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Bachurin G.N., Kapitonova L.V. (2014) Aspects of biological compatibility between the Oriental cuckoo *Cuculus (saturatus) opatus* and its host species on Sakhalin Island, Russia // *Far East. J.Orn.* 4: 42—56.

SUMMARY

We conducted an analysis of the ecological compatibility the Oriental cuckoo with known and potential host species on Sakhalin Island, and compared oological parameters of this brood parasite and its hosts on both the mainland and island regions of the Russian Far East. Variation of oological parameters of Oriental cuckoo and host eggs were examined here for the first time. We documented fundamentally-similar egg coloration among Oriental cuckoo and Pallas's leaf warblers, which supports the assertion by N.N. Balatskii that there is a distinct race that parasitizes Pallas's leaf warbler nests. The high level of similarity among Oriental cuckoo eggs collected from the mainland and island regions of the Russian Far East reflects broad parasitism of this shared host species, and is evidence of the common origin of these populations.

The referred figures and tables are in the original article in Russian, pp. 42—56

The reproductive biology of the Oriental cuckoo *Cuculus (saturatus) optatus* is poorly understood despite the species' wide distribution in the Palearctic and locally-high population size. Specific data are only known from a handful of locations and most information was collected by chance or tangentially to another research project.

The breeding success of the Oriental cuckoo and other obligate nest parasites depends on the degree of biocompatibility with its host species. Important compatibility parameters include a high nesting population of the host species, nest accessibility for egg-laying by cuckoos, and the duration of the reproduction period, among others. This determines regional and geographical specificity in the selection of primary host species (Numerov, 2003). Another important element of biocompatibility is a phenomenon common among cuckoos of the *Cuculus* genus: intraspecific differentiation by egg coloration - that is, the ability of females of one species to produce eggs of a different color, thereby copying the egg color of the primary host species. This biological attribute was the basis of intraspecific division of cuckoos into biological races (Malchevskii, 1958) which are referred to as "gens" (plural is "gentes;" Jourdain, 1925). However, no universally-accepted opinion has been produced to date either regarding the mechanisms of formation and maintenance of gentes, or in terms of a clear definition of the concept of «race» in relation to cuckoos. The reason for this incongruity is the lack of targeted studies (including genetic) and, consequently, the lack of regional egg collections. There are two hypotheses to explain the similarity of egg coloration of brood parasites and their host species. First, that the similarity is based on inheritance at the population level (i.e., resulting in gentes of cuckoos within a species), and second that the match between egg color of brood parasite and host was random and without any evolutionary influence (Malchevskii, 1987).

Supporters of the ecological view of gentes consider the possibility of division not by the color of cuckoo eggs, but by the primary host species (Numerov, 2003). In this case, the gentes indicator is dictated by the host species dominant in a region. It should be a species tolerant of brood parasite eggs of any color and be able to successfully raise its offspring.

Kislenko and Naumov (1967) suggested that ecological gentes of cuckoo should be divided based on the type of egg coloring, specifically: (1) those

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with «brown spots» (which are typical for Common chiffchaff *Phylloscopus collybita* of Western and Central Siberia); (2) those with «red spots» (which are typical for Arctic warbler *Ph. borealis* and Yellow-browed warbler *Ph. inornatus* of Eastern Siberia and the Russian Far East); and (3) those with completely white eggs (which are typical for eggs of Two-barred greenish warbler *Ph. trochiloides*, Pale-legged leaf warbler *Ph. tenellipes*, Eastern crowned warbler *Ph. coronatus*, and Dusky warbler *Ph. fuscatus* of the Russian Far East. This nomenclature was adopted by a number of Russian scientific papers (e.g., Malchevskii, 1987; Nechaev, 1993; Numerov, 2003). It should be emphasized that the first two types (brown spot, red spot) are documented, but to date no reliable data regarding the «white gents» of Oriental cuckoos have been uncovered[1].

