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Striking difference in response to expanding brood parasites by birds in western and eastern Beringia

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ABSTRACT. Two species of obligate brood-parasitic *Cuculus* cuckoos are expanding their ranges in Beringia. Both now breed on the Asian side, close to the Bering Strait, and are found in Alaska during the breeding season. From May to July 2017, we used painted 3D-printed model eggs of two cuckoo host-races breeding in northeastern Siberia to test behavioral responses of native songbirds on both sides of the Bering Strait, with particular attention to species that are known cuckoo hosts in their Siberian range. Each host nest was tested after the second egg was laid and, if possible, again 4 days later with a model of a different type. Although our Siberian study site was also outside the known breeding ranges of the cuckoos, we found that Siberian birds had strong anti-parasite responses, with 14 of 22 models rejected. In contrast, birds in Alaska had virtually no detectable anti-parasite behaviors, with only one of 96 models rejected; the rejecters were Red-throated Pipits (*Anthus cervinus*). Such differences suggest that the cuckoos might successfully parasitize naïve hosts and become established in North America whether or not their historic host species are widely available.

RESUMEN. **Sorprendente diferencia en respuesta a la expansión de parásitos de cría por aves en el oeste y el este de Beringia**

Dos especies de parásitos de cría obligatorios del genero *Cuculus* están expandiendo sus rangos en Berinigia. Las dos especies ahora se reproducen en el lado Asiático cerca del estrecho de Bering y pueden ser encontrados en Alaska durante la temporada de reproducción. Entre Mayo y Julio de 2017, utilizamos huevos impresos en 3D y pintados representativos de dos razas huéspedes de *Cuculus* que se reproducen en el noreste de Siberia con el fin de poner a prueba las respuestas comportamentales de aves paseriformes nativas en los dos lados de estrecho de Bering, enfocándonos principalmente, en las especies que se conocen como hospederos de las especies de *Cuculus* a través de su rango en Siberia. Cada par de huéspedes fue puesto a prueba después que el segundo huevo había sido puesto en el nido y de ser posible, cuatro días después con un modelo de diferente tipo. A pesar que nuestro sitio de estudio en Siberia esta fuera del rango conocido de las especies de *Cuculus*, encontramos que las aves de Siberia tienen comportamientos anti-parasíticos marcados, con 14 de los 22 modelos rechazados. Contrario a esto, las aves en Alaska no tuvieron ningún comportamiento anti -parasítico detectable, con solo uno de los 96 modelos rechazado; la especie que rechazo el huevo fue una pareja de *Anthus cervinus*. Estas diferencias sugieren que las especies de *Cuculus* pueden exitosamente parasitar hospederos ingenuos y establecerse en Norte América independientemente de que sus hospederos tradicionales estén ampliamente disponibles.

Key words: climate change, Common Cuckoo, *Cuculus canorus*, *Cuculus saturatus*, invasive species, Oriental Cuckoo, parasitism

Common Cuckoos (*Cuculus canorus*) and Oriental Cuckoos (*C. saturatus*) are expanding their ranges in Beringia, likely as a consequence of vegetation changes caused by anthropogenic climate change (Crowley 2000, Pearson et al. 2013, Dinets et al. 2015). They now breed on the Asian side close to the Bering Strait (Fig. 1) and are frequently present in Alaska during the breeding season, with multiple individuals recorded in most years (Dinets et al. 2015). Common Cuckoos have advanced further than Oriental Cuckoos, and now breed in Siberia within 300 km of the Bering Strait. Moreover, a courting pair has been observed on an island off the Alaskan Peninsula, and some observations suggest that cuckoos might be establishing a new migratory route to California (Lyon and

