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Vocalization of the Ground Jays Supports their Subdivision into two Genera: *Podoces* and *Eupodoces*

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Abstract
In this study, we used a comparative approach to describe, for the first time, vocalizations of adults and nestlings in all four species of ground jays. The analysis of two main types of adult calls of the ground jays clearly separated them into two groups: black-breasted ground jays (– Iranian and Turkestan Ground Jays) and black-crowned ground jays (– Mongolian and Xinjiang Ground Jays). This separation was further supported by the marked differences between Turkestan Ground Jay and Mongolian Ground Jay in their nestling vocalization. These data along with earlier findings on morphology of adults and nestlings, structure of nest, and some biology and behavior features, could serve as a basis for altering the taxonomic status of these two groups, placing them in two genera: black-breasted ground jays (genus *Podoces: P. pleskei* and *P. panderi*) and black-crowned ground jays (genus *Eupodoces*: *E. hendersoni* and *E. biddulphi).*

1. Introduction

Ground Jays (*Podoces*) are small corvids (Corvidae) that are confined to arid and semiarid deserts from Iran through Turkmenistan and Kazakhstan to China and Mongolia. There are four species of *Podoces*: Iranian Ground Jay *P. pleskei* Zarudny, 1896; Turkestan Ground Jay *P. panderi* Fischer, 1821; Mongolian Ground Jay *P. hendersoni* Hume, 1871; and Xinjiang Ground Jay *P. biddulphi* Hume, 1874 (del Hoyo & Collar 2016). Already more than a century ago, on the base of elongated upper major tail coverts and their protruding beyond the middle of the length of tail feathers in *P. hendersoni* and *P. biddulphi* (but not in *P. panderi* and *P. pleskei*), the genus *Podoces* was separated into two subgenera: the subgenus of *Podoces,* so-called black-breasted ground jays (Iranian and Turkestan Ground Jays), and the subgenus *Eupodoces*, so-called black-crowned ground jays (Mongolian and Xinjiang Ground Jays) (Zarudny & Loudon 1902). But the validity of *Eupodoces* had not been supported by most authors in that time and was thus rejected (Sharpe 1909; Hartert 1910). However, it was noted that black-crowned ground jays also differ from black-breasted ground jays by their long dark legs, black patches on the head and the absence of black patch on the breast (Amadon 1944). On these grounds also, some authors have suggested that ground jays can be divided into two subgenera or even genera (del Hoyo & Collar 2016; del Hoyo *et al.* 2009).

Additionally, E.V. Kozlova (1975) pointed out the differences between *hendersoni*/*biddulphi* and *pleskei*/*panderi* in the comparative analysis of morphology of certain elements of the skull, the patterns of colouration of the plumage in ontogeny, and the wing formula, as well as distribution and habitats. Recently, it was found that *hendersoni*/*biddulphi* differ from *pleskei*/*panderi* in certain aspects of their breeding biology. The black-crowned ground jays, unlike black-breasted ground jays, have the following features: their nests have a cup-shaped form without a roof, and

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have a base made from camel excrement; nestlings hatch with developed natal down; both parents, probably, incubate a clutch. In contrast, black-breasted ground jays often build a shelter roof over the nest that provides protection from the sun, and hide the nest from predators; newly-hatched nestlings are naked; only females incubate eggs. All these data served as a basis for altering the taxonomic status of these two groups at the genus level (Ilyashenko *et al.* 2017; Ilyashenko 2018).

In passerine birds, morphology, DNA and vocal data are the ones most often used to resolve the taxonomy of groups (Martens *et al.* 2011; del Hoyo & Collar 2016). In particular, vocal analysis can offer robust classifications because many acoustic features were found to vary strongly along phylogenetic lines, especially with respect to groups of species from a single or several related genera (McCracken & Sheldon 1997; Price & Lanyon 2002; Farnsworth & Lovette 2008; Seneviratne *et al.* 2012). Some authors argued, however, that the presence of high phylogenetic signal in the vocal data does not necessarily guarantee reliable taxonomic information at the genus level (Cardoso *et al.* 2012). Nevertheless, in several instances, vocal analysis along with the DNA studies had led to altering the taxonomic status of a group at the genus level (Alström *et al.* 2018).