Balatskii (1998) offered a more fractional approach, allowing for the existence of distinct gentes of Oriental cuckoo parasitizing, in particular, Pallas's leaf warbler *Phylloscopus proregulus* and Yellow-browed warbler. We, in the views on the nature of gentes formation in the Oriental cuckoo, adhere to the genetic approach and interpretation of the concept of gentes as an independent population unit characterized by specific egg coloring that was inherited as a discrete feature. Discreteness implies the existence of certain limits of the variability range of egg coloration elements inside each gens, and that there is no overlap of range between gentes.

The vast majority (82.9%) of eggs and chicks of the Oriental cuckoo discovered in the Russian portion of its global range were concentrated to 10 species of the *Phylloscopus* genus (Numerov, 2003), indicating that warblers are its primary host species. Data published from the mainland of the Russian Far East detailing specifics of reproduction and egg morphology of the Oriental cuckoo have been collected by various researchers in southern Primorskii Krai and the Bikin River on the western slope of the Sikhote-Alin Mountains (e.g., Malchevskii, 1987; Balatskii, 1991, 1997; Mikhailov and Balatskii, 1997; Numerov, 2003), however not all these records have been confirmed by collection materials.

On Sakhalin Island, four bird species are known to be parasitized by the Oriental cuckoo: Pallas's leaf warbler, Arctic warbler, Dusky warbler, and Masked bunting *Ocyris (spodocephala) personata*. Nechaev (1991) collected eggs and provided morphological characteristics. Our material here allows for an expansion of what is known about the reproductive biology of Oriental cuckoo on Sakhalin Island. In particular, we give a description of eggs found in nests of previously-unknown host species, and consider aspects of cuckoo biocompatibility with these species. Our data also allows for a comparative analysis of oometrical characteristics of brood parasites and their host species.

MATERIALS AND METHODS

Studies were conducted in June and July of 2008-2009 in the Nogliki, Tymovskii, Makarovskii, Dolinskii, and Aniva Counties of Sakhalin Island (Fig. 1), areas that contain habitat representative of the entire island. We selected sites by surveying for areas with local concentrations of Oriental cuckoo. In locations with the greatest number of females, nest searches were conducted with an emphasis on known and potential host species. In total, we found 127 nests of seven species of passerines at different stages of the nesting cycle (Table 1). Eggs of Oriental cuckoo were found only in Radde's warbler (two nests with one egg in each nest) and Yellow-browed warbler (one nest with one egg). We also examined eggs found by other researchers on Sakhalin: V.N. Sotnikov (one egg in a Dusky warbler nest, 2006), S.F. Akulinkin (1 egg from a Yellow-browed warbler nest, 2009), V.A. Nechaev (3 eggs, various years). We also gathered information about eggs collected from the oviducts of female Oriental cuckoos collected by Y.A. Redkin (2009; N = 9).

We used Bachurin (2011) as a reference for Oriental cuckoo eggs; these were eggs collected from the Russian Far East mainland. The eggs found during our research (and those collected by V.N. Sotnikov and S.F. Akulinkin, described above), are listed in this publication as well. The only egg measurements not directly taken by us came from Nechaev (1991) and

1) The only confirmed, fully-white egg of an Oriental cuckoo known to us was found in the nest of a Common chiffchaff in 1963 by S.P. Chunikhinii in southern Siberia (Salairskii Ridge). It was among a clutch of three host eggs. This egg, part of Y.P. Spangenberg's collection, is now housed in the Zoological Museum of the Siberian Branch of the Russian Academy of Sciences in Novosibirsk. In our opinion this instance should be considered an anomaly due to, for example, a pigment deficiency.

Balatskii (1991, 1997).

Only fully-developed clutches were used for comparative analysis of egg coloring. Newly-laid eggs typically appear pinkish-yellow-translucent due to the presence of moisture in the shell which emphasizes the yolk (much like transparent wax paper). The spots, especially those located deep in the shell, are emphasized and appear more saturated. This effect disappears during incubation and gradual moisture evaporation from the shell. Then, the background turns white, and spots, especially the internal ones, fade. Similar changes occur in museum collections when a shell is dried for the purposes of long-term storage.

