egg size on the growth of nestling Pied Flycatchers *Ficedula hypoleuca*. Ann. Zool. Fenn. 21:213–216.

KARLSSON J., AND S. G. NILSSON. 1977. The influence of nest-box area on clutch size in some hole-nesting passerines. Ibis 119:207–211.

KENNEDY, E. D. 1991. Determinate and indeterminate egg-laying patterns: a review. Condor 93:106–124.

KENNEDY, E. D., AND H. W. POWER. 1990. Experiments on indeterminate laying in House Wrens and European Starlings. Condor 92:861–865.

KERN, M. D., AND R. J. COWIE. 1996. The size and shape of eggs from a Welsh population of Pied Flycatchers—testing Hoyt's use of egg dimensions to ascertain egg volume. J. Field Ornithol. 67:72–81.

LUNDBERG, A., AND R. V. ALATALO. 1992. The Pied Flycatcher. T. and A. D. Poyser, London.

MACWHIRTER, R. B. 1989. On the rarity of intraspecific brood parasitism. Condor 91:485–492.

MORENO, J., L. GUSTAFSSON, A. CARLSON, AND T. PÄRT. 1991. The cost of incubation in relation to clutch-size in the Collared Flycatcher *Ficedula albicollis*. Ibis 133:186–193.

NUR, N. 1988. The cost of reproduction in birds: an examination of the evidence. Ardea 76:155–168.

POWER, H. W., E. D. KENNEDY, L. C. ROMAGNANO, M. P. LOMBARDO, A. S. HOFFENBERG, P. C. STOUFFER, AND T. R. MCGUIRE. 1989. The parasitism insurance hypothesis: why starlings leave space for parasitic eggs. Condor 91:753–765.

POTTI, J. 1993. Environmental, ontogenetic, and genetic variation in egg size of Pied Flycatchers. Can. J. Zool. 71:1534–1542.

SANZ, J. J., AND J. MORENO. 1995. Experimentally induced clutch size enlargements affect reproductive success in the Pied Flycatcher. Oecologia 103:358–364.

SIIKAMÄKI, P. 1995. Habitat quality and reproductive traits in the Pied Flycatcher—an experiment. Ecology 76:308–312.

SILVERIN, B. 1980. Seasonal development of reproductive organs in the female Pied Flycatcher *Ficedula hypoleuca* and experimental studies on duration of her re-nesting ability. J. Zool. 190:241–257.

SILVERIN, B., AND J. C. WINGFIELD. 1982. Patterns of breeding behaviour and plasma levels of hormones in a free-living population of Pied Flycatchers, *Ficedula hypoleuca*. J. Zool. 198:117–129.

VON HAARTMAN, L. 1967. Clutch-size in the Pied Flycatcher. Proc. Int. Ornithol. Congr. 14:155–164.

EGG RECOGNITION IN YELLOW-BILLED AND BLACK-BILLED MAGPIES IN THE ABSENCE OF INTERSPECIFIC PARASITISM: IMPLICATIONS FOR PARASITE-HOST COEVOLUTION[1]

GINGER M. BOLEN[2]
Museum of Vertebrate Zoology, 3101 VLSB, University of California, Berkeley, CA 94720

STEPHEN I. ROTHSTEIN
Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106

CHARLES H. TROST
Department of Biology, Idaho State University, Box 8007, Pocatello, ID 83209

Abstract. Yellow-billed Magpies (*Pica nuttalli*) ejected 100% of nonmimetic eggs placed in their nests despite such behavior having no detectable present day benefits. They are not currently parasitized, nor is there any evidence of a recently extinct brood parasite. Furthermore, there was no molecular evidence of conspecific parasitism, and Yellow-billed Magpies accepted

eight of nine conspecific eggs transferred between nests, so recognition would rarely be of benefit if conspecific parasitism occurred. Thus, we suggest that egg recognition in Yellow-billed Magpies is a plesiomorphic trait, a primitive character inherited from a remote ancestor, its nearest relative, the Black-billed Magpie (*Pica pica*). The latter suffers from parasitism by Great Spotted Cuckoos (*Clamator glandarius*) in Eurasia and displays rejection behavior throughout Europe in populations that are allopatric and sympatric with this cuckoo. As would be expected if Yellow-billed Magpies inherited rejection behavior from the Black-billed Magpie, or the common ancestor of both species, we found that North American Black-billed

Magpies also have well developed egg recognition despite being unaffected by interspecific parasitism. The long-term retention of host defenses as is indicated by magpies has major implications for the coevolutionary interactions between brood parasites and their hosts.