With respect to ground jays, there have been no taxonomic studies based on DNA sequences and/or vocalizations. Mitochondrial genomes have been sequenced either completely or partly (i.e. cytB gene) in the two black-crowned ground jays species only (Ericson *et al*. 2005; Ke *et al*. 2010), and no nuclear markers have been studied at all. Ground jays vocalizations have been described only briefly in some species, and there have been no comparative studies. Here, we used a comparative approach to analyze the vocalizations of all species of ground jays. We assessed whether the vocalizations would or would not support the separation of ground jays into the two groups (i.e. genera): *hendersoni*/*biddulphi* and *pleskei*/*panderi*. To achieve this goal, we recorded and collected sound library vocalizations of individuals of all four species of ground jays.

2. Materials and Methods

Mongolian Ground Jay was studied in the field. Field work was carried out in Southern Gobi Desert, Mongolia (N 42–43°, E 104–107°) on 22–30 April 2017. The calls of Turkestan Ground Jay were extracted from the documentary film "The Pander's Ground Jay of the Ile" produced by A.Z. Zhatkanbayev (2006). Additional recordings of all ground jays species were downloaded from Xeno-canto (www.xeno-canto.org), AVoCet (www.avocet.zoology.msu.edu) and the Internet Bird Collection (www.hbw.com). Sonograms were produced and analyzed using Syrinx PC v. 2.6 (John Burt, www.syrinxpc.com) with an FFT size = 256, and a window type = Hanning.

Ground jays have individual repertoires of several call types, and no song in the conventional sense have been described in these species. However, the data on this matter are still scarce. Two types of adult vocalizations were analyzed, as only these two types were presented in the recordings of all four species: trill and alarm call (Fig. 1). These vocalizations produce by both male and female. The trill was defined as a rapid sequence of short tonal elements. The number of elements in the trill and trill length varied widely both within and among species. In each trill element, we measured the duration, and the minimum and maximum fundamental frequencies, and then calculated medians of a trill. Also, in each alarm call, we measured the duration, and the minimum and maximum fundamental frequencies. For each individual (= recording: see Supplementary Table S1) we measured either 1–15 (median 4.5) trills or 4–15 (median 5) alarm calls.

Median values of an individual were calculated and used in the analysis. In total, we measured 50 trills and 630 elements within them in 10 individuals of the four ground jay species, and 64 alarm calls in 11 individuals (Supplementary Table S1). In some cases, we analyzed both trill and alarm calls from the same individual.

We also described the nestlings' vocalizations of the Turkestan Ground Jay and Mongolian Ground Jay. In Mongolian Ground Jay, we used our own recordings at two nests: one nest had nestlings 5–8 days old, and the nestlings' age in another nest was 15 days. Several recordings of Turkestan Ground Jays nestlings and fledglings at ages from 5 to 18 days (at two nests) were extracted from the documentary film "The Pander's Ground Jay of the Ile" (Supplementary Table S1). For each nestling call, we measured the duration, and the minimum and maximum fundamental frequencies.

All species of ground jays are monotypic, except *Podoces panderi* that has two isolated subspecies (but treated as monotypic in: del Hoyo & Collar 2016): *P.p. panderi* Fischer, 1821 (Transcaspia) and *P. p. ilensis* Menzbier et Schnitnikov, 1915 (eastern Kazakhstan). In this study, we analyzed vocalizations of both subspecies jointly (see Supplementary Table S1 for details), as the sample size was too small for any comparisons between these two subspecies.

Statistical analysis was performed in R environment (v.3.3.2) (R Core Team 2016). The hierarchical cluster analysis with Euclidean distance and method Ward.D in the 'pvclust' package in R (Suzuki & Shimodaira 2015) was used to classify the four ground jays species into groups. The medians of the time-and-frequency parameters of both trills and alarm calls of a species were used in this analysis. When comparing calls of nestlings of different ages, and those of adults, we used Mann-Whitney *U* test with Bonferroni correction procedure for multiple comparison.

3. Results

Ground jays seemed to produce trills in a wide array of contexts. We have observed Mongolian Ground Jay calling either from a bush top or while approaching the nest or moving away from the nest. Besides, incubating females of Turkestan Ground Jay, while sitting at the nest, emitted trills to the male before he approaches, to encourage him to feed her.

