Notes

Egg Laying in Inappropriate Nests by the Brown-headed Cowbird (*Molothrus ater*): Acts of Parasitism or Emergency Egg Dumping?

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The generalist, brood-parasitic Brown-headed Cowbird (*Molothrus ater*) has been found to parasitize the nests of about 220 species, mostly passerine birds. Among the thousands of documented cases of parasitism are rare records of egg laying in nests in which the cowbird stands no chance of success, because its diet or developmental strategy are incompatible with those of the "host" species. Forty-four nests of 16 such inappropriate host species are reviewed: 23 nests of nine precocial species (water birds and shorebirds) plus 21 nests of seven altricial species (a raptor, doves, cuckoos, a hummingbird, and a woodpecker). Two hypotheses explain inappropriate egg laying. In the "normal laying" hypothesis, Brown-headed Cowbirds may lay dozens of eggs in nests they encounter, including the occasional inappropriate nest. In the "emergency laying" hypothesis, females, on discovering that a selected nest has failed, must lay or "dump" her eggs elsewhere, in nests of inappropriate hosts or already-parasitized nests of regular hosts. Support for either hypothesis will require electronic surveillance of movements of nest-searching and laying Brown-headed Cowbirds to generate fine-scale spatial data that confirm whether parasitism on inappropriate nests occurs at the usual laying time for pre-selected nests (around sunrise) or later in the day if the chosen nest has failed and emergency laying is required.

Key Words: brood parasitism; Brown-headed Cowbird; egg dumping; emergency egg laying; host incompatibility; host selection; laying time; multiple parasitism; *Molothrus ater*

Introduction

Obligate avian brood parasitism is a reproductive strategy in which a female lays all of her eggs in another species' nest and relies on the "host" to rear her young. Hosts that accept the parasitic young usually experience reduced reproductive success, which has resulted in the evolution of a suite of adaptations by hosts to counter these costs (Payne 1977; Rothstein 1990; Ortega 1998; Davies 2000). The success of parasitism among potential host species is variable and, therefore, we may ask: what constitutes a good host? When any bird lays an egg in another bird's nest, the probability of success is increased if the host species is able to raise the parasite's offspring to independence. Friedmann (1929, 1963) proposed four requirements with respect to the suitability of hosts of parasitic cowbirds (*Molothrus* spp.): (1) they exhibit an altricial post-hatching pattern of development, (2) they lay eggs not much larger than the cowbird's, (3) they exhibit the "normal method" of feeding nestlings, i.e., adults placing food into the nestlings' gaping bills, and (4) they feed young a "typical passerine" (arthropod) diet that will also sustain the cowbird's development (also see Ortega 1998; Peer and Bollinger 1998). Underlying these conditions is the basic one that the host accepts foreign eggs (Rothstein 1975).

Eggs of the obligate brood-parasitic Brown-headed Cowbird (*Molothrus ater*) have been found in nests of more than 220 species of birds, of which more than 140 species of passerine birds have been documented as fledging the parasite's young (Lowther 2010). The Brown-headed Cowbird, therefore, has been designated a generalist parasite because of its use of so many hosts, in contrast to many species of parasitic cuckoos in which females parasitize only a single host species (Davies 2000). Among the species whose clutches have been recorded receiving one or more Brown-headed Cowbird eggs are ones in which the young parasite, even if hatched, stands no chance of survival because the patterns of development of host and cowbird are completely incompatible. This is termed "inappropriate" laying, although it has also been called "egg-dumping" and "freak" or "accidental" laying by other authors (e.g., Friedmann 1966; Friedmann *et al.* 1977). The host species may be precocial (e.g., ducks and shorebirds) and, because the young leave the nest within a few hours of hatching, the cowbird is left behind. Other inappropriate hosts, however, may be altricial (e.g., doves and cuckoos); although the young develop in the nest, the cowbird's diet requirements are not met. Speculation on the reasons for inappropriate laying has focused on indiscriminate laying by Brown-headed Cowbirds or females committed to laying their eggs on a given morning forced at the last minute to lay elsewhere, after discovering their previously selected nest has been destroyed.

Objectives

The first objective of this review was to compile the anecdotal records of inappropriate laying by the Brown-headed Cowbird that are scattered throughout the liter-

ature, although most have been included in host catalogues and supplements compiled by Friedmann (1931, 1963, 1966, 1971), Friedmann *et al.* (1977), and Friedmann and Kiff (1985) and, more recently, listed in Ortega (1998) and Lowther (2010). I corresponded with curators of egg collections and, if possible, original observers to augment details of records and clarify information on the provenance of clutches and success of host and cowbird. This met with variable success, but I summarized the information available for each record regardless of completeness to bring the records up to date.

The second objective was to examine the act of inappropriate laying in the context of results of recent studies of nest-searching behaviour and time of day of laying by Brown-headed Cowbirds and hosts and to suggest studies using techniques of electronic surveillance of nest-searching and laying females to remove the anecdotal records from the realm of speculation.

In the "normal laying" hypothesis, Brown-headed Cowbirds lay dozens of eggs in random nests as encountered, including the occasional inappropriate nest or already-parasitized nest of a regular host. In the "emergency laying" hypothesis, females that discover that a previously selected nest has been destroyed, unable to retain their hard-shelled eggs in the oviduct for more than a few hours, need another place to lay. Laying in inappropriate nests would be expected to occur around sunrise, at the cowbird's normal laying time (Scott 1991; McMaster *et al.* 2004), if nests are preselected, or later in the day if laying is an emergency.