Oriental cuckoo eggs (as compared to other cuckoo eggs) can be visually identified with great confidence due to their elongated oval shape. Furthermore, Balatskii (2003) reported one hundred percent accuracy of species identification by measuring dry weight of the shell. For Oriental cuckoos, egg weight varies from 0.08-0.15 g and did not overlap the minimum threshold (0.19 g) of the dry weight of an Eurasian cuckoo egg shell. We determined if different eggs belonged to the one or more females by comparing the dry weight of shells, and the size, shape, and color of eggs. As we were not focused on species surveys, data concerning relative abundance of Oriental cuckoo host species were based on data from Nechaev (1991). Pairs/km2 were estimated based on the number of singing males, rather than the number of potential nesting sites. It is worth noting however that in species with «unconventional» mating systems (such as warblers) the number of singing males may not be a reliable indicator of breeding pairs.

Bird names in the original Russian follow (Koblik et al., 2006), whereas this English translation follows Brazil (2009).

RESULTS AND DISCUSSION

The Oriental cuckoo is a common breeding species on Sakhalin Island. It is distributed broadly across the island and inhabits various forest types, but prefers coniferous-birch and conifer plantations at different altitudinal zones, as well as trees and shrubland in places where coniferous and mixed forests overlap (Nechaev, 1991). According to our observations, the species tends to have an uneven distribution. The highest density we observed was in the wide floodplains of the central part of the island and in the coniferous and mixed forests on the slopes of the middle portion of the island. This species is very poorly represented or almost completely absent along the coast.

We propose that the distribution of the Oriental cuckoo can be determined not only by the distribution of potential host species, but also by trophic specifics of the brood parasite. As such, along the coast of Lunskii and Chaivo Bays, where the Dusky warbler is quite common (including in areas of Japanese stone pine) and where Pallas's leaf warbler is ubiquitous, Oriental cuckoos only appear in appreciable numbers some 10-20 km from the coast. Perhaps this is explained by the more severe climatic conditions of the coastal and mountainous areas of Sakhalin, which adversely influence insect species composition and abundance (preferred food of the Oriental cuckoo). The milder climate of central Sakhalin, in tandem with the region's greater variety of forest types, floodplains, and undulating mountain slopes, provide the best conditions to foster high densities of passerines, including those warbler species that Oriental cuckoos parasitize.

Territory use, sex ratio, and the relationship between males and females of the Oriental cuckoo are not well understood. Apparently, they are in many respects similar to descriptions found in Numerov (2003) of the obligate nest parasite Eurasian cuckoo.

In different parts of Sakhalin, where the Oriental cuckoo is common or relatively rare, during the breeding season males and females live in habitats typical for their primary host species. The home range of females is determined by the nesting density of specific host species. All common species of the Sakhalin *Phylloscopus* warblers, in our opinion, have a tendency to form nesting aggregations. The presence of dense nesting groups of the primary host species is undoubtedly a positive for Oriental cuckoo. This reduces females' energy consumption when searching for nests, when synchronizing maturation of eggs with the start of egg laying in the host species, and when defending a territory: all these characteristics generally improve breeding success. According to our observations, the area where a female Oriental cuckoo concentrates her egg-laying overlaps with one or more such nesting areas of warblers, and rarely

exceeds 200-300 m in diameter.

An extended breeding period of a host species is one of the most important factors determining the success of parasitism of Oriental cuckoo on that species. The breeding season of Dusky and Radde's warbler Phylloscopus schwarzi, based on the nests found on Sakhalin (Nechaev, 1991), falls from mid-June to mid-July, and for Pallas's leaf warbler: the first ten days of June to the end of July. Such a protracted breeding period in a species with a monocyclic system of reproduction can be explained by the late start of breeding of birds nesting for the first time and also by repeated egg-laying after the destruction of first clutches. The fact that some warbler species exhibit polygynous mating behavior apparently contributes to the length of nesting period as well.

Overview of host species of Oriental cuckoo

Of the eight species of warblers recorded on Sakhalin Island (Nechaev, 1991), five of them (Arctic, Yellow-browed, Pallas's leaf, Dusky, and Radde's warblers) can be considered suitable Oriental cuckoo host species. Two warbler species (Two-barred greenish and Eastern crowned warblers) can only be regarded as random hosts due to the localized distribution and low densities of those birds on Sakhalin. One species (Sakhalin leaf warbler Ph. borealoides) is an unlikely host due to the difficulties of nest accessibility for cuckoos[2]. The following is an overview of each host species of Oriental cuckoo on Sakhalin Island in terms of biocompatibility.