The structure of trill elements was very similar between Mongolian and Xinjiang Ground Jays. Trills of both species were composed of short low-pitched ascending elements. In contrast, trill elements of Turkestan and Iranian Ground Jays were longer and more high-pitched (Fig. 1, 2, Table 1). The latter two species thus had trills that were more similar among themselves than to both Mongolian and Xinjiang Ground Jays.

The alarm call data also separated the four species of ground jays into two groups (Table 2). The two species of black-breasted ground jays produced very similar calls that had four (two 'pairs') short tonal ascending elements each. The alarm calls of the two black-crowned ground jays were longer and were composed of 2–3 different frequency-modulated tonal elements (Fig. 1). Besides, the Mongolian Ground Jay was found to be able to produce two different types of alarm call in a single sequence (Fig. 1, c).

Finally, cluster analysis based on trill and alarm call measurements divided the four studied species into two well-defined groups (Fig. 3).

The duration, the minimum and maximum fundamental frequencies of calls of the Turkestan Ground Jay nestlings did not differ (1) between 5^{th} and 12^{th} days of their life (Mann-Whitney *U* test, $P>0.05$ for all variables), and (2) between 15^{th} and 18^{th} days of life ($P>0.05$ for all variables). Nestlings of 5- and 12-days old produced significantly high-pitched and longer calls than did 15- and 18-days old nestlings

(P<0.0002 for all variables). Thus, the time-and-frequency parameters of nestlings' calls in Turkestan Ground Jay appeared to change dramatically between their 12th and 15th days of life. In that time, nestlings switched from producing the trill-like high-pitched signals to emitting adult-type alarm calls (Fig. 4, a), as the time-and-frequency parameters of calls of 15–18-days old nestlings did not differ from those of adult alarm calls (Mann-Whitney U test, P>0.05 for all variables).

Trills, but not alarm calls, seem to develop early in life of the Mongolian Ground Jay nestlings (Fig. 4). The 5-days old nestlings of this species produced high-pitched trills that were much longer than the calls of the Turkestan Ground Jay nestlings of the same age. When 15-days old, the nestlings of the Mongolian Ground Jay emitted trills that were rather similar to adult trills but higher-pitched (Mann-Whitney U test, P<0.003) and longer (Mann-Whitney U test, P<0.003). Therefore, the vocalizations of nestlings and their developmental patterns differed markedly between Turkestan and Mongolian Ground Jays.

Table 1. Univariate statistics for measurements of the trill elements of the four species of ground jays. The values are medians, and min-max and number of individuals (*n*) given in parentheses.

Species	Duration, sec	Minimal frequency, kHz	Maximum frequency, kHz
panderi (*n*=2)	0.10 (0.09–0.10)	3.63 (3.58–3.68)	4.42 (4.13–4.72)
pleskei (*n*=1)	0.06	3.69	5.21
hendersoni (*n*=5)	0.02 (0.01–0.02)	1.82 (1.65–1.85)	2.35 (2.31–2.62)
biddulphi (*n*=2)	0.03 (0.02–0.04)	1.74 (1.69–1.79)	2.26 (2.24–2.28)

Table 2. Univariate statistics for measurements of the alarm calls of the four species of ground jays. The values are medians, and min-max and number of individuals (*n*) given in parentheses.

Species	Duration, sec	Minimal frequency, kHz	Maximum frequency, kHz
panderi (*n*=2)	0.07 (0.07–0.08)	2.94 (2.41–3.47)	5.34 (5.26–5.42)
pleskei (*n*=3)	0.07 (0.07–0.07)	3.20 (3.06–3.57)	5.42 (5.21–5.50)
hendersoni (*n*=5)	0.09 (0.06–0.09)	1.95 (1.58–2.07)	7.73 (7.07–9.03)
biddulphi (*n*=1)	0.18	2.17	6.28