Records of Inappropriate Laying

Inappropriate laying is a rare event. Forty-four nests of 16 inappropriate "host" species have been recorded: 23 nests of nine precocial species, i.e., water birds and shorebirds, and 21 of seven altricial species, i.e., a raptor, doves, cuckoos, a hummingbird, and a woodpecker (Appendix I). All nests received one cowbird egg, except for a Blue-winged Teal (*Anas discors*) nest that received two cowbird eggs plus a third cowbird egg discovered on the ground nearby and two Wilson's Phalarope (*Steganopus tricolor*) nests that each received two cowbird eggs. Sixteen (69.5%) of the 23 cases of inappropriate parasitism on precocial species involved four species of shorebird, but, among these, eight (50%) were of parasitism on the Spotted Sandpiper (*Actitis macularius*). Frequency of parasitism on the 21 altricial species involved eight records (38.1%) of doves and 10 records (47.6%) of cuckoos.

The rarity of cowbird parasitism on two inappropriate host species listed in Appendix I (Mourning Dove [*Zenaida macroura*] and Black-billed Cuckoo [*Coccyzus erythropthalmus*]) was confirmed by co-workers and me; we recorded no parasitism on over 400 nests of the former species and over 60 nests of the latter, examined over more than 35 years (1974–2010) of monitoring a Brown-headed Cowbird host community at Delta Marsh, Manitoba. Mourning Doves eject some cowbird eggs from their nests (Peer and Bollinger 1998), but we likely would have recorded some parasitism on this species, even if it had occurred infrequently.

Of the 23 parasitized nests of precocial species, (1) six failed (three depredated, two flooded, and one deserted before cowbird eggs were laid); (2) cowbird egg(s) disappeared from three (one nest later depredated); (3) a cowbird egg was collected from one nest, but the host clutch remained active; (4) host eggs but not cowbird eggs hatched at three nests; and (5) fates were undetermined at 10 nests. Of the 22 parasitized nests of altricial species, (1) two failed (one depredated and one deserted); (2) a cowbird egg disappeared from one nest that was later depredated; (3) parasitized clutches were collected from five nests; (4) a cowbird egg hatched, but the nestling disappeared from one nest; (5) unsubstantiated record of cowbird fledging from one nest; and (6) fates were undetermined at 11 nests.

Discussion

Parasitism on nests in which a young Brown-headed Cowbird stands no chance of success is extremely rare, in light of the thousands of reports of parasitism on nests of passerine species that traditionally serve as hosts (lists compiled by Herbert Friedmann and colleagues [also references in Appendix I]; also Ortega 1998; Lowther 2010). This parasitism is probably inconsequential to the reproductive success of parasite and host and, therefore, of little evolutionary importance. Nests that failed apparently did so unrelated to parasitism or the clutches were collected by oologists; nests that remained active generally were not inspected frequently enough to determine the outcome (Appendix I). The cowbird's success was limited in the first place because of its 10- to 11-day incubation period (Briskie and Sealy 1990); thus, if hatching had occurred, the cowbird would have hatched before host young and perished from lack of parental care.

It is most interesting that this laying occurs at all, in light of the time of day of nest searching and laying by Brown-headed Cowbirds. Were these nests previously selected for parasitism or were they used as receptacles for eggs laid in an emergency after the cowbird discovered its chosen nest had failed? Studies of ovarian development of cowbirds, based on dissections of gravid females collected over the breeding season (Payne 1976; Scott and Ankney 1980, 1983) or keeping track of eggs laid in aviaries (e.g., King 1979; Holford and Roby 1993) have shown that some females are capable of laying up to several dozen eggs during the breeding season. This has led some authors to suggest that females parasitize nests as they encounter them, regardless of the potential for success, i.e., a "shotgun" approach (e.g., Preston 1948; Rothstein 1976), in the likelihood that a young cowbird will be reared. Recent studies involving molecular genetic techniques, however, have revealed that cowbirds lay fewer, more valu-

able eggs during the breeding season, which suggests selectivity among nests parasitized (reviewed *in* Sealy *et al.* 2002).

The following scenario may be envisioned, leading up to a Brown-headed Cowbird laying in an inappropriate nest. Laying occurs during a remarkably short and consistent 20-minute "window" around sunrise (Scott 1991; McMaster *et al.* 2004; Ellison and Sealy 2007), before potential hosts have laid (Neudorf and Sealy 1994). Females then generally search for and apparently select the next nest for parasitism, although nothing is known about whether females "line up" nests for parasitism. By late morning, females have generally left the host nesting area and travelled to areas to forage, eventually flying to a roost site in the evening (e.g., Rothstein *et al.* 1984; Curson *et al.* 2000). Before sunrise the next morning, females fly directly to the selected nest, approach it "stealthily," often in the dark (Scott 1991; Sealy *et al.* 2000; Sealy and McMaster 2004), and parasitize it within a few seconds (Sealy *et al.* 1995). If the selected nest has been depredated, has failed because of inclement weather, or the cowbird's attempt to parasitize it is thwarted by aggressive adults (Neudorf and Sealy 1994; also see Ellison and Sealy 2007), the female is forced to lay its egg elsewhere, which possibly accounts for records of laying 2–3 h after sunrise (e.g., Friedmann 1929; Kinser 1973).

