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Predicting the responses of native birds to transoceanic invasions by avian brood parasites

Vladimir Dinets,[1,5] Peter Samaš,[2] Rebecca Croston,[3,4] Tomáš Grim,[2] and Mark E. Hauber[3]

[1]*Department of Psychology, University of Tennessee, Knoxville, Tennessee 37996, USA*
[2]*Department of Zoology and Laboratory of Ornithology, Palacký University, Olomouc 77146, Czech Republic*
[3]*Department of Psychology, Hunter College and the Graduate Center, City University of New York, New York, New York 10065, USA*
[4]*Department of Biology, University of Nevada, Reno, Nevada 89557, USA*

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ABSTRACT. Three species of brood parasites are increasingly being recorded as transoceanic vagrants in the Northern Hemisphere, including two *Cuculus* cuckoos from Asia to North America and a *Molothrus* cowbird from North America to Eurasia. Vagrancy patterns suggest that their establishment on new continents is feasible, possibly as a consequence of recent range increases in response to a warming climate. The impacts of invasive brood parasites are predicted to differ between continents because many host species of cowbirds in North America lack egg rejection defenses against native and presumably also against invasive parasites, whereas many hosts of Eurasian cuckoos frequently reject non-mimetic, and even some mimetic, parasitic eggs from their nests. During the 2014 breeding season, we tested the responses of native egg-rejecter songbirds to model eggs matching in size and color the eggs of two potentially invasive brood parasites. American Robins (*Turdus migratorius*) are among the few rejecters of the eggs of Brown-headed Cowbirds (*M. ater*), sympatric brood parasites. In our experiments, robins rejected one type of model eggs of a Common Cuckoo (*C. canorus*) host-race, but accepted model eggs of a second cuckoo host-race as well as robin-mimetic control eggs. Common Redstarts (*Phoenicurus phoenicurus*), frequent hosts of Common Cuckoos in Eurasia, rejected ~50% of model Brown-headed Cowbird eggs and accepted most redstart-mimetic control eggs. Our results suggest that even though some hosts have evolved egg-rejection defenses against native brood parasites, the invasion of brood parasites into new continents may negatively impact both naïve accepter and coevolved rejecter songbirds in the Northern Hemisphere.

RESUMEN. **Prediciendo la respuesta de aves nativas a la invasión trans-oceánica de aves parásitas de nido**
Tres especies de parásitos de nido han sido registradas en aumento como errantes trans-oceánicos en el Hemisferio Norte, incluyendo a dos cucos *Cuculus* desde Asia a Norte América y un tordo *Molothrus* desde Norte América a Eurasia. Los patrones de vagabundeo sugieren que el establecimiento en el Nuevo continente es posible, probablemente como consecuencia de expansiones de rango recientes en respuesta al calentamiento global. Se predice que el impacto de la invasión de parásitos de nido diferirá entre continente debido a que muchas especies huéspedes de tordos en Norte América no poseen defensas de rechazo de huevos en contra de parásitos nativos y presumiblemente en contra de parásitos invasores, mientras que muchos hospedadores de los cucos en Eurasia frecuentemente rechazan huevos parásitos no miméticos, y aún algunos miméticos, de sus nidos. Durante la temporada reproductiva del 2014, pusimos a prueba la respuesta de aves canoras que naturalmente rechazan huevos frente a modelos de huevos que semejaban en tamaño y color a los huevos de dos especies potencialmente invasoras. El Mirlo primavera (*Turdus migratorius*) está entre los pocos hospedadores que rechazan huevos de un parásito de nido simpátrico, el Tordo cabeza café (*M. ater*). En nuestro experimento, el Mirlo primavera rechazó un tipo de modelo de huevo de una raza-hospedadora del Cuco común, pero aceptó los huevos modelo de una segunda raza-hospedadora del cuco al igual que un huevo mimético de Mirlo. El Colirrojo real (*Phoenicurus phoenicurus*), hospedador frecuente de Cuco común en Eurasia, rechazó ~50% de los huevos modelo del Tordo cabeza café y aceptó las mayoría de los huevos control miméticos a los del Colirrojo real. Nuestros resultados sugieren que aún cuando algunos hospedadores han desarrollado defensas de rechazo de huevo contra parásitos de nido nativos, la invasión de parásitos hacia nuevos continentes puede tener un impacto negativo en aves canoras, tanto para las que son aceptadoras ingenuas como para las que han co-evolucionado estrategias de rechazo de huevos, en el Hemisferio Norte.