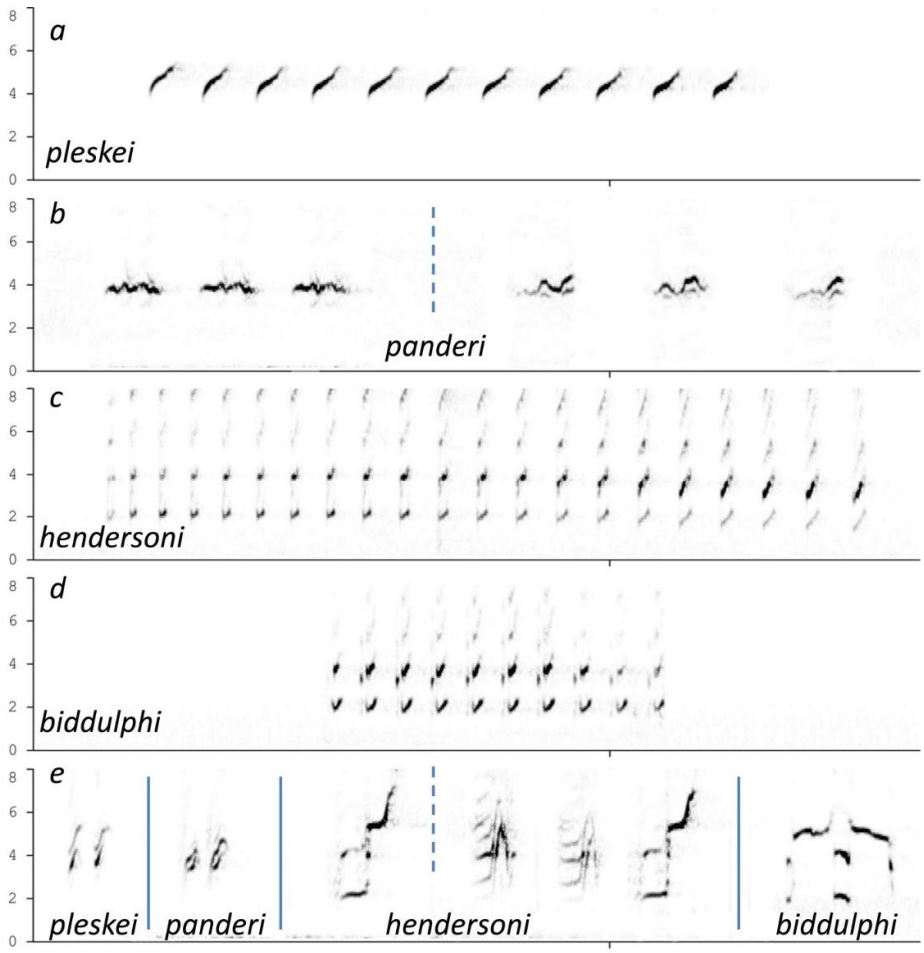

Fig. 1. Spectrograms of adult trills (*a*-*d*) and alarm calls (*e*) of the four species of ground jays. Trills of *panderi* separated by dotted line (*b*) are from different individuals, and alarm calls of *hendersoni* separated by dotted line (*e*) are from the same individual.