Knowledge of the time of day cowbirds parasitized a sandpiper's, duck's, or dove's nest should reveal whether the nest has been selected originally for parasitism or parasitized in an emergency. If selected previously, the nest would be expected to have been parasitized around sunrise, the cowbird's usual laying time; if the cowbird had been forced to use the nest as an alternative receptacle, parasitism would probably have occurred later in the day. If no alternative nest is available, the cowbird may be forced to lay the egg on the ground, possibly eating it and gaining nutrients (Scott *et al.* 1992). Rather than discard the egg in an emergency, however, cowbirds may benefit by laying in already-parasitized nests.

Friedmann (1929) noted in passing that, in an emergency, a cowbird may lay in a nest of one of its regular hosts, even if it or another female has already parasitized it. In this case, young may be produced, which would account for the rarity of finding cowbird eggs laid on the ground. Multiple parasitism (more than one cowbird egg in a clutch) occurs frequently in many host populations (e.g., Ortega 1998; Trine 2000), including three species of hosts at Delta Marsh (Sealy 1992; Woolfenden *et al.* 2004). Using techniques of molecular genetics, two different groups of female Brown-headed Cowbirds were identified laying in already-parasitized nests: different females parasitizing the same nest and the same females parasitizing a nest again (McLaren *et al.* 2003; also see Ellison *et al.* 2006). Females that re-parasitize a nest may be laying in an emergency, possibly later in the morning, but without information on the time of day of laying by all cowbirds at multiply parasitized nests, repeated parasitism has been assumed to be normal laying. Data on timing of multiple parasitism in southern Texas (Ellison and Sealy 2007), obtained through watches at host nests of Brown-headed Cowbirds and Bronzed Cowbirds (*M. aeneus*), revealed that despite frequent multiple parasitism, usually by several females on the same nest and morning (Ellison *et al.* 2006), cowbirds tended to visit nests alone. More than one Brown-headed Cowbird arrived at the same nest only twice and, in each case, both cowbirds parasitized the nests. It was not known, however, whether both individuals had selected these nests for parasitism on those particular mornings.

Future Directions

Explanations for parasitism by Brown-headed Cowbirds on inappropriate hosts and elucidation of details of nest-searching behaviour in general will remain mostly speculative until researchers employ recent advances in electronic surveillance, such as passive integrated transponder technology, with passive readers and antennae (Smyth and Nebel 2013) or radio-telemetry in the same way (Wyllie 1981; Honza *et al.* 2002) to track the female cowbird's every movement during the breeding season. This technology may enable collection of the fine-scale spatial data necessary to reveal which nests are selected for parasitism and parasitized. Perch sites and the time spent on them by females could be measured in relation to the nest that is to be parasitized, linking perch site and host nest and, thus, confirming parasitism on selected nests at dawn (Scott 1991; McMaster *et al.* 2004). Nests inspected later by the researcher would confirm parasitism, because the tracking system would only reveal that the nest had been visited by a particular cowbird at a particular time, not that the cowbird had parasitized it. (Video cameras positioned above [open-cup] nests may confirm that parasitism occurred [Sealy *et al.* 2000], whereas nests would be inspected daily to monitor contents leading up to parasitism.) Information processed by nest-searching female Brown-headed Cowbirds and other brood parasites likely involves interactions among body condition and fecundity, availability of suitable hosts, responses to features of the landscape, and spatial memory; gathering such information requires continuing studies in the laboratory and detailed monitoring of movements of free-ranging individuals (e.g., Rothstein *et al.* 1987; Gates and Evans 1998; White *et al.* 2009; Guigueno *et al.* 2014).

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Literature Cited

Anonymous. 1891. Brief notes. Ornithologist and Oologist 16: 108–109.

Bendire, C. E. 1895. The cowbirds. Pages 587–624 *in* Report of the United States National Museum, Smithsonian Institution, for Year Ending June 30, 1893.

Briskie, J. V., and **S. G. Sealy.** 1990. Evolution of short incubation periods in the parasitic cowbirds, *Molothrus* spp. Auk 107: 789–794.

Buckle, D. J. 1969. Cowbird egg in Mourning Dove nest. Blue Jay 27: 170.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, and **M. C. E. McNall.** 1990. The birds of British Columbia. Volume 2, Royal British Columbia Museum, Victoria, British Columbia, Canada. 636 pages.

Coues, E. 1884. Egg of the cowbird in nest of Carolina Dove. Auk 1: 293.

Curson, D. R., C. B. Goguen, and **N. E. Mathews.** 2000. Long-distance commuting by Brown-headed Cowbirds in New Mexico. Auk 117: 795–799.

Davie, O. 1898. Nests and Eggs of North American Birds (fifth edition). Landon Press, Columbus, Ohio, USA. 509 pages.

Davies, N. B. 2000. Cuckoos, Cowbirds and Other Cheats. T and AD Poyser, London, UK. 310 pages.

Davis, S. K., J. R. Duncan, K. M. Mazur, and **P. A. Duncan.** 1999. Brown-headed Cowbird parasitizes Upland Sandpiper nest. Blue Jay 57: 73–74.

Ellison, K., and **S. G. Sealy.** 2007. Small hosts infrequently disrupt laying by Brown-headed Cowbirds and Bronzed Cowbirds. Journal of Field Ornithology 78: 379–389.

