, 88 от самцов и 109 от самок, определены частоты проявления 10 признаков, обеспечивающих адаптивность мощного клюва данного вида. Из них 7 признаков проявляются только у птенцов, частота двух меняется с возрастом и для одного остаётся постоянной. У самцов и самок признаки проявляются одинаково. По частоте встречаемости булавочного отверстия в парасфеноиде и перепонки в межглазничной перегородке обнаружено значимое различие между популяциями Сахалина и Хоккайдо, тогда как по другим признакам и между остальными парами популяций различия статистически незначимы. Полученные результаты не совпадают ни с подвидовым делением на *C. m. mandshuricus* и *C. m. japonensis*, ни с полученными ранее генетическими данными по митохондриальной ДНК, выявившими островную и материковую группы гаплотипов (Kryukov *et al.* 2012). В то же время, результаты применённого неметрического морфологического (фенетического) популяционного анализа черепа позволяют локализовать место встречи двух волн расселения в районе пролива Лаперуза, хотя современный поток генов нивелирует эти различия.

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