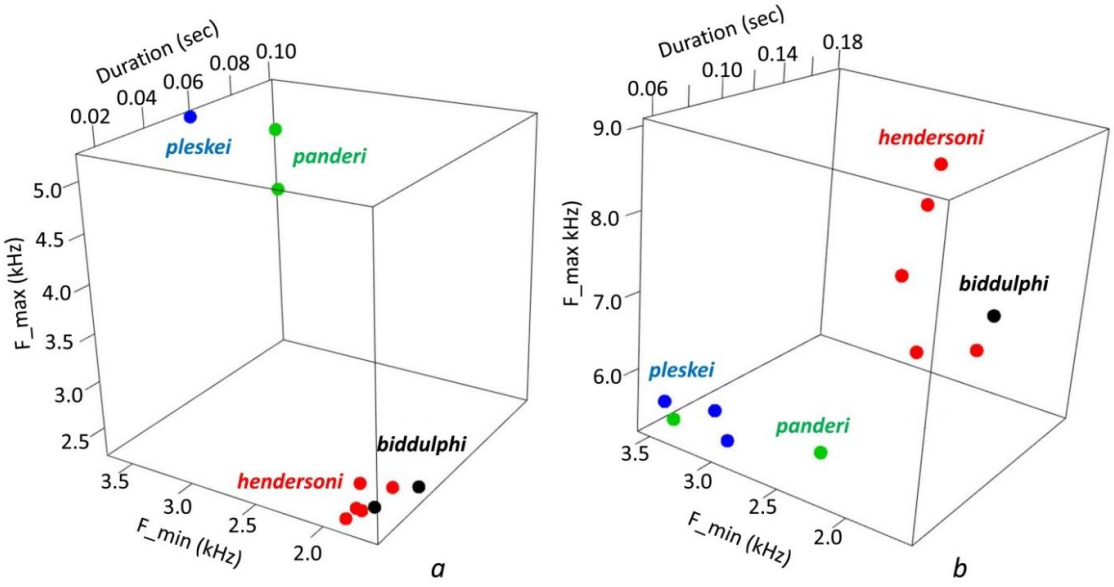

Fig. 2. 3D Boxplot of the time-and-frequency parameters of trills (*a*) and alarm calls (*b*) of adult individuals of the four species of ground jays (F_min = minimal fundamental frequency, F_max = maximum fundamental frequency).

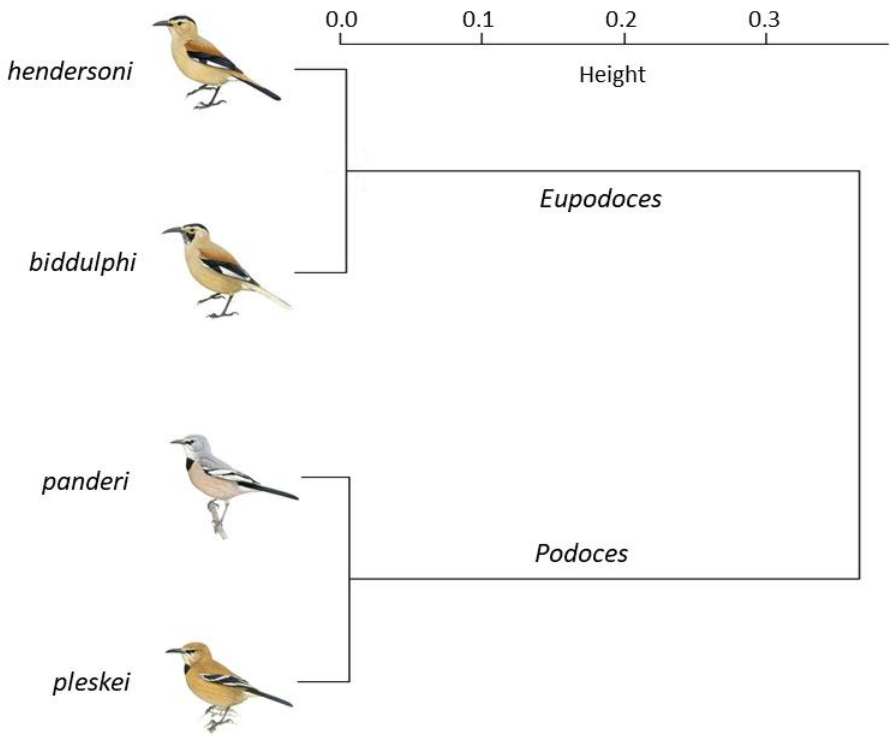

Fig. 3. Cladogram of the time-and-frequency parameters of trills and alarm calls.