Ellison K., S. G. Sealy, and **H. L. Gibbs.** 2006. Genetic elucidation of host use by individual sympatric Bronzed Cowbirds (*Molothrus aeneus*) and Brown-headed Cowbirds (*M. ater*). Canadian Journal of Zoology 84: 1269–1280.

Friedmann, H. 1929. The Cowbirds: A Study in the Biology of Social Parasitism. Charles C. Thomas, Springfield, Illinois, USA. 421 pages.

Friedmann, H. 1931. Additions to the list of birds known to be parasitized by the cowbirds. Auk 48: 52–65.

Friedmann, H. 1934. Further additions to the list of birds victimized by the cowbird. Wilson Bulletin 46: 25–36,

Friedmann, H. 1943. Further additions to the list of birds known to be parasitized by the cowbirds. Auk 60: 350–356.

Friedmann, H. 1949. Additional data on victims of parasitic cowbirds. Auk 66: 154–162.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. United States National Museum Bulletin 233. Smithsonian Institution, Washington, DC, USA. 276 pages.

Friedmann, H. 1966. Additional data on the host relations of the parasitic cowbirds. Smithsonian Miscellaneous Collection 149: 1–12.

Friedmann, H. 1971. Further information on the host relations of the parasitic cowbirds. Auk 88: 239–255.

Friedmann, H., and **L. F. Kiff.** 1985. The parasitic cowbirds and their hosts. Proceedings of the Western Foundation of Vertebrate Zoology 2: 226–302.

Friedmann, H., L. F. Kiff, and **S. I. Rothstein.** 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contributions to Zoology 235: 1–75.

Gardner, K. A. 1981. Birds of Oak Hammock Marsh Wildlife Management Area. Manitoba Department of Natural Resources, Winnipeg, Manitoba, Canada. 172 pages.

Gates, J. E., and **D. R. Evans.** 1998. Cowbirds breeding in the central Appalachians: spatial and temporal patterns and habitat selection. Ecological Applications 8: 27–40.

Guigueno, M. F., D. A. Snow, S. A. MacDougall-Shackelton, and **D. F. Sherry.** 2014. Female cowbirds have more accurate spatial memory than males. Biology Letters 10: 20140026. Accessed 8 November 2014. http://dx.doi.org/10.1098/rsbl.2014.0026.

Hamilton, W. J., III. 1957. Blue-winged Teal nest parasitized by Brown-headed Cowbird. Wilson Bulletin 69: 279.

Hatch, D. R. M. 1971. Brown-headed Cowbird parasitism on Spotted Sandpiper and Wilson's Phalarope. Blue Jay 29: 17–18.

Hicks, L. E. 1934. A summary of cowbird host species in Ohio. Auk 51: 385–386.

Higgins, K. F. 1971. Cowbird parasitism of an Upland Plover nest. Prairie Naturalist 3: 79.

Higgins, K. F., and **L. M. Kirsch.** 1975. Some aspects of the breeding biology of the Upland Sandpiper in North Dakota. Wilson Bulletin 87: 96–102.

Holford, K. C., and **D. D. Roby.** 1993. Factors limiting fecundity of captive Brown-headed Cowbirds. Condor 95: 536–545.

Hooper, D. F. 1992. Birds of east-central Saskatchewan. Special Publication 18. Saskatchewan Natural History Society, Regina, Saskatchewan, Canada. 160 pages.

Honza, M., B. Taborsky, Y. Teuschl, W. Vogl, A. Moknes, and **E. Røskaft.** 2002. Behaviour of female Common Cuckoos, *Cuculus canorus*, in the vicinity of the host nests before and during laying: a radiotelemetry study. Animal Behaviour 64: 861–868.

Houston, C. S. 1975. Eggs of other species in Great Horned Owl nests. Auk 92: 377–378.

Houston, C. S., and **P. W. Brown.** 1982. Cowbird egg in Common Tern nest. Journal of Field Ornithology 53: 57.

Kellogg, C. D. 1900. Cowbird in a dove's nest. Bird-Lore 2: 121.

King, A. P. 1979. Variables affecting parasitism in the North American cowbird (*Molothrus ater*). PhD dissertation, Cornell University, Ithaca, New York. 109 pages.

Kinser, Jr., G. W. 1973. Ecology and behavior of the Cardinal, *Richmondena cardinalis* (L), in southern Indiana. PhD dissertation. University of Indiana, Bloomington, Indiana, USA. 200 pages.

Koons, D. N. 2000. First record of Brown-headed Cowbird egg in a Lesser Scaup nest. Wilson Bulletin 112: 544.

Lister, R. 1964. Northern Great Plains region. Audubon Field Notes 18: 515–519.

Lowther, P. E. 2010. Lists of victims and hosts of the parasitic cowbirds (*Molothrus*). Version 22. The Field Museum, Chicago, Illinois, USA. Accessed 12 September 2011 XXXX. http://fm1.fieldmuseum.org/aa/Files/lowther/CB List.pdf

McLaren, C. M., B. E. Woolfenden, H. L. Gibbs, and **S. G. Sealy.** 2003. Genetic and temporal patterns of multiple parasitism by Brown-headed Cowbirds (*Molothrus ater*) on Song Sparrows (*Melospiza melodia*). Canadian Journal of Zoology 81: 281–286.

McMaster, D. G., D. L. H. Neudorf, S. G. Sealy, and **T. E. Pitcher.** 2004. A comparative analysis of laying times in passerine birds. Journal of Field Ornithology 75: 113–122.