Pallas's leaf warbler

In our opinion, this is one of the most abundant and widespread of Oriental cuckoo host species on Sakhalin Island. It is found throughout the island and in all forest types, with the exception of coastal regions dominated by Japanese stone pine, continuous and extensive tracts of burnt forest, and wetlands. The population density of this species in the most suitable habitats (mainly in coniferous and mixed forests of varying densities, both in flatlands and on mountain slopes) is so high that according to our data, from one survey point we could hear up to 10 singing males. According to Nechaev (1991), the largest number (10-15 pairs/1 km of survey route) was detected in coniferous and birch-coniferous forests and «less than 5 pairs» in stone-birch forests with a mixture of conifers and small-leafed lowland forests. Our data support Nechaev's (1991) assertion that the lowest densities were in secondary small-leafed forests and forests of broad floodplains, although they are evenly distributed there.

Pallas's leaf warbler was considered a host species of Oriental cuckoo by Nechaev (1991) based on two discoveries: 1 egg on the Onor River on 25 June 1977 and 1 chick in the vicinity of the city of Yuzhno-Sakhalinsk, on 12 August 1972.

According to our data, the relationship between Oriental cuckoo and Pallas's leaf warbler is stable and uniform across most of the island. This is confirmed by numerous observations of territorial Oriental cuckoo females lingering near Pallas's leaf warblers and in an absence of other potential congeneric host species.

Pallas's leaf warblers exhibit considerable variation in height of nest placement in relation to ground level, from the shrub layer to the tops of tree crowns. Nechaev (1991) provided data on nest height and found the mean height was 2.35 m (range: 0.55-10.0 m; N = 28). Our data complement this data: we found a mean nest height of 2.60 m (range: 1.20-6.50 m; N = 16).

The extent that Oriental cuckoos parasitize Pallas's leaf warbler nests may be underestimated due to the difficulties associated with finding these nests to sample. They are small, concealed, and often placed high off the ground.

The nuances of mating behavior and habitat use by Pallas's leaf warbler have been poorly studied. We collected data that can be considered indirect evidence of polygynous mating in dense congregations of Pallas's leaf warbler on Sakhalin Island. Here we provide an example from the Listvennitsa River in Dolinsk County: there, in a small valley covered by Kuril bamboo ~ 1.75 m tall located between the floodplain and floodplain terraces of pine forest, we found a cluster of 4 nests of this warbler species. Three nests were located at a distance of 30-40 m from one another and one more at a distance of about 80 m. On opposite sides of this group, higher on the hill slopes, we heard two males singing. The first was on the

2) According to Nechaev (1991), the Sakhalin leaf warbler is a common nesting species in specific habitats of southern and central Sakhalin Island (with up to 5 pairs/1 km of survey transect), but its nests are poorly accessible to Oriental cuckoo given their location in deep crevasses of cliffs and banks among rocks and roots

edge of the floodplain terraces and bamboo plain, at a distance of 100-200 m from the nests, and the second was on the opposite side of the river, at a distance of 300-350 m. Biserov (1999) described a similar, very dense cluster of three nests of Pallas's leaf warbler on a 0.5 ha site in Bureinskii Nature Reserve, where the distance between active nests was 25-30 m. The probability of polygyny, and the tendency for Pallas's leaf warbler to form breeding groups, can make this species an attractive host for Oriental cuckoos.

Descriptions of Pallas's leaf warbler egg coloration vary by author, but the presence of reddish spots is the most common. Ptushenko (1954) described the eggs as white and covered by «small violet-gray and red-brown spots and dots scattered randomly at the sharp end of the egg, and tightly concentrated at the blunt end." Balatskii (1997) noted the uniformity of Pallas's leaf warbler and Oriental cuckoo eggs from the upper reaches of the Bikin River and gave the following description: «the base color is white with a cream tint....the whole egg is covered by a brownish-red surface with small, deep rosy pink and gray spots, and speckles and dots of irregular shape.»