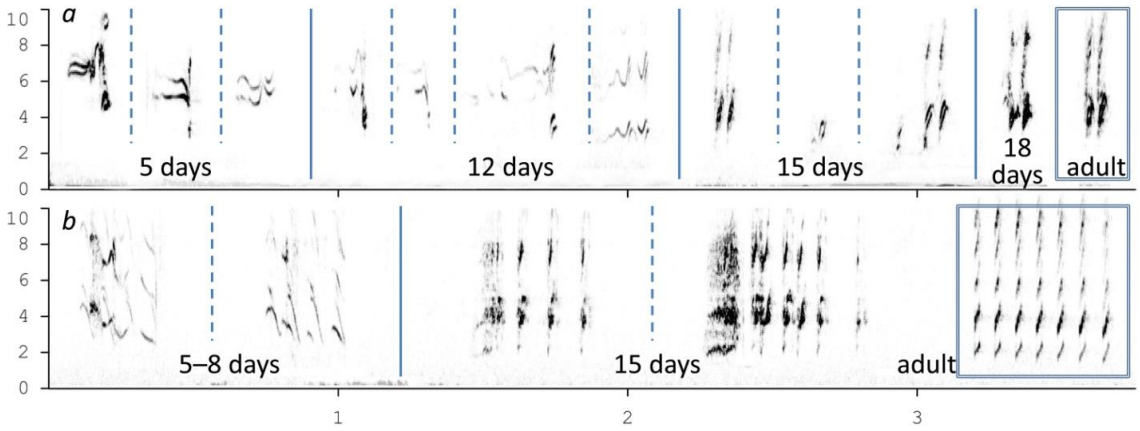

Fig. 4. Spectrograms of calls of nestlings and fledglings of different ages of the Turkestan Ground Jay (*a*) and Mongolian Ground Jay (*b*). The examples of adult Turkestan Ground Jay alarm call (a) and Mongolian Ground Jay trill (b) are given for comparison.

4. Discussion

The vocal data clearly separated the four species of ground jays into two groups: black-breasted ground jays (Iranian and Turkestan Ground Jays) and black-crowned ground jays (Mongolian and Xinjiang Ground Jays). Adult vocalization of all four species of ground jays consists of at least two main call types: trill and alarm call. Both Iranian and Turkestan Ground Jays have 'slow' trills of rather long and high-pitched elements. By contrast, a 'fast' low-pitched trill is characteristic for Mongolian and Xinjiang Ground Jays. The alarm calls of Iranian and Turkestan Ground Jays are very similar and have two 'pairs' of short elements each. The alarm calls of black-crowned ground jays are longer and are of 2–3 elements each. The separation of black-breasted ground jays and black-crowned ground jays was further supported by the marked differences in nestling vocalizations between *panderi* and *hendersoni*.

In passerine birds, vocalizations are often used to resolve the taxonomy of groups (Martens *et al.* 2011; del Hoyo & Collar 2016). Bird vocalizations can be divided into songs and calls, with songs being used for phylogeny reconstructions much more often than calls (Catchpole & Slater 2008). Nevertheless, calls have been found to vary strongly along phylogenetic lines, and have been thus used to resolve species- and genera-level taxonomy. This is especially true for Corvids, because many species lack a typical song, and calls not songs are predominately used for communication in these birds. Indeed, calls have been used successfully in several taxonomic and phylogeographic studies of Corvidae (Martens *et al.* 2000; Kryokov *et al.* 2017).

However, vocalization alone is not sufficient to resolve the taxonomy of a group. In the present study, we found that vocal data supported division within ground jays based on certain aspects of their breeding biology (Ilyashenko *et al.* 2017; Ilyashenko 2018). Therefore, the vocal analysis clearly confirmed earlier findings, and supports grouping the four species of ground jays into two genera: *Podoces* (*P. pleskei* and *P. panderi*) and *Eupodoces* (*E. hendersoni* and *E. biddulphi*).

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Supplementary Table S1. Recordings of individuals used in the present analysis.