McNicholl, M. 1968. Cowbird egg in Mourning Dove nest. Blue Jay 26: 22–23.

McNicholl, M. K. 2009. Additional records of Brown-headed Cowbird eggs in nests of Spotted Sandpiper. Wildlife Afield 6: 168–169.

Mossop, H. 1963. Cowbirds easily adopted. Chickadee Notes 452. Winnipeg Free Press, 14 September 1963.

Neudorf, D. L., and **Sealy, S. G.** 1994. Sunrise nest attentiveness in cowbird hosts. Condor 96: 162–169.

Ortega, C. P. 1998. Cowbirds and Other Brood Parasites. University of Arizona Press, Tucson, Arizona, USA. 371 pages.

Payne, R. B. 1976. The clutch size and numbers of eggs of Brown-headed Cowbirds: effects of latitude and breeding season. Condor 78: 337–342.

Payne, R. B. 1977. The ecology of brood parasitism in birds. Annual Review of Ecology and Systematics 8: 1–28.

Peck, G. K., and **R. D. James.** 1983. Breeding Birds of Ontario, Nidiology and Distribution, Volume 1: Nonpasserines. Life Sciences Miscellaneous Publication. Royal Ontario Museum, Toronto, Ontario, Canada. 321 pages.

Peer, B. D., and **E. K. Bollinger.** 1998. Rejection of cowbird eggs by Mourning Doves: a manifestation of nest usurpation? Auk 115: 1057–1062.

Preston, F. W. 1948. The cowbird (*M. ater*) and the cuckoo (*C. canorus*). Ecology 29: 115–116.

Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250–271.

Rothstein, S. I. 1976. Cowbird parasitism of the Cedar Waxwing and its evolutionary implications. Auk 93: 498–509.

Rothstein, S. I. 1990. A model system for coevolution: avian brood parasitism. Annual Review of Ecology and Systematics 21: 481–508.

Rothstein, S. I., J. Verner, and **E. Stevens.** 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65: 77–88.

Rothstein, S. I., D. A. Yokel, and **R. C. Fleischer.** 1987. Social dominance, mating and spacing systems, female fecundity, and vocal dialects in captive and free-ranging Brown-headed Cowbirds. Pages 127–185 *in* Current Ornithology, Volume 3. *Edited by* R. F. Johnston, Plenum, New York, USA. 522 pages.

Sadler, T. S., and **M. T. Myres.** 1976. Alberta birds 1961–1970. Occasional Paper 1. Provincial Museum of Alberta, Natural History Section, Edmonton, Alberta, Canada. 314 pages.

Scott, D. M. 1991. The time of day of egg laying by the Brown-headed Cowbird and other icterines. Canadian Journal of Zoology 69: 2093–2099.

Scott, D. M., and **C. D. Ankney.** 1980. Fecundity of the Brown-headed Cowbird in southern Ontario. Auk 97: 677–683.

Scott, D. M., and **C. D. Ankney.** 1983. The laying cycle of Brown-headed Cowbirds: passerine chickens? Auk 100: 583–592.

Scott, D. M., P. J. Weatherhead, and **C. D. Ankney.** 1992. Egg-eating by female Brown-headed Cowbirds. Condor 94: 579–584.

Sealy, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. Condor 94: 40–54.

Sealy, S. G., and **D. G. McMaster.** 2004. Two additional observations of egg laying by parasitic Brown-headed Cowbirds. Blue Jay 62: 24–27.

Sealy, S. G., D. G. McMaster, S. A. Gill, and **D. L. Neudorf.** 2000. Yellow Warbler nest attentiveness before sunrise: antiparasite strategy or onset of incubation? Pages 169–177 *in* Ecology and Management of Cowbirds and Their Hosts: Studies in the Conservation of North American Passerine Birds. *Edited by* J. N. M. Smith, T. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, University of Texas Press, Austin, Texas, USA. 388 pages.

Sealy, S. G., D. G. McMaster, and **B. D. Peer.** 2002. Tactics of obligate brood parasites to secure suitable incubators. Pages 254–269 *in* Avian Incubation: Behaviour, Environment, and Evolution. *Edited by* D. C. Deeming, Oxford University Press, Oxford, UK. 421 pages.

Sealy, S. G., D. L. Neudorf, and **D. P. Hill.** 1995. Rapid laying by Brown-headed Cowbirds *Molothrus ater* and other parasitic birds. Ibis 137: 76–84.

Siddle, C. 2008. British Columbia record of a Brown-headed Cowbird egg in a Spotted Sandpiper nest. Wildlife Afield 5: 215–216.

Smyth, B., and **S. Nebel.** 2013. Passive integrated transponder (PIT) tags in the study of animal movement. Nature Education Knowledge 4(3): 3. [On-line.]

Stewart, R. E. 1975. Breeding Birds of North Dakota. Tri-College Center for Environmental Studies, Fargo, North Dakota, USA. 295 pages.

Stewart, R. E., and **C. S. Robbins.** 1958. Birds of Maryland and the District of Columbia. North American Fauna 62. United States Department of the Interior, Fish and Wildlife Service, Washington, DC, USA. 401 pages.

Trautman, M. B. 1940. The birds of Buckeye Lake, Ohio. Miscellaneous Publication 44. University of Michigan, Ann Arbor, Michigan, USA. 466 pages.