Key words: American Robin, climate change, Common Redstart, cowbird, cuckoo, egg rejection, invasive species

Earth's changing climate is causing many bird species to expand their ranges toward the poles, sometimes lengthening migratory routes or improving the chances of survival for overwintering individuals (Walther et al. 2002, Hitch and Leberg 2007). Range expansions are of particular concern in the case of interspecific brood parasites that exploit hosts by laying eggs in

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[5] Corresponding author. Email: dinets@gmail.com

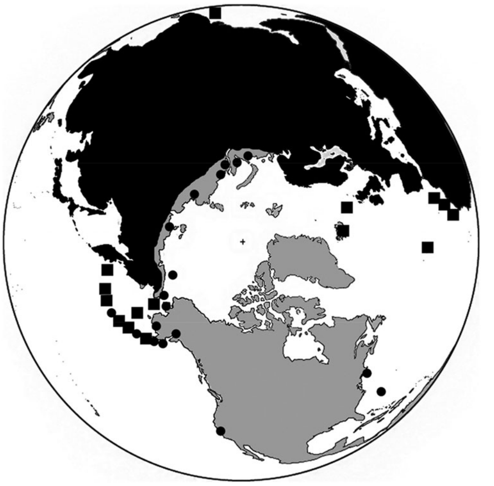

Fig. 1. Current range (black) and records of vagrancy of Common Cuckoos, with single records indicated by circles and multiple records by squares (based on Gavrilov et al. 1993, Payne 1997, Howell et al. 2014, and University of Alaska's Museum of the North catalog).

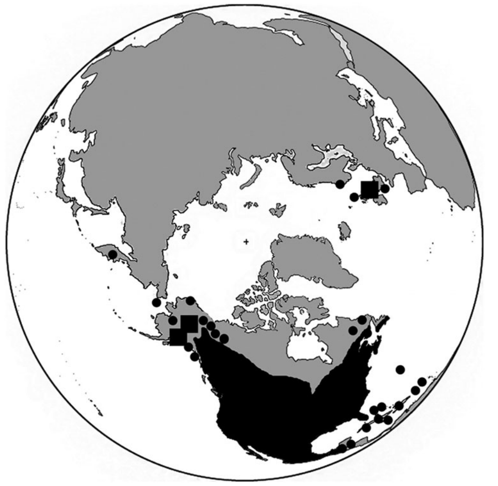

Fig. 2. Current range (black) and records of vagrancy of Brown-headed Cowbirds with single records indicated by circles and multiple records by squares (based on Hudson 2010, Fraga 2011, and E. Koblik, pers. comm.

host nests and reduce the fitness of foster parents by hijacking costly parental care (Davies 2000). For several species of Holarctic avian brood parasites, northward range expansions will likely result in access to and potential colonization of new continents in the near future. For example, Common (*Cuculus canorus*) and Oriental (*C. optatus*) cuckoos are native to temperate Eurasia, but have begun to colonize northeastern Siberia; these obligate parasitic species now breed within 300 km of the Bering Strait (Gavrilov et al. 1993) and are common within 600 km of it (Tomkovich 2012). Both cuckoos are now regularly recorded as vagrants in both mainland Alaska and its archipelagos (Howell et al. 2014; Fig. 1).

Common Cuckoos are brood parasites of particular potential impact because multiple individuals have been recorded in North America simultaneously, and they are known for their extreme habitat flexibility, occurring as a breeding species in shrubby tundra, reed beds, steppes, boreal taiga, and subalpine meadows among other habitats (Payne 1997, Boeme et al. 1998). Furthermore, a courting pair has already been observed in Alaska, and at least one individual wintered in California in 2012 (Howell et al. 2014). Considering how sparse the observational coverage of Alaska is, these records suggest that Common Cuckoos could already be breeding in North America and using a novel migration route.