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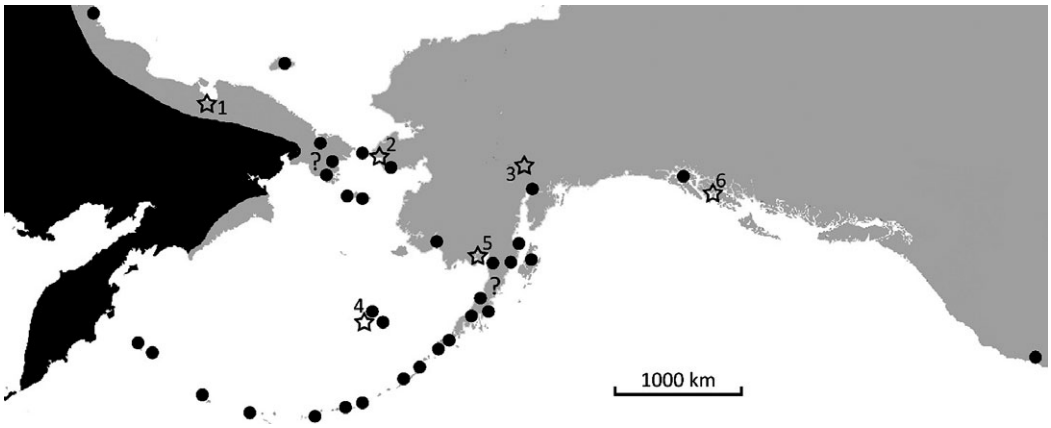

Fig. 1. Study sites in Siberia and Alaska (stars): 1—Chaun, 2—Seward Peninsula, 3—Denali Highway, 4—St. Paul I., 5—Bristol Bay, and 6—Alaska Panhandle. Black is the estimated current range of *Cuculus* cuckoos, with dots marking vagrancy records and question marks indicating possible breeding.

Gilbert 2013, Howell et al. 2014, Dinets et al. 2015, Goff 2015).

Introduced or expanding populations of brood parasites can have negative fitness consequences for naïve hosts, potentially causing declines in host populations and possibly even extinctions of native bird species if the latter lack adequate behavioral defenses against parasitism (Davies 2000, Grim and Stokke 2016, Crystal-Ornelas et al. 2017). Dinets et al. (2015) found that even typically strong foreign-egg rejecter hosts, such as American Robins (*Turdus migratorius*), may accept novel parasitism if the egg coloration of the cuckoo host-race is sufficiently similar to that of their own eggs. Therefore, understanding the possible consequences of the invasion of North America by cuckoos is of growing importance. We tested the behavioral responses of native birds in Alaska and northeastern Siberia to models of cuckoo eggs painted either plain blue or pale blue with spots, representing egg morphs of two Common Cuckoo host-races.

METHODS

Study sites. Our study was conducted from May to July 2017 at six different locations spanning Beringia (Table 1, Fig. 1). In

Table 1. Study sites in Siberia and Alaska where the behavioral responses of native songbirds to models of cuckoo eggs were tested in 2017.

Site	Coordinates	Elevation (m)	Habitats	Dates
Chaun (Siberia)	68°45′N 170°35′E	5–6	Typical tundra, alder and willow groves	4–21 June
Alaska sites:				
Seward Pen.	65°00-37′N 168°06-59′W	0–300	Typical and alpine tundra, willow groves	15 June – 3 July
Denali Highway	63°02-04′N 147°07-09′W	1300–1400	Alpine tundra	14–28 June
St. Paul Is.	57°08′N 170°13′W	5–20	Typical tundra, oceanic meadows	4–12 June
Bristol Bay	59°00-20′N 158°19′-160°22′W	10–300	Shrubby tundra, spruce forest, willow groves	25 May – 14 June
Panhandle	55°24-48′N 131°33′-133°09′W	200–700	Alpine tundra, spruce forest, willow groves	31 May – 30 June

Siberia, our study site (Chaun Research Station) was within the shared delta of the Palyavaam, Chaun, and Puchveyem rivers in northeastern Chukotka (Fig. 1). Cuckoos have not been recorded there (Kretchmar et al.1991, Solovyeva 2012), but they currently breed in Anadyr Basin ~200 km to the south (P. Tomkovich, pers. comm.). In Alaska, most study sites were near where vagrant cuckoos have either been observed or collected (Dinets et al. 2015), including the Seward Peninsula (Fig. 1), located on the American side of the Bering Strait, St. Paul Island (Fig. 1), where multiple cuckoos of both species have been seen over the years (Howell et al. 2014), a site in central Alaska (Denali Highway, Fig. 1) where one of our target species (see below) was particularly easy to find, the shores of Bristol Bay (Fig. 1), north of where a courting pair of Common Cuckoos was observed (Howell et al. 2014), and the Alaskan Panhandle (Fig. 1), just south of where a Common Cuckoo was recently observed, apparently on spring migration from California (Goff 2015).