Trine, C. L. 2000. Effects of multiple parasitism on cowbird and Wood Thrush nesting success. Pages 135–144 *in* Ecology and Management of Cowbirds and Their Hosts: Studies in the Conservation of North American Passerine Birds. *Edited by* J. N. M. Smith, T. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, University of Texas Press, Austin, Texas, USA. 388 pages.

White, D. F., L. Ho, and **G. Freed-Brown.** 2009. Counting chicks before they hatch: female cowbirds can time readiness of a host nest for parasitism. Psychological Science 20: 1140–1145.

Williams, C. S., and **A. H. Trowbridge.** 1939. Wilson's Phalarope host of Nevada Cowbird. Auk 56: 77.

"Woods" [pseudonym for Robert Sutherland]. 1972. Two cowbird hosts new to Kansas. Kansas Ornithological Society Bulletin 23: 14–15.

Woolfenden, B. E., H. L. Gibbs, C. M. McLaren, and **S. G. Sealy.** 2004. Community-level patterns of parasitism: use of three common hosts by a brood parasitic bird, the Brown-headed Cowbird. Écoscience 11: 238–248.

Wyllie, I. 1981. The Cuckoo. Universe Books, New York, New York, USA. 176 pages.

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APPENDIX I. Records of egg laying by Brown-headed Cowbirds (*Molothrus ater*) in the nests of inappropriate species of birds.

Host species	Notes[1]
Precocial[2]	
Blue-winged Teal (*Anas discors*)	1. Manitoba, 8 June 1956: 3 he, 2 ce. The Blue-winged Teal flushed from an empty nest bowl on 2 June; 6 days later, three teal eggs had been depredated, apparently by a Striped Skunk (*Mephitis mephitis*), but two intact cowbird eggs were present in the nest bowl and a third cowbird egg was on the ground "about 30 yards from the destroyed nest," on 11 June (Hamilton 1957: 279). It was not known whether the teal was still attending the nest when the first cowbird egg was laid (Friedmann 1963: 45). 2. Manitoba, 30 May 1976: 4 he, 1 ce. Nest contained seven Blue-winged Teal eggs and no cowbird egg on 1 June (Gardner 1981: 151).
Lesser Scaup (*Aythya affinis*)	1. Manitoba, 16 June 1999: 6 he, 1 ce. By 22 June, 10 Lesser Scaup eggs were being incubated, but the Brown-headed Cowbird egg was missing; the nest was depredated by 26 June (Koons 2000: 554). The disappearance of the cowbird egg was interpreted as an act of ejection (Koons 2000). Laying of successive eggs, including the cowbird egg, followed by its disappearance, conform to the criteria for ejection by a host (Rothstein 1975), i.e., the parasite's egg disappeared and, in this case, the Lesser Scaup continued to attend the clutch, laying four additional eggs after the cowbird egg disappeared.
Virginia Rail (*Rallus limicola*)	1. Ontario, 7 June 1971: 8 he, 1 ce. The Virginia Rail was observed on, or flushed, from the nest five times between 6 and 11 June, with eight rail eggs recorded in total (cowbird egg was collected); two young rails were observed with adults on 11 July (ONRS, Royal Ontario Museum; confirmed by M. Peck, email, 31 October 2011; also see Friedmann *et al.* 1977: 10; Peck and James 1983: 153).
Killdeer (*Charadrius vociferus*)	1. Manitoba, 1963: 4 he, 1 ce. Reported by Mossop (1963: 24) but details are incomplete: "[Brown-headed] cowbird egg resting snugly with the usual foursome of Killdeer's very much larger eggs" (also see Hatch 1971: 18; Friedmann *et al.* 1977: 10).
Spotted Sandpiper (*Actitis macularius*)	1. Alberta, 5 June 1960:[3,4] Reported with no details by Friedmann *et al.* (1977: 10). 2. Alberta, 1964[3], 1 ce. Reported by R. W. Turner as "another cowbird egg was found in a Spotted Sandpiper nest" (Lister 1964: 518; also see Friedmann 1966: 2; Sadler and Myres 1976: 233). 3. Ontario, 5 June 1965: 4 he, 1 ce. No other details (ONRS; confirmed by M. Peck, email, 31 October 2011; also see Friedmann *et al.* 1977: 10; Peck and James 1983: 179). 4. Utah, 2 June 1968:[3], 1 ce. M. F. Baker discovered a Spotted Sandpiper nest with one cowbird egg, but no other details are available (Friedmann 1971: 241). 5. British Columbia, June 1964: 3 he, 1 ce. Record extracted from field notes of the late J. G. Sarles by R. W. Campbell, communicated to McNicholl (2009: 168). 6. Manitoba, 26 June 1970: 4 he, 1 ce. Brown-headed Cowbird egg surrounded by "the usual four" Spotted Sandpiper eggs, each pointing inward, "suggesting that the egg had been accepted"; the nest had been destroyed by 8 July before fates of the eggs could be determined (Hatch 1971: 17-18; also see Friedmann *et al.* 1977: 10). 7. Minnesota[3,4] . Oring (1997: 18; email, 1 November 2011) reported "parasitism by… Brown-headed Cowbird observed twice in 19 [years] in [north-]central Minnesota, but hatching [of cowbirds] unsuccessful." 8. British Columbia, 6 June 1984: 3 he, 1 ce. Spotted Sandpiper flushed from nest containing four warm eggs, one of which was a Brown-headed Cowbird egg (Siddle 2008: 215; also see Campbell *et al.* 1992: 152).