We examined eggs from Pallas's leaf warbler on Sakhalin Island and found that they were practically the same as the eggs of this species from Khabarovskii and Primorskii Krais on the mainland. Shells had a white base color, with surface stains that were brightly expressed and had at least two layers of different intensities: in our opinion reddish-brown (almost chestnut brown[3]). The color of spots located within the shell ranged from pale pink to pale gray, depending on the depth of the stain. In newly-laid eggs the stains appeared more saturated and gave the eggs a more reddish appearance.

The shape and size of these and other spots in eggs of various clutches and, to some extent, within a clutch varied from very small (almost a dot) to relatively large (1.5-2 mm) and expansive. The proportion of spots, variation in depth (internal and surface), and dimensional characteristics (large and small) of different clutches could be quite different. Their distribution on the surface of the shell could also be different: they were either disperse (with intensification at blunt end, or formed a dense cluster in the form of a halo. In general, the pattern of spotting on the shell had a stable color: it was largely constant in different clutches and is a species-specific feature (Fig. 2). No other warbler species has such a broad spatial distribution on Sakhalin. Other species are tied to specific habitats where they may form dense settlements and, depending on the location, can be considered ubiquitous. But when the entire island is considered, all species are outnumbered by Pallas's leaf warbler.

Dusky warbler

This species occurs mainly in the northern and central regions of Sakhalin. It is common in all types of open spaces, from coastal to alpine Japanese stone pine. It inhabits shrub and grass-shrub thickets. In some places the numbers can be high—up to 30 pairs/1 km of survey route (e.g., on the coasts of Chaivo and Piltun Bays (Nechaev, 1991). Nechaev (1991) described an observation of a Dusky warbler feeding fledgling Oriental cuckoos near Cape Maria (on the Schmidt Peninsula) on 10 August 1976. In the area adjacent to Chaivo, (the Shivchibin River, a right tributary of the Bolshoi Garomai River), on 02 August 2006 a nest with Dusky warbler fledglings was found during surveys. There was a whole Oriental cuckoo egg in the nest (V.N. Sotnikov, pers. comm.).

We failed to obtain direct evidence of brood parasitism by Oriental cuckoos of Dusky warblers, but our repeated discoveries of locations with high concentrations of both species with a complete lack of (or poor representation by) other potential host species for cuckoos can be construed as evidence of an obvious connection. Such a case was noted in post-burn forests with tall Labrador tea thickets on the floodplain of the Tym River. During two field seasons near the Bauri River, a female Oriental cuckoo was regularly observed at a site overgrown with Alder by a train track and bordered by larch swamp. The concentration of Dusky warblers there in both years was no less than 10 pairs, and other warbler species were practically absent (only one singing male Pallas's leaf warbler and an Arctic warbler were detected).

Most nests of Dusky warblers were discovered by us during the nest-building phase or shortly before egg laying. The location of these nests, and the entry paths to them within a shrub, would not likely hamper access by a brood parasite.

3. The brown tint is more characteristics of another representative of the Phylloscopus genus: the Common chiffchaff Ph. collybita.

Our observations allow us to consider Dusky warbler as a convenient host species for Oriental cuckoos in disparate locations in the northern part of Sakhalin Island.

Arctic warbler

This species is distributed in the northern and central regions of Sakhalin Island in sparse coniferous and mixed forests, plains, and mountain slopes. It prefers deciduous forests with birch and shrubs, the edges of mixed forests, overgrown post-burn forests, and places of deforestation. Nechaev (1991) recorded 4-5 pairs/1 km of survey route. In our opinion, Arctic warbler is most common in damp riparian forest floodplains. Individuals of this species often nest at considerable distances from each other but they occasionally form loose groups of several nesting pairs. Nesting territories are generally large in size. Nests on Sakhalin, as in other parts of species range, are located low to the ground and are quite difficult to find. Nechaev (1991) gave a description of only one nest, found on 12 July 1979, in the Bolshoi Uangi River valley (along the northwest coast of the island). It contained a recently hatched clutch of 4 eggs of the host, and a single egg of an Oriental cuckoo.