Species studied. In Siberia, we focused on locally occurring species known to serve as cuckoo hosts in the region. In Alaska, we paid particular attention to five species with trans-Beringian ranges that are known to serve as cuckoo hosts in Siberia (Table 2) because these familiar species can be expected to be the initial hosts of invading cuckoos.

The only host-race of Common Cuckoo known to occur in northeastern Siberia is the pipit race that lays variably colored, spotted eggs with whitish to light bluish backgrounds that are mimetic to the eggs of their known hosts (Fig. 2). Although Common Cuckoos have only been studied opportunistically in this region (Kistschinsky 1968, Malchevsky 1987, Tomkovich 2012), they are known to regularly parasitize Red-throated Pipits (*A. cervinus*), and, at least occasionally, to parasitize other *Anthus* pipits, White Wagtails (*Motacilla alba*), Eastern Yellow Wagtails (*M. tschutschensis*), various buntings (*Emberiza* spp.), and leaf-warblers (*Phylloscopus* spp.) (Kistschinsky 1968, Malchevsky 1987, Tomkovich 2012). All these species have spotted eggs with light background coloration. A few hundred kilometers to the south and west, another host-race (Bluethroat race) is known to lay immaculate blue eggs in nests of Bluethroats (*Luscinia svecica*), Siberian Rubythroats (*L. calliope*), and, occasionally, leaf-warblers (Malchevsky 1987, Egorov and Larionov 2016). The only known host of Oriental Cuckoos in the region is the Arctic Warbler (*P. borealis*), which lays spotted eggs with a nearly white background (Malchevsky 1987).

Six of these Siberian species also breed in Alaska, including Red-throated and Buff-bellied (*A. rubescens*) pipits, White and Eastern Yellow wagtails, Bluethroats, and Arctic Warblers. We made a special effort to find nests of these species in Alaska. Unfortunately, we were unable to get extensive data on Red-throated Pipits in either Siberia or Alaska. We also tested many common Alaskan species that have open nests and provision young with insects, making them potential novel hosts of cuckoos (Table 2). Among those were Pacific Wrens (*Troglodytes pacificus*), closely related to Eurasian Wrens (*T. troglodytes*) that are often parasitized by Common Cuckoos in western Eurasia (Malchevsky 1987), and Grey-crowned Rosy-finches (*Leucosticte tephrocotis*) that are the only songbirds on St. Paul Island with a breeding population of more than a hundred pairs (Palmer 1899, C. Cox, pers. comm., V. D., pers. obs.).

Testing behavioral responses. We tested the responses of the birds to painted 3D-printed model eggs (Igic et al. 2015) that were 2.25 × 1.69 cm in size, near the middle of the egg size range of Common Cuckoos (2.1–2.3 × 1.5–1.8 cm, Malchevsky 1987). We used two types of models: (1) light grey-blue with brown spots, like the eggs of the pipit host-race of Common Cuckoos and of Oriental Cuckoos, and (2) blue, like the eggs of the Bluethroat race of Common Cuckoos. The light blue ground color was made using a mixture of high quality Koh-i-Noor acrylic paints: white (0100), cyan (0405), brown (0640), and green light (0500). Spot colors were made by mixing Koh-i-Noor white (0100) with Grumbacher burnt umber (C024), raw umber (C172), and mars black (C134). These two model types have been widely used in previous studies in Eurasia (e.g., Grim et al. 2011), allowing for meaningful comparison of our results.

We followed the same procedure as Dinets et al. (2015), with minor modifications described below. In brief, we located the nests

Table 2. Test results for each species and at our study sites in Siberia and Alaska. The first number in each cell is the sample size of the spotted model eggs, and the second is the sample size of the blue model eggs. The larger of these two numbers is the total number of nests checked, except for Little Buntings (*Emberiza pusilla*), with two nests tested with one model each, and White Wagtails (*Motacilla alba*), with seven nests tested in Siberia, but some abandoned after the first test. For each species, the numbers of mimetic models are underlined (the spotted model was considered mimetic if the species has pale eggs with small dark spots; the blue model was considered mimetic if the species has immaculate blue eggs). Numbers of rejections (if not zero) are in parentheses. Species known to be cuckoo hosts are in bold font.