Species	Vocalization type	Number of trills (in parenthesis: number of trill elements) or calls measured)	Location, data	Source	Author
Eupodoces hendersoni	trill	1 (21)	Mongolia, Southern Gobi Desert, 23.04.2017	own data	Elena Ilyashenko
Eupodoces hendersoni	trill	11 (130)	Mongolia, Southern Gobi Desert, 25.04.2017	own data	Amarkhuu Gungaa, Valentin Ilyashenko, Elena Ilyashenko
Eupodoces hendersoni	trill	6 (73)	China, Qinghai, Chaka Salt Works, Chaka, 13.08.2008	AvoCet: AV4075	Paul I. Holt
Eupodoces hendersoni	trill	1 (19)	Mongolia, SW of Dalanzadgad, Omnogovi, 10.05.2013	Xeno-canto: XC149809	Frank Lambert
Eupodoces hendersoni	trill	1 (3)	China, Qinghai, Haixi, 3.07.2014	Xeno-canto: XC191473	Mike Nelson
Eupodoces biddulphi	trill	4 (85)	China, Xinjiang, just outside Jinlucun, 10.05.2011	Xeno-canto: XC225255, XC225256, XC225257, XC225259	Alexander Hellquist
Eupodoces biddulphi	trill	5 (50)	China, Xinjiang, Puhui Dunes, south-south-west of Korla, 14.08.2005	AvoCet: AV4074	Paul I. Holt
Podoces panderi panderi	trill	1 (51)	Uzbekistan, Uchkuduk District, Navoyi Province, 1.05.2013	Xeno-canto: XC148565	Tom Martin
Podoces panderi ilensis	trill	15 (15)	Kazakhstan, South Balkhash Area, Saryssik Atyrau, 2002–2006	The documentary film "The Pander's Ground Jay of the Ile"	Altay Zhatkanbayev
Podoces pleskei	trill	5 (183)	Iran, Khar Turan National Park, Shahrud, Semnan, 19.04.2017	Xeno-canto: XC366328	Patrik Åberg
Eupodoces hendersoni	alarm call	5	Mongolia, Southern Gobi Desert, 23.04.2017, bird #1	own data	Elena Ilyashenko
Eupodoces hendersoni	alarm call	5	Mongolia, Southern Gobi Desert, 23.04.2017, bird #2	own data	Elena Ilyashenko
Eupodoces hendersoni	alarm call	5	Mongolia, Southern Gobi Desert, 29.04.2017	own data	Elena Ilyashenko
Eupodoces hendersoni	alarm call	5	Mongolia, Southern Gobi Desert, 30.04.2017	own data	Amarkhuu Gungaa
Eupodoces hendersoni	alarm call	5	China, Qinghai, Haixi, 4.08.2005	Xeno-canto: XC206465	Keith Blomerley
Eupodoces biddulphi	alarm call	5	China, Qinghai, Chaka Salt Works, Chaka, 13.08.2008	AvoCet: AV4075	Paul I. Holt
Podoces panderi panderi	alarm call	5	Uzbekistan, Kyzyl Kum Desert, 13.05.2008	Internet Bird Collection: IBC1130404	Greg Baker
Podoces panderi ilensis	alarm call	15	Kazakhstan, South Balkhash Area, Saryssik Atyrau, 2002–2006	The documentary film "The Pander's Ground Jay of the Ile"	Altay Zhatkanbayev
Podoces pleskei	alarm call	5	Iran, Khar Turan National Park, Shahrud, Semnan, 28.08.2009	Xeno-canto: XC174761	Amir Jafari
Podoces pleskei	alarm call	4	Iran, Khar Turan National Park, Shahrud, Semnan, 19.04.2017 (bird #1)	Xeno-canto: XC366331	Patrik Åberg

Podoces pleskei	alarm call	5	Iran, Khar Turan National Park, Shahrud, Semnan, 19.04.2017 (bird #2)	Xeno-canto: XC366331	Patrik Åberg
Eupodoces hendersoni	trill of nestling (5–8 days old)	5 (22)	Mongolia, Southern Gobi Desert, 25.04.2017	own data	Amarkhuu Gungaa, Valentin Ilyashenko, Elena Ilyashenko
Eupodoces hendersoni	trill of nestling (15 days old)	10 (41)	Mongolia, Southern Gobi Desert, 23.04.2017	own data	Elena Ilyashenko
Podoces panderi ilensis	call of nestling (5 days old)	6	Kazakhstan, South Balkhash Area, Saryssik Atyrau, 2002–2006	The documentary film "The Pander's Ground Jay of the Ile"	Altay Zhatkanbayev
Podoces panderi ilensis	call of nestling (12 days old)	8	Kazakhstan, South Balkhash Area, Saryssik Atyrau, 2002–2006	The documentary film "The Pander's Ground Jay of the Ile"	Altay Zhatkanbayev
Podoces panderi ilensis	call of nestling (15 days old)	4	Kazakhstan, South Balkhash Area, Saryssik Atyrau, 2002–2006	The documentary film "The Pander's Ground Jay of the Ile"	Altay Zhatkanbayev
Podoces panderi ilensis	call of fledgling (18 days old)	8	Kazakhstan, South Balkhash Area, Saryssik Atyrau, 2002–2006	The documentary film "The Pander's Ground Jay of the Ile"	Altay Zhatkanbayev

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