The Arctic warbler is considered a host species for Oriental cuckoo in Japan (Austin and Kuroda, 1953; Royama, 1963; cited in Kislenko and Naumov, 1967). During the course of two field seasons we found only two nests of the species despite its high abundance in those locations. The first nest was found in Nogliki County in the coniferous forest floodplain of the Yasynge River on 26 June, 2008. A female was actively constructing it. The nest was shaped like a sphere and attached to the side of a mossy, fallen tree trunk. The nest was almost complete but still lacked an inner lining. The nest was constructed with pieces of split stems and bast fibers as well as a lot of green moss. The second nest was examined on 20 July, 2009 in Tymovskii County. It had been built on the slope of an overgrown ditch in a floodplain of alder-willow forest on the left bank of the Tym River. The clutch contained 5 fresh eggs. Egg size (mm) was as follows: 20.2 x 13.0; 20.6 x 13.0; 20.5 x 12.9; 20.2 x 13.1; 20.7 x 12.8; 20.7 x 13.4. The base color of these shells was pure white. The pattern was formed of pale spots of varying intensity and concentrated in a halo on the blunt end. Deep spots were of a pinkish color while surface spots were a bright, brick-red color with a slight reddish shade (Fig. 2). The nest was made of vegetable matter—pieces of stems and green moss—and was difficult to distinguish from the surrounding substrate. The entrances to both nests were obstruction-free and quite convenient and accessible for a cuckoo. This species has been documented by Nechaev (1991) as certainly a host species for Oriental cuckoos, and it is widespread on Sakhalin. However, we tend to consider it a secondary host species for Oriental cuckoo for two reasons: first, Arctic warbler nests are found at extremely low densities, and second, the warbler nests are well concealed.

Yellow-browed warbler

This species was identified as an Oriental cuckoo host species on Sakhalin Island for the first time by this study. According to Nechaev (1991) this is a rare breeder in northern Sakhalin, with nesting confirmed only by the presence of fledglings along the northwest coast of Sakhalin in the Tenga River valley (on the Schmidt Peninsula). More recent data shows that the species' nesting range extends considerably further south on the North Sakhalin Plain, to the left bank of the Tym River (and possibly further south; O.P. Valchuk, V.N. Sotnikov, unpubl. data).

Yellow-browed warbler nesting clusters are found in larch and birch floodplain forests with creeping alder and Labrador tea in the understory, most often along the edge of a wetland with scattered tree stands. A cluster of 5-6 pairs was located at the edge of a wetland in a secondary alder-willow forest with sparse larches. One nest was found on the ground near a trunk of an alder under the thin layer of dry grass; the entrance was open and stretched horizontally with dimensions 37 x 45 mm, oriented to the north. There were 7 hatchlings in the nest, not more than a day old, and under them was an Oriental cuckoo egg with an embryo younger than 2 days. It was probably laid at the last day of incubation; most likely the brood parasite was forced into doing this, possibly due to the destruction of a nest where it had planned to lay eggs. Around this nesting cluster we observed two males Oriental cuckoos and several singing males Dusky and Arctic warblers, and one male Eastern crowned warbler.

Another Yellow-browed warbler nest with an Oriental cuckoo egg was found by S.F. Akulinkin on

09 July 2009 in a floodplain of tall larch forest near the village of Val. The nest was located on the ground among dense moss. The nest depression contained three thoroughly-incubated eggs of the host and a single egg of the brood parasite with an embryo lagging in development behind the host embryos by 4-5 days (It was laid in a fully-incubated clutch).

On the mainland in the Russian Far East, the Yellow-browed warbler is considered a host species for Oriental cuckoo based on a discovery in the upper reaches of the Bikin River (on the western slope of the Sikhote-Alin Mountains; Balatskii, 1997). Yellow-browed warbler seems to be a good and prospective host species for Oriental cuckoo given that it appears to be expanding its range on Sakhalin Island, tends to nest in clusters, and has simple nest access.

Black-browed reed warbler *Acrocephalus bistrigiceps*

Malchevskii (1987) considered this to be an Oriental cuckoo host species based on the works of Y.B. Pukinskii on the Bikin River in Primorskii Krai. The absence of any mention of Oriental cuckoo parasitism on this warbler in previous ornithological studies of Sakhalin Island, as well as our own observations, lends support to the idea that the Black-browed reed warbler is not a regular host species for Oriental cuckoos.