Species		Study sites Siberia: Chaun (Siberia)	Study sites Alaska: Seward Pen.	Denali highway	St. Paul I.	Bristol Bay	Pan-handle	Alaska total
Arctic Warbler[a]	***Phylloscopus borealis***[a]	–	1/1	–	–	2/2	–	3/3
Willow Warbler	***P. trochilus***	2/4(3)	–	–	–	–	–	–
Bluethroat[a]	***Luscinia svecica***[a]	2(2)/1(1)	2/2	–	–	–	–	2/2
Northern Wheatear[a]	*Oenanthe oenanthe*[a]	–	2/1	–	–	–	–	2/1
American Robin	*Turdus migratorius*	–	–	–	–	0/1	1/1	1/2
Gray-cheeked Thrush[a]	*Catharus minimus*[a]	–	1/0	–	–	1/1	–	2/1
Swainson's Thrush	*C. ustulatus*	–	–	–	–	–	1/1	1/1
Hermit Thrush	*C. guttatus*	–	–	–	–	1/1	1/0	2/1
Pacific Wren	*Troglodytes pacificus*	–	–	–	–	–	1/1	1/1
White Wagtail[a]	***Motacilla alba***[a]	4(2)/5(4)	2/2	–	–	–	–	2/2
Eastern Yellow Wagtail[a]	***M. tschutschensis***[a]	–	1/1	–	–	2/2	–	3/3
American Pipit[a]	*Anthus rubescens*[a]	–	1/1	1/4	–	–	–	2/5
Red-throated Pipit[a]	***A. cervinus***[a]	1/1	2/2(1)	–	–	–	–	2/2(1)
Orange-crowned Warbler	*Oreothlypis celata*	–	–	–	–	1/1	1/1	2/2
Yellow Warbler	*Setophaga petechia*	–	–	–	–	1/1	1/1	2/2
Yellow-rumped Warbler	*S. coronata*	–	–	–	–	1/1	1/1	2/2
Wilson's Warbler	*Cardellina pusilla*	–	–	–	–	1/1	1/1	2/2
American Tree Sparrow	*Spizella arborea*	–	–	–	–	2/1	–	2/1
Savannah Sparrow[a]	*Passerculus sandwichensis*[a]	–	–	–	–	1/1	–	1/1
Song Sparrow	*Melospiza melodia*	–	–	–	–	0/1	1/1	1/2
Red Fox Sparrow	*Passerella iliaca*	–	–	–	–	1/1	–	1/1
Sooty Fox Sparrow	*P. unalaschcensis*	–	–	–	–	0/1	1/1	1/2
White-crowned Sparrow	*Zonotrichia leucophrys*	–	–	–	–	1/1	1/1	2/2
Golden-crowned Sparrow	*Z. atricapilla*	—	–	–	–	2/2	1/1	3/3
Dark-eyed Junco	*Junco hyemalis*	–	–	–	–	1/1	2/2	3/3

Table 2. Continued

Species		Study sites: Chaun (Siberia)	Alaska: Seward Pen.	Denali highway	St. Paul I.	Bristol Bay	Pan-handle	Alaska total
Little Bunting	***Emberiza pusilla***	1(1)/1(1)	–	–	–	–	–	–
Gray-crowned Rosy-finch[a]	*Leucosticte tephrocotis*[a]	–	–	–	2/2	–	–	2/2
Total		10(5)/12(9)						47(0)/49(1)

[a]Species breeding in both Siberia and Alaska.

of potential cuckoo hosts by following birds carrying nest material or, in some cases, accidentally, checked nests daily until two eggs were present, and added (not replaced) a single model egg. In previous work, adding a model egg rather than replacing an existing host egg with it made no difference in the rejection rates of some cuckoo hosts (Grim et al. 2011), so we decided to avoid unnecessary loss of host eggs, especially considering that some of the species tested have small populations in North America. The color of the first model used for each species at each location was determined by a coin toss, and model colors were alternated at subsequent nests. We then checked nests after four days to assess the content and the outcome of the experimental manipulation (acceptance, egg ejection, or nest abandonment; the latter determined by egg temperature). If the nest was still active, we removed the first model, added another model of the other type (following Aidala et al. 2015), and checked the nest again after four more days. The color of the first model used in the first nest of each species at each study site was determined by a coin toss; in subsequent nests of the same species at the same location, the color of the first model to be inserted was alternated. This allowed us to avoid order bias because both model types were equally likely to be used earlier and later in the laying process. We checked the results after four days, rather than six as in most previous studies, because our observations during own previous studies have shown that most rejections happen within a few hours after model placement (Dinets et al. 2015, V. Dinets, pers. obs.), and it allowed us to conduct the second trial either before or soon after the start of incubation, thus minimizing the effects of nest progress on the likelihood of rejection. Among the 14 nests where at least one model was rejected (Table 3), the first model was rejected 10 times out of 14, and the second model five times out of five, suggesting that birds with more advanced nests were not more likely to accept the models. On the other hand, some species ejected non-mimetic models more often, irrespective of the order of placement (Table 3), but the numbers are too small for significance testing.