APPENDIX I. *(continued)*

Host species	Notes[1]
Precocial[2]	
Upland Sandpiper (*Bartramia longicauda*)	1. Minnesota: 4 he, 1 ce. "[Brown-headed] Cowbird's egg was almost buried in the bottom of the nest" (Friedmann 1931: 60); the parasitized clutch was originally in the J. Hooper Bowles egg collection, but it was not located. 2. North Dakota, 18 June 1971: 3 he, 1 ce. Upland Sandpiper flushed from nest (18 and 28 June); shell fragments and membranes of hatched sandpiper eggs and a punctured Brown-headed Cowbird egg were present on 12 July (Higgins 1971: 79; also see Stewart 1975: 235). 3. North Dakota, 1 June: 3 he, 1 ce. Adult flushed from nest on 1 and 3 June, but the clutch of three Upland Sandpiper eggs was destroyed by 5 June (Higgins and Kirsch 1975: 98). 4. Manitoba, 6 July 1991: 3 he, 1 hy, 1 ce. Upland Sandpiper was flushed from the nest, but nest could not be located on 8 July to confirm hatching of the other sandpiper eggs or the Brown-headed Cowbird egg (Davis *et al.* 1999).
Wilson's Phalarope (*Steganopus tricolor*)	1. Utah, 6 June 1938: 4 he, 2 ce. This and the following Wilson's Phalarope nest were about 7.5 m apart on a small artificial island in a marsh; the four phalarope eggs in one nest had hatched by 21 June, but the two Brown-headed Cowbird eggs remained and were later flooded; one cowbird egg "was evidently infertile, but the others [including two from the nest below] were advanced in development" (Williams and Trowbridge 1939: 77; also see Friedmann 1943: 353). 2. Utah, 6 June 1938: 4 he, 2 ce. On 28 June, three phalarope eggs had hatched, but the fourth egg, which was pipped, and both cowbird eggs had been destroyed by flooding (Williams and Trowbridge 1939: 77; also see Friedmann 1943: 353). 3. Manitoba, 15 June 1970: 4 he, 1 ce. The cowbird egg rested along the edge of the phalarope eggs, but the fate of the eggs was not determined (Hatch 1971: 17; also see Friedmann *et al.* 1977: 10).
California Gull (*Larus californicus*)	1. North Dakota, June 1899:[3,4]. A California Gull nest contained "several eggs of its own and one of the [Brown-headed] cowbird" Friedmann (1963: 46).
Common Tern (*Sterna hirundo*)	1. Saskatchewan, 7 July 1979: 2 he, 1 ce. This was the only record of a Brown-headed Cowbird egg in a tern or any other nest in 18 years of banding at Redberry Lake (Houston and Brown 1982: 57; also see Freidmann and Kiff 1985: 244).
Altricial[2]	
Ferruginous Hawk (*Buteo regalis*)	1. North Dakota, 3 May 1894: 4 he, 1 ce. A. Eastgate reported a nest with a Brown-headed Cowbird egg that Friedmann (1929: 206) described as "a purely accidental host." In fact, the cowbird egg may not have been laid there in the first place. Houston (1975) recorded eggs of three prey species in Great Horned Owl (*Bubo virginianus*) nests, possibly discarded when prey was being apportioned for the young. However, this hawk's nest already contained eggs when the cowbird's egg appeared, rendering this scenario unlikely. The cowbird may have targeted a House Sparrow's (*Passer domesticus*) nest built on the side of the hawk's nest, as this sparrow is occasionally parasitized (Friedmann *et al.* 1977: 32).
Mourning Dove (*Zenaida macroura*)	1. Iowa:[3,4]. A report by E. H. King is lacking details, but noted that "the [Mourning] Dove is the largest bird [King] had known to be chosen as the Cowbird's foster-parent" (Coues 1884; also see Friedmann 1929: 206). 2. Pennsylvania, 25 May 1899: 2 he, 1 ce. A dubious record reported by Kellogg (1900: 121) of "a [Brown-headed] Cowbird flutter[ing] off an old Grackle's nest, [which] on examination… the nest [was found] to contain a Cowbird's egg." Three days later a clutch of two Mourning