The eggs of a Black-browed reed warbler are fundamentally different from leaf warbler eggs. They are densely covered with spots, sometimes almost entirely covering the greenish-gray base color. The spots are arranged in several layers: the internal spots are grayish-brown, and the outer ones are brownish-olive. Black-browed reed warblers can form nesting clusters, sometimes in the same habitats as leaf warblers. Her nests are open and easily accessible. This warbler shows no discriminatory behavior to the appearance of larger, differently colored eggs in clutches and is considered as a host for Eurasian cuckoo on Sakhalin (based on two records from Nechaev (1991) and two records from V.V. Grichik, pers. comm.). Therefore the Black-browed reed warbler can be considered a possible but random host species for Oriental cuckoo on Sakhalin Island.

Bunting species

Bunting species are also possible host species for Oriental cuckoos on Sakhalin Island. Nechaev (1991) reported the discoveries of two Oriental cuckoo eggs in the nests of Masked buntings: the first on the Onor River (in central Sakhalin) and the second on the Kuznetsovka River (in southern Sakhalin). In general, buntings have only rarely been recorded as host species of Oriental cuckoo on the mainland. Numerov (2003), citing data from the Y.B. Pukinskii, noted one case of parasitism on the Yellow-throated bunting *Cristemberiza elegans;* Balatskii (1997) cited a case of the laying eggs to the Black-faced bunting *Ocyris spodocephala*; and Bachurin (2011) noted an Oriental cuckoo egg in the nest of a Tristram's bunting *O. tristrami*. All of these records are from the Bikin River basin (on the western slope of the Sikhote-Alin Mountains).

According to various authors, Japanese yellow bunting O. sulphurata and Masked bunting are considered host species of Oriental Cuckoo in Japan (Numerov, 2003).

Oriental cuckoo, being mostly an obligate brood parasite on leaf warblers that lay quite small eggs, is adapted to small passerine eggs. Buntings are larger birds than warblers and their eggs are consequently much larger than leaf warbler eggs. The average egg size of a Masked bunting is 20.8 x 15.5 mm (Nechaev, 1991), and these eggs are intensely spotted and polymorphic. Reddish-brown or grayish-brown-olive tones prevails in the coloration, which differentiates them from the egg coloring of leaf warblers living in similar habitats. We have repeatedly recorded nesting Masked bunting in areas of dense nesting of various types of warblers and female Oriental cuckoos patrolling those areas. However, we did not detect a single case of contact between buntings and cuckoos. These facts, as well as the lack of specific records from both Sakhalin and the neighboring areas of Japan, do not give grounds to any stability in the relationship between Oriental cuckoo and Masked bunting. The cases found by Nechaev (1991) may have been random. We have similarly not found any indication in the literature that Oriental cuckoos parasitize Black-faced bunting, a species common in northern Sakhalin.

Oomorphological criteria to identify the primary host species of Oriental Cuckoo

Despite the obvious convenience of warblers

species such as Dusky warbler, Radde's warbler, Arctic warbler and yellow-browed warbler for Oriental cuckoo, only Pallas's leaf warbler, due to its widespread distribution and a higher density, can be considered the most common host species for Oriental cuckoo. The high degree of compatibility of Oriental cuckoo and Pallas's leaf warbler is confirmed by comparing some oomorphological characteristics of brood parasite eggs and the above-mentioned host species. Figure 2 shows eggs of the Oriental cuckoo collected by us, showing a series of color variations and spot patterns on the shell surface. All eggs undoubtedly belong to different females (as they were collected in different areas of Sakhalin). Oriental cuckoo eggs from the collection of Nechaev were compared with our samples based on previously-taken photographs and did not reveal any significant differences from the eggs of our collection. Given the uniformity of the samples presented, these features can be considered specific and inherited for in the whole Sakhalin population of Oriental cuckoo. At the same time, the variational series of Oriental cuckoo eggs shows almost absolute similarity with the variational series of Pallas's leaf warbler eggs in all species-specific characteristics. Moreover, despite the significantly larger size of the Oriental cuckoo eggs, and accordingly much greater shell surface area, even the largest size spots are not visually larger than the spots on the eggs of Pallas's leaf warbler. In other words, for any of the Oriental Cuckoo egg coloration options we see we can find a corresponding match in egg coloration of Pallas's leaf warbler as well (Fig. 2).