Testing each nest twice, although a standard practice in egg rejection studies (e. g.

Fig. 2. A. Egg (uppermost) of the pipit host-race of the Common Cuckoo (*Cuculus canorus*) in a Buff-bellied Pipit (*Anthus rubescens*) clutch at Anadyr River, Siberia (collected by P. Tomkovich). B. Model egg (left side) of the pipit host-race of Common Cuckoos (*Cuculus canorus*) in a Little Bunting (*Emberiza pusilla*) nest at Chaun Research Station, Siberia (photo by Harald Ris, used with permission).

Table 3. Detailed results of tests with bird nests at Chaun (Siberia). For each species, the mimetic models (if any) are underlined (the spotted model was considered mimetic if the species has pale eggs with small dark spots; the blue model was considered mimetic if the species has immaculate blue eggs).

Species		1st model	Result	2nd model	Result
Willow Warbler	*Phylloscopus trochilus*	Spotted	Accepted	Blue	Abandoned
Willow Warbler	*Phylloscopus trochilus*	Blue	Abandoned	–	–
Willow Warbler	*Phylloscopus trochilus*	Blue	Abandoned	–	–
Willow Warbler	*Phylloscopus trochilus*	Spotted	Accepted	Blue	Accepted
Bluethroat	*Luscinia svecica*	Blue	Ejected	Spotted	Ejected
Bluethroat	*Luscinia svecica*	Spotted	Ejected	–	–
White Wagtail	*Motacilla alba*	Spotted	Accepted	Blue	Abandoned
White Wagtail	*Motacilla alba*	Blue	Abandoned	–	–
White Wagtail	*Motacilla alba*	Spotted	Accepted	Blue	Abandoned
White Wagtail	*Motacilla alba*	Blue	Abandoned	–	–
White Wagtail	*Motacilla alba*	Spotted	Abandoned	–	–
White Wagtail	*Motacilla alba*	Spotted	Abandoned	–	–
White Wagtail	*Motacilla alba*	Blue	Accepted	–	–
Red-throated Pipit	*Anthus cervinus*	Spotted	Accepted	Blue	Accepted
Little Bunting	*Emberiza pusilla*	Spotted	Abandoned	–	–
Little Bunting	*Emberiza pusilla*	Blue	Abandoned	–	–

Grim et al. 2011), can cause pseudoreplication, but not in our study because we did not run any statistical tests. We were more interested in observing responses to both mimetic and non-mimetic models, even when a small number of nests was available, than in

obtaining a large number of independent test results. Because of logistical constrains of working in remote locations, only a small number of nests of each species was tested (Table 1); nevertheless, this allowed us to examine geographic patterns of the most common responses to experimental parasitism, including acceptance, egg ejection, and nest abandonment.

RESULTS

We conducted 118 tests on 71 nests of 27 species (Table 2). Only nine nests were lost to predation during our study.

In Siberia, only eight of 22 models were accepted. All Willow Warblers (*P. trochilus*) accepted spotted (mimetic) models, but three of four pairs abandoned their clutches when an immaculate blue (non-mimetic) model was inserted (Table 3). Little Buntings (*E. pusilla*) abandoned their clutches after a model of either type was inserted (neither of the two egg types was mimetic, Fig. 2B). Bluethroats removed both blue (mimetic) and spotted (non-mimetic) models from their nests. White Wagtails rejected a half of spotted (mimetic) models and all but one blue (non-mimetic) ones. A pair of Red-throated Pipits accepted both spotted (mimetic) and blue (non-mimetic) models.