Brown-headed Cowbirds (*Molothrus ater*), North America's most common obligate brood parasites, have greatly expanded their range in eastern North America over the last four centuries in parallel with deforestation and cattle farming (Fraga 2011). This expansion continues at their northern range limit, and may be aided by the warming climate. Brown-headed Cowbirds colonized Newfoundland in the late 1950s, and were first recorded in Labrador only two decades ago (Maybank 1993). Along with their northward expansion and lengthening of their migratory routes within North America, Brown-headed Cowbirds of both sexes are increasingly being recorded as vagrants in Eurasia, particularly in Western Europe (Fig. 2). The first two records were in the late 1980s and, more recently, cowbirds have been recorded almost annually (Hudson 2010). This increase in sightings is unlikely to be due to growing observer effort because observational coverage in Europe has remained extensive since well before 1988 (Moss 2004), and this species is clearly different in appearance from most European birds. In 2009, multiple individuals were observed in Britain simultaneously (Hudson 2010); such simultaneous occurrences are the ones most likely to result in successful invasion and establishment. In 2014, a Brown-headed Cowbird was also recorded in Kamchatka (northeastern Siberia) during fall migration; in contrast to Western Europe, observational coverage of this vast area is extremely poor (E. Koblik, pers. comm.). In their non-breeding ecology in North America (Fraga 2011), cowbirds are similar to European Starlings (*Sturnus vulgaris*), extraordinarily successful invasives in North America (Craig and Feare 2009). Much like invasive starlings, Brown-headed Cowbirds inhabit a wide variety of open and semi-open habitats, ranging from short-grass prairies to fragmented forests and urban landscapes (Fraga 2011). This flexibility may facilitate successful invasion into varied Eurasian landscapes.

Both *Cuculus* cuckoos and *Molothrus* cowbirds are obligate brood parasites (Payne 1997, Davies 2000), and this is a critical consideration in estimating the respective impact of invasion on potential passerine host populations. However, there are also important differences between these brood parasites. *Cuculus* cuckoos are virulent parasites whose young evict all host eggs and young from nests, eliminating any host reproductive success (Grim et al. 2009). Common Cuckoos impact a wide variety of songbird species, with female cuckoos from different host-races (gentes) successfully mimicking the egg colors of their respective hosts, thus circumventing the hosts' defensive mechanism of rejecting foreign eggs from the nest (Davies 2000). As an outcome of the co-evolutionary arms race with cuckoos, and considering the possible invasion by cowbirds into Europe, native hosts of the many cuckoo gentes should show strong egg rejection behaviors in response to non-mimetic cowbird eggs in their nests. A cowbird invasion of northeastern Siberia would likely have more serious consequences because, in contrast to cuckoos in Western Europe that parasitize more than 10 genera of songbirds (Malchevski 1987, Payne 1997, Davies 2000), cuckoos in northeastern Siberia regularly parasitize few avian genera, namely *Anthus*, *Phylloscopus*, and, possibly, *Motacilla* and *Luscinia* (Malchevski 1987, Gavrilov et al. 1993, Tomkovich 2012).

In contrast to cuckoos, cowbirds are generalist brood parasites not only at the level of the species, but also at the level of individual females, many of which lay eggs in nests of different host species (Woolfenden et al. 2003). Cowbirds do not specifically mimic the egg color of their hosts, and lay eggs of consistent coloration across different host species (Ortega 1998). Cowbirds are moderately virulent parasites; their chicks do not evict hosts, but they can beg more intensively and out-compete smaller and later-hatched host young in nests (Hauber 2003). Even with moderate virulence, cowbirds can contribute to declines in native songbird populations. For example, Kirtland's Warblers (*Setophaga kirtlandii*) remain in need of active protection from extinction, including management that includes the culling of cowbirds within their small breeding range (Kelly and DeCapita 1982, but see Rothstein and Peer 2005). In addition, most passerines living in- and outside the historic range of cowbirds typically accept both mimetic and non-mimetic parasite eggs (Rothstein 1990) and thus pay the full costs of cowbird parasitism (Hauber 2003).

To determine if hosts of native brood parasites respond differentially to parasitism by their most likely transcontinental invader parasite, we conducted two parallel sets of experimental studies, using strong inference rather than preformulated hypotheses. In the first study, we placed model eggs designed to resemble Brown-headed Cowbird eggs in nests of Common Redstarts (*Phoenicurus phoenicurus*), a native European species regularly parasitized by Common Cuckoos (Rutila et al. 2002). In the second study, we placed models resembling the eggs of one of two Common Cuckoo gentes occurring in northeastern Siberia in nests of American Robins (*Turdus migratorius*), one of only few North American cowbird host species known to reject cowbird eggs (Rothstein 1982). In both sets of studies, we also used control model eggs mimicking the eggs of the respective hosts, and which are known to be accepted in these nests (Grim et al. 2009, Croston and Hauber 2014).