In our opinion, the eggs of other warbler species that can be considered host species are very different (or not at all similar) to the eggs of Pallas's leaf warbler and Oriental cuckoo:

Visual comparison of eggs of Arctic warbler found in Sakhalin and in other parts of its range, particularly in the Urals and Western Siberia, shows their uniformity. Spotting is always light, sometimes barely noticeable, and spots are paler and colored differently than those of Pallas's leaf warbler.

Dusky warbler has white eggs without pigmentation. Eggs of Radde's warbler are characterized by yellow and yellowish-brown spots and are quite similar to the eggs of other warblers in the Russian Far East. Yellow-browed warbler and Pallas's leaf warbler are systematically related species grouped in the subgenus Reguloides (Stepanyan, 2003). Nevertheless, their eggs are well distinguished by the characteristic features of the color pattern of the shell. We had the opportunity to see collections of eggs of Yellow-browed warbler from Western Siberia, Transbaikalia, and from Primorskii Krai (Bikin River).

The main difference between the coloration of these warbler eggs and those from Pallas's leaf warbler eggs (and Oriental cuckoo eggs) is that their spots have a rusty-brown tint (closer to tan) and not reddish like in Pallas's leaf warbler (Fig. 2). In addition, eggs of Yellow-browed warbler are characterized by having diffuse pigment in the shell structure, giving it a pinkish tint against the light. In the Pallas's leaf warbler egg shell (as in the eggs of Oriental cuckoos) such diffuse pigment is not present, and it's slightly yellowish-white.

Comparison of Oriental cuckoo and Pallas's leaf warbler eggs in candling further confirms the similarity in color and placement of internal spots. The base color of the shell is yellowish-white against the light in both cases, albeit somewhat richer for the cuckoo due to the higher density of its shell. In some eggs this effect also appears externally, giving the base color of Oriental cuckoo eggs a light cream shade.

The coloration of Oriental cuckoo eggs collected from Sakhalin Island is not visually different from those of the Russian Far East mainland (Fig. 2). A comparison of oometrical characteristics (length and width of eggs) also supports their similarity: the average length and width of eggs from the mainland was 21.16 and 13.4 (range: 19.9-22.5 and 13.0-14.4; n = 15) respectively, and 21.20 and 13.9 (range: 19.7-22.0 and 12.9-15.0; n = 9) from Sakhalin, respectively. A Chi-square test showed that these two samples were not different ($r = 0.22$ for length and $r = 0.21$ for width; using the Fisher precise probability criteria $r = 0.15$).

CONCLUSION

The information we provide here leads to the conclusion that Sakhalin Island (and the nearby mainland) is inhabited by a single population of Oriental cuckoo, females of which lay eggs with oometrically-similar characteristics across that range. The high level of similarity, in our opinion, is explained by parasitism of birds from both regions

on the same host species - Pallas's leaf warbler. The stable and apparently genetically fixed similarity of the brood parasite's egg coloration with eggs of Pallas's leaf warbler qualifies this population as an independent gen.

Apparently, its formation took place on the mainland. Pallas's leaf warbler, being a relatively young species for the avifauna of Sakhalin, entered the island about 3,000 years ago (Nazarenko, 1977; Nazarenko, 1982; Nechaev, 1991) and currently occupies all suitable habitat. The described gen of Oriental cuckoo spread throughout the island following it.

Sakhalin Island also contains groups of Oriental cuckoos specializing in parasitizing other convenient and biocompatible species of warblers: Dusky warbler, Arctic warbler, Yellow-browed warbler, and Radde's warbler. These species are good additional (and in some areas of the island even primary) host species for Oriental cuckoos due to their tendency to form breeding clusters, and due to the lack of discriminatory behavior towards eggs of this brood parasite (Nechaev, 1993).

However, use of these other species as hosts has not yet led to a disruption of mechanisms that support the genetic line of Pallas's leaf warbler's egg features, or even a dilution of these features.

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