In Alaska, 95 of 96 model eggs were accepted. The exception was a blue (non-mimetic) model, rejected by a pair of Red-throated Pipits at Seward Peninsula. A spotted (mimetic) model was earlier accepted by the same pair; the other pair tested in the same area accepted both spotted and blue models. Unlike in Siberia, all Bluethroats and White Wagtails accepted each model type.

DISCUSSION

Siberia vs. Alaska. The striking differences in responses between birds in Alaska and Siberia were surprising because study sites in both areas are outside the active breeding ranges of cuckoos, and because other investigators (e.g., Soler and Møller 1996, Grim et al. 2011) have found high intraspecific consistency in such responses among most cuckoo hosts from different populations. Birds at the Siberian site likely have anti-parasite responses in the absence of parasites because of sufficiently high gene flow from nearby cuckoo-exposed populations (Moskát et al. 2008). They may have also retained anti-parasitic responses since colonizing this region from the south (where the cuckoos are present). All species studied in Siberia are of Palearctic origin, and the colonization of northeastern Siberia is known to have happened relatively recently for at least some of the potential cuckoo host species we studied, e.g., Willow Warblers colonized Chukotka only after the last glacial maximum, as evidenced by the lack of genetic structure (Lundberg et al. 2017).

In Alaska, most species tested are of Nearctic origin and it is unlikely that they have been exposed to any form of avian brood parasitism in the past. However, since the second half of the 20th century, birds in the Alaskan Panhandle have been exposed to brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Fraga 2011). Birds of Palearctic origin may have been genetically isolated in North America long enough to lose the behavioral defenses that their Siberian conspecifics exhibit, although some hosts of avian brood parasites have reportedly retained anti-parasitic responses for prolonged periods of time (Bolen et al. 2000, Rothstein 2001, Peer et al. 2011, Samas et al. 2014). The single observed rejection by a pair of Red-breasted Pipits in Alaska is probably an indication of recent colonization. This species is widespread in Eurasia, but has only a narrow breeding range on the American side of the Bering Strait, with an estimated population size of fewer than 100 individuals (Price et al. 1995). *Anthus* pipits elsewhere in Siberia often reject eggs that are not mimetic (Larionov 1992), although the only Siberian pair tested in this study did not do so (see above).

Possible scenarios of cuckoo range expansion. Once breeding populations of Common and Oriental cuckoos are established in North America, both species will encounter many naïve potential hosts. At least initially, these parasites can be expected to search for nests of their Siberian hosts, which might lead to differential success between the two cuckoo species. Oriental Cuckoos will find their historic host, Arctic Warblers, to be relatively common and widespread in habitats in Alaska that are similar to those they inhabit in Siberia (Price et al. 1995, Boeme et al.

1998, V. D., pers. obs.). However, although Common Cuckoos will find several familiar host species in Alaska, nests in this new range are found in open tundra habitats, as in the case of the Red-throated and Buff-bellied pipits, White and Eastern Yellow wagtails, and Bluethroats (Price et al. 1995, Tyler 2004, V. Dinets, pers. obs.), whereas, in Siberia, these species, except Buff-bellied Pipits, are also found in more densely vegetated habitats suitable for cuckoo nest-searching and foraging behaviors (Boeme et al. 1998, Vogl et al. 2002, Tyler 2004, V. Dinets, pers. obs.). In addition, the two songbird species believed to be the most frequent hosts of Common Cuckoos in northeastern Siberia—Red-throated Pipits and White Wagtails—have narrow ranges and populations of fewer than 100 individuals, likely too small to sustain a breeding population of cuckoos in Alaska (Price et al. 1995). Thus, although Oriental Cuckoos may remain parasites of Arctic Warblers at least initially in North America, Common Cuckoos will be more likely to abandon their host fidelity and parasitize naïve North American-only species. Our results show that native Alaskan birds lack behavioral defenses and will be highly vulnerable to cuckoo parasitism. Such a host shift will also be facilitated by the similarity in coloration and patterning of the eggs of about two-thirds of Alaskan songbirds to those of the Common Cuckoo's pipit host-race (Baicich and Harrison 2005), and by the similarity between the adult plumage patterns of cuckoos and small *Accipiter* hawks on both sides of Beringia. This plumage mimicry provokes mobbing responses and facilitates searching for host nests by the cuckoos (Malchevsky 1987), and there is indirect evidence that it will be as effective in North America as in Eurasia (Lyon and Gilbert 2013).

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