METHODS

Study species and sites. Common Redstarts were studied near Ruokolahti in southeastern Finland (61°24'N, 28°37'E) from May to July 2014. About 300 nest boxes had been set up in cultivated pine forests (for details see Grim et al. 2009). Redstarts lay pale blue eggs and are parasitized by a host-specific race of Common Cuckoos laying highly mimetic, pale blue eggs (Igic et al. 2012). This study population is sympatric with Common Cuckoos, with a parasitism rate of ~20% of nests with one or more cuckoo eggs (Grim et al. 2009). Redstarts reject non-mimetic eggs about five times as often as they do mimetic eggs, at rates of 44–46% vs. 6–8%, respectively (Rutila et al. 2002, Hauber et al. 2014).

American Robins were studied near Tioga Pass, California (37°57'N, 119°16'W), at elevations of 2900–3200 m from May to June 2014. Robins in this area nest in short lodgepole pines (*Pinus contorta*), and form loose colonies of 3–10 pairs. Brown-headed Cowbirds colonized the Sierra Nevada in the 1930s and parasitize a variety of species, but not American Robins (Rothstein et al. 1980). Elsewhere throughout the United States, in regions of sympatry, American Robins are uncommon hosts of Brown-headed Cowbirds and are strong rejecters of cowbird eggs, always (100%) grasp-ejecting both natural and model cowbird eggs from experimentally parasitized nests (Rothstein 1982, Croston and Hauber 2014).

Egg-rejection experiments. Redstart nests were parasitized by adding one of three types of artificial egg models. We manufactured egg models from plaster-of-Paris and painted them with acrylic paint for egg experiments. The size, mass, and shape of artificial egg models matched those of cowbird eggs (detailed in Croston and Hauber 2014). The cowbird egg model (invasive parasite) was creamy-white in background color, and we added either immaculate model eggs or those spotted with brown speckles concentrated around the blunt pole of eggs (Fig. 3); the latter models resembled a real cowbird egg (Croston and Hauber 2014). The blue egg model (control) was the same size as the cowbird egg model, but was painted a blue color designed to resemble those of the cuckoo race that parasitizes redstarts (described in Samaš et al. 2014).

Each nest was parasitized by an experimenter (PS) during the egg-laying stage or the first 7 d of incubation. The experimenter added an experimental egg in the nest cup and did not remove any host eggs. Based on previous research, egg addition vs. exchange has no effect on rejection probability in cuckoo or cowbird hosts relative to exchange of one host egg for one experimental parasitic egg (Davies and Brooke 1989, Grim et al. 2011, Croston and Hauber 2014).

Fig. 3. Model egg of a Brown-headed Cowbird in a nest of a Common Redstart at our Finland study site.

We checked nest contents every 2–3 d and employed the standard 6-d exposure period to evaluate host responses as acceptance or rejection of cuckoo parasitism (Grim et al. 2011). The egg model was assumed to be accepted if found in an active nest on the sixth day after placement. After each acceptance, we removed the egg model and sometimes re-used it in other experimental nest, but only after the model was cleaned and found to have no signs of peck-marks or other damage. In four of 29 nests, we performed two experimental trials in randomly chosen order, but always with different types of egg models. In these repeated experiments, we followed the methods of Samaš et al. (2011); 2 d after the outcome of the first trial (acceptance or rejection), we placed a model of the other type into the nest. Again, we checked the nest daily until ejection or acceptance up to 6 d. Nest desertion (Kosciuch et al. 2006) was not a specific response to parasitism in redstarts because desertion rate of experimental (3 of 32) and control (2 of 16) nests did not differ ($\chi^2 = 0.1$, $P = 0.74$).