APPENDIX I. *(continued)*

Host species	Notes[1]
Altricial[2]	
Mourning Dove (*Zenaida macroura*)	Dove eggs had been laid in the nest, but three weeks later the nest contained "a Cowbird ready to fly." The record is accompanied by a photograph showing the young cowbird and two dove eggs, but Friedmann (1963: 47) found this record unconvincing because adult doves were not observed at the nest; the grackles that built the nest may have taken it over and reared the cowbird; and the Mourning Dove's method of feeding young is incompatible with feeding of a young cowbird.
	3. Ohio:[3,4]. Without details, one dove's nest was reported as parasitized among 41 host species recorded by Hicks (1934; also see Friedmann 1963: 46).
	4. Manitoba, 15 June 1965: 1 he, 1 ce. One dove egg was present on 4 June; cowbird egg laid 15 June but gone by 17 June; two dove eggs later disappeared (McNicholl 1968: 22).
	5. Saskatchewan, 4 June 1967: 1 he, 1 ce. Nest contained one dove egg on 20 May 1967; by 4 June the nest was deserted but contained one egg each of dove and cowbird; underneath the nest was a broken dove egg (Buckle 1969: 170; also see Hooper 1992: 84).
Common Ground-Dove (*Columbina passerina*)	1. Texas, 23 May 1925: 2 he, 1 ce. Friedmann found this nest, reporting that it was the only one parasitized among 10 Common Ground-Dove nests examined. Another parasitized nest discovered "from the same district years earlier" was reported without details by R. D. Camp to Friedmann (1929: 206; also see Friedmann 1963: 48).
	2. Texas, 24 May 1927: 2 he, 1 ce. R. D. Camp collected a parasitized clutch of the Common Ground-Dove that is now WFVZ no. 59610 (R. Corado, email, 7 April 2014; also see Friedmann 1929: 206).
	3. Texas, 4 June 1927:[3,4]. Friedmann *et al.* (1977: 11) reported that this parasitized clutch was in the museum of Oregon State University, but there is no record of it in that collection (B. D. Dugger, email, 26 March 2014).
Yellow-billed Cuckoo (*Coccyzus americanus*)	1. Connecticut, 8 June 1875:[3,4]. Friedmann (1963: 48) reported this parasitized egg set, collected by F. Benners, catalogued in the (Bell) Museum of Natural History (no. 39), University of Minnesota; however, the host was recorded as the Black-billed Cuckoo and both the single Black-billed Cuckoo's egg and presumably the single cowbird's egg are missing (R. Zink, email, 16 January 2014).
	2. Illinois, before 1893:[3,4], 1 ce. Record of nest with one cowbird egg observed by W. E. Loucks, without supporting evidence, "sometime prior to 1893" (Friedmann 1934: 29, 1949: 158, 1963: 48). This record formed the basis for inclusion of this species in Bendire's (1895: 594) list of host species of the Brown-headed Cowbird.
	3. Pennsylvania, 30 April 1912: 4 he, 1 ce. Friedmann (1971: 242) reported this parasitized clutch, collected by A. Benners and originally housed in the Rockbridge Alum Springs Biological Laboratory, Goshen, Virginia (M. Brodsky, email, 13 January 2014). The egg set is now WFVZ no. 59747 (R. Corado, email, 7 April 2014).
	4. Ohio, before 1934: 5 he, 1 ce. One of eight Yellow-billed Cuckoo nests inspected 1922–1934, but dates of observations of the nests, including the parasitized nest, were not given (Trautman 1940: 273, 393; also see Friedmann 1949: 158).
	5. Kansas, 20 June 1962: 1 he, 1 ce. The nest was empty on 25 June ("Woods" 1972: 14-15; also see Friedmann *et al.* 1977: 11).
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	1. New York:[3], 1 ce. This record was obtained by F. Morris and E. A. Eames who documented it in the botanical literature; Friedmann (1943: 353) pointed it out to ornithologists.
	2. Maryland, 26 May 1932: 1 he, 1 ce. Details were provided by R. E. Stewart to Friedmann (1963: 48; also see Stewart and Robbins 1958: 329).

APPENDIX I. *(continued)*

Host species	Notes[1]
Altricial[2]	
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	3. Quebec, 15 June 1938: 2 he, 1 ce. The information pertaining to this clutch was sent to Friedmann (1963: 48) by L. M. Terrill. 4. Michigan, 24 June 1969: 2 hy, 1 ce. One of 14 Black-billed Cuckoo nests inspected in 1968 and 1969 by S. I. Rothstein. At the parasitized nest, the cowbird egg was gone on 27 June, but "2 half-shells from it were found almost directly beneath the nest. The half-shells were dried out, indicating that the cowbird egg had hatched. Probably, since the usual food of cuckoos — bristly caterpillars — was unsuitable to the cowbird infant, it died shortly after hatching and its dead body was removed by the host" (Friedmann *et al.* 1977: 11). 5. Wisconsin, 13 July 1957: 2 he, 1 ce. Egg set collected by C. H. Richter and housed in Richter Natural History Collection, University of Wisconsin, Green Bay (Friedmann and Kiff 1985: 244). Sent to J. Hurley, Yakima, Washington, on 21 October 1958 (T. Erdman, email, 15 January 2014), but current whereabouts of the Hurly collection, including this egg set, is not known.
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	1. Ohio:[3]. Listed as a host of the Brown-headed Cowbird, without supporting data, by Bendire (1895: 594) and Davie (1898: 339). Friedmann (1963: 49) referred to another vague record communicated to him by L. Jones, who wrote that he had taken a cowbird's egg from a nest of [Red-headed Woodpecker] in Ohio "many years ago," but supplied no details.
Ruby-throated Hummingbird (*Archilochus colubris*)	1. Massachusetts, July 1890: 0 he, 1 ce. Report of a Ruby-throated Hummingbird's nest "completely filled" by a Brown-headed Cowbird's egg (Anonymous 1891: 109). Friedmann (1929: 206-207) initially doubted this record, believing the nest was likely that of an Eastern Wood Peewee (*Contopus virens*), but he decided later to accept this improbable record because a cowbird egg would not fill the cup of a peewee's nest (Friedmann 1963: 58).

Note: he = host egg(s), hy = host young, ce = Brown-headed Cowbird eggs, ONRS = Ontario Nest Record Scheme, WFVZ = Western Foundation of Vertebrate Zoology.

[1]Location, date, and contents of nest recorded when first inspected.

[2]Post-hatching mode of development.

[3] Number of host eggs unknown.

[4] Number of cowbird eggs unknown.