American Robin nests were parasitized using model plaster-of-Paris cuckoo eggs (Fig. 4). We again used three types of model eggs, all matching the size of Common Cuckoo eggs from

Fig. 4. (1) Two eggs of an American Robin, (2) redstart type of a model Common Cuckoo egg, (3) pipit type of a model Common Cuckoo egg, and (4) a model egg intended to be mimetic of an American Robin egg from our California study site.

the host race (gens) that parasitized Common Redstarts (detailed in Samaš et al. 2014). One cuckoo egg type (hereafter redstart model; Grim et al. 2011) was immaculate pale blue, painted to resemble the egg of the cuckoo's redstart gens (see above), but also similar to the eggs of cuckoo gens that parasitizes Bluethroats (*Luscinia svecica*) and, occasionally, *Turdus* thrushes in Siberia (Malchevsky 1987). The second cuckoo egg type (hereafter pipit model; Grim et al. 2011) was gray-blue and spotted with brown spots, similar to the eggs of cuckoo gens that parasitize pipits (*Anthus* spp.) in Europe (Davies 2000) and northeastern Siberia (Tomkovich 2012). The third type was blue-green in color and mimicked the color of American Robin eggs (detailed in Croston and Hauber 2014).

American Robin nests were found (by VD) during nest construction. As soon as a nest was found to contain two robin eggs, a model was added, with the order of colors determined by rolling a dice. For robins, we re-visited nests after 5 d (Aidala et al. 2015) and removed the first model (if still present); in some cases, a second model (always of a different color, determined by a coin toss) was added. The latency of robin egg rejection is always 4 d or less (Croston and Hauber 2014), thus our conclusions would not be affected by using a 6-d rejection criterion. If a nest received a new model egg, it was then re-visited after another 5 d to evaluate the outcome (presence/absence) and remove the second model (if still present). Each model egg was used only once. Experiments continued until at least 10 trials were successfully completed for each of the cuckoo egg model types. No nests with eggs were abandoned during the study, but seven were lost to predation or during a strong thunderstorm.

Statistical analyses. We ran nominal logistic models to analyze the outcome (acceptance/ejection) of model presentations for both species pooled, with the following predictors in the full model: host species, parasite vs. control model egg, spotting nested within parasite eggs, and presentation order. For significance, we set $\alpha = 0.05$ and sequentially removed each non-significant terms starting with the highest P value from the model until we arrived to a minimal adequate model. We present the test statistics and P values for each predictor from the model just before it was removed or, for significant terms, from the final model.

RESULTS

The logistic regression revealed significant effects of the parasitic vs. control model egg treatments ($\chi^2_{1,4} = 4.8$, $P = 0.029$) and of the spotting vs. immaculate nested within the parasitic models ($\chi^2_{1,4} = 15.4$, $P < 0.0001$), irrespective of experimental order ($\chi^2_{1,1} = 0.1$, $P = 0.74$), host species identity ($\chi^2_{1,1} = 0.55$, $P = 0.46$), and with a non-significant species x treatment effect ($\chi^2_{1,1} = 1.9$, $P = 0.16$). Specifically, redstarts rejected spotted cowbird models (N = 12) most often and mimetic control eggs (N = 10) least often (Fig. 5). Similarly, robins rejected spotted parasite (pipit-cuckoo, N = 11) models the most often, but did not reject either immaculate parasite (redstart-cuckoo, N = 10) or mimetic control eggs (N = 7, Fig. 5).

DISCUSSION

Our results suggest that transoceanic invasions by brood parasites will likely have complex consequences. In North America, the short-term effects of invasion by Common Cuckoos may depend on which one gens or multiple gentes are involved in colonizing and parasitizing which new sites and particular new host species. We predict the acceptance of all cuckoo eggs by acceptor hosts of Brown-headed Cowbirds irrespective of cuckoo host race and egg coloration

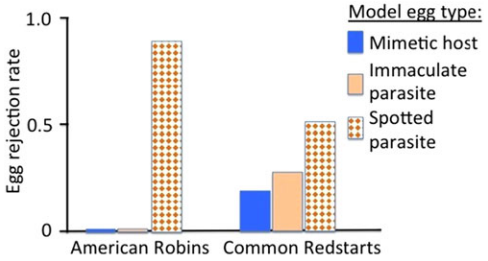

Fig. 5. Rejection responses of American Robins in California and Common Cuckoos in Finland to experimentally introduced parasitic egg model types of Common Cuckoos and Brown-headed Cowbirds, potentially invasive brood parasite species.

(Abernathy and Peer 2014). Our results also suggest that some cuckoo gentes might even be successful in parasitizing American Robin nests (a host that rejects cowbird eggs). In addition, robins and perhaps other rejecter host species in Alaska may show reduced behavioral defenses against cuckoos compared to those in California, just as they do against cowbird eggs (Kuehn et al. 2014); Alaska is outside the native range of cowbirds and will most likely be the foothold area for cuckoo colonization. For more accurate predictions, we would need a behavioral and experimental survey of breeding songbirds of western Alaska, particularly those that are the most likely first victims of cuckoo parasitism because they or their close relatives occur on both continents or serve as cuckoo hosts in Siberia, that is, American Pipits (*A. rubescens*), Red-throated Pipits (*A. cervinus*), Arctic Warblers (*Phylloscopus borealis*), Bluethroats, and, possibly, Yellow Wagtails (*Motacilla flava*) (Kistschinsky 1968, Malchevsky 1987, Tomkovich 2012). However, it is worth noting that most cuckoo hosts show high intraspecific consistency (repeatability for data from different populations) in their responses to parasitism, that is, even a single population may be reasonably representative of the typical species anti-parasite responses (e.g., Soler and Møller 1996, Grim et al. 2011).

Determining whether cuckoo chicks can be successfully raised and hatched in nests of acceptor American Robins would also require further experimentation, especially because Eurasian *Turdus* thrushes are notoriously rare and poor hosts of Common Cuckoos due to their unusual nest cup structure or unwillingness to care for parasite chicks (Grim et al. 2011). Over a longer time scale, cuckoos faced with a naïve avifauna can be expected to rapidly evolve greater behavioral flexibility in host choice (Lahti et al. 2009) than in Siberia, and to eventually evolve new egg morphs that might be mimetic of new hosts, as seen in Cuckoo Finches (*Anomalospiza imberbis)* during the 20th century (Spottiswoode and Stevens 2012). However, this process will likely require several generations and might give native species a better chance to at least partially adapt to the novel threat (Cruz et al. 2008).

In Europe, the prevalence of egg rejection among passerine hosts is much greater than in North America (Aviles et al. 2006), and the implications of our experiments here are different. Common Redstarts rejected model cowbird eggs at rates similar to non-mimetic model and painted natural eggs (Rutila et al. 2002, Hauber et al. 2014), and many other European songbirds have also evolved defenses against cuckoo parasitism that should largely protect them from cowbird invasion (except in cases when the cowbird egg happens to match a host's own egg coloration; Klippenstein and Sealy 2010). However, ~50% of spotted cowbird model eggs were still accepted by redstarts, implying partial success of even non-mimetic parasites in these nests. Also, many cuckoo hosts learn to defend their nests vigorously from approaching cuckoo adults (Thorogood and Davies 2012). Recordings of natural parasitism events even showed that Eurasian Reed-warblers (*Acrocephalus scirpaceus*) strongly reject natural cuckoo eggs only when they detected a cuckoo female during laying; when a cuckoo was not observed during the act of laying, cuckoo eggs were always accepted (Moksnes et al. 2000, see also Hanley et al. 2015). Cowbirds may not elicit nest defense behaviors and, consequently, without a shift in the acceptance thresholds of hosts, egg rejection rates of non-mimetic cowbird eggs could be lower than for non-mimetic cuckoo eggs (Hauber et al. 2006). Cowbirds, in contrast to cuckoos, do not have longer nesting periods than both current and potential hosts, thus their fitness and spread cannot be limited, even in principle, by host chick discrimination without recognition (Grim et al. 2003, Grim 2007). Finally, cowbirds are known to parasitize many species that would not be suitable hosts for cuckoos, such as cavity nesters with small entrances (e.g., *Protonotaria* warblers) and large thrush species (e.g., American Robins, *Turdus* thrushes; Friedmann and Kiff 1985). Such species in Europe may not reject parasitic eggs of any kind (Davies and Brooke 1989, Grim et al. 2014). Again, predicting the possible short-term effects of cowbird invasion more accurately would require conducting egg rejection studies with songbirds in the region most likely to be the cowbirds' initial foothold (i.e., the British Isles). Because cowbirds do not have host-specific gentes, their choice of potential hosts in Europe remains uncertain, although *Emberiza* buntings might be most at risk as the only European birds closely related to some of the most frequent hosts in eastern Canada (Terrill 1961). The potential effects of a cowbird invasion of northeastern Siberia are more difficult to predict because the responses of native birds of the region to any kind of brood parasitism remain virtually unknown.

Overall, our results indicate that transoceanic invasions by brood parasites will likely have complex consequences, and that more extensive studies are needed for making more accurate predictions of the impact of these potentially impending events. To assess possible effects of invasion, we recommend monitoring the populations of hosts most likely to be exposed.

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