Key words: Black-billed Magpie, brood parasitism, coevolution, egg recognition, Pica nuttalli, Pica pica, Yellow-billed Magpie.

A generalization arising from previous studies of egg recognition is that it is well developed in many species that are actual or potentially suitable hosts of current brood parasites (Rothstein 1975, 1990, Moksnes et al. 1991). Such suitable host species are currently parasitized or could be parasitized given basic aspects of their breeding biology, such as the food they feed their nestlings and nests that are accessible to known obligate parasites. Although many actual and potential hosts lack egg recognition (Rothstein 1975a), most likely due to evolutionary lag (Rothstein 1990) or costs incurred by host defenses (Rohwer and Spaw 1988, Lotem et al. 1995), recognition behavior is much more prevalent among these species than among species that are unsuitable as hosts. This difference between the behavior of suitable and unsuitable hosts is strong evidence that obligate brood parasites are the primary selective pressure responsible for the evolution of egg recognition (Davies and Brooke 1989a, Rothstein 1990, Moksnes et al. 1991).

A particularly interesting category of suitable hosts are populations that are no longer parasitized, either because they have become allopatric with respect to parasites that could victimize them or because parasites have shifted to other hosts (Soler et al. 1998). Retention of egg recognition in the absence of selection has significant implications for the long-term coevolution between parasitic birds and their hosts (Rothstein 1990).

Here we present evidence for the retention of egg recognition in the absence of brood parasitism in Yellow-billed Magpies (*Pica nuttalli*). We studied this species for two reasons. First, the Yellow-billed Magpie is well beyond the size range of birds that can be parasitized successfully (Friedmann and Kiff 1985) by its only sympatric brood parasite, the Brown-headed Cowbird (*Molothrus ater*). Furthermore, the latter has been sympatric with the Yellow-billed Magpie for less than a century (Rothstein 1994) and no other obligate brood parasite is known to have been sympatric with the species during the period of historical records.

Second, its only congener, the Black-billed Magpie (*P. pica*), shows highly developed egg discrimination in parts of Europe where it is heavily parasitized by the Great Spotted Cuckoo (*Clamator glandarius*). The Black-billed Magpie also is a host of the Koel (*Eudynamys scolopacea*), a cuckoo with which it is sympatric in Asia (Johnsgard 1997). Both cuckoos lay eggs similar to those of the magpie. Soler and Møller (1990) reported that parasitized populations of Black-billed Magpies in Spain show varying levels of discrimination of mimetic cuckoo eggs that relate to the duration of each population's sympatry with Great Spotted Cuckoos. Extensive experiments on six other European Black-billed Magpie populations allopatric with this cuckoo show that each exhibits rejection rates of 52.9% to 100% for nonmimetic eggs (Soler et al. 1999). Thus, direct contact with cuckoos is not necessary to maintain high levels of egg recognition in Black-billed Magpies.

Given the Yellow-billed Magpie's lack of recent contact with brood parasites and the widespread presence of egg recognition in European Black-billed Magpies, we assumed that a demonstration of egg recognition in Yellow-billed Magpies would indicate that this behavior may be retained for extremely long periods of time (thousands of generations), possibly even through a speciation event. This hypothesis depends on three assumptions concerning the Yellow-billed Magpie: (1) neither inter- nor intra-specific parasitism is currently maintaining egg recognition, (2) neither inter- nor intra-specific parasitism has occurred during the recent history of the species, and (3) the species is descended from an allopatric population that diverged from the Black-billed Magpie.

In addition to reporting on Yellow-billed Magpie responses to nonmimetic eggs, we report on their response to conspecific eggs as a partial test of the possible importance of intraspecific parasitism. Finally, we report the responses of North American Black-billed Magpies (*P. p. hudsonia*) to nonmimetic eggs as a partial test of the hypothesis that Yellow-billed Magpies retained egg-recognition from a Black-billed Magpie ancestor.

METHODS

Experiments on Yellow-billed Magpies were conducted at Hastings Natural History Reservation and the adjacent Oak Ridge Ranch in Carmel Valley, California. Most of this area is steep hillside with scattered, open oak savanna.

Experiments with nonmimetic eggs were initiated by placing a single nonmimetic egg in each of 12 nests. Nonmimetic eggs were either model eggs cast in plaster of Paris and painted red, blue, or white, or real quail (*Coturnix* sp.) eggs given a red coat of paint that allowed the egg markings to show through. Previous studies have shown that rejecter species respond to plaster eggs in the same ways as to real eggs (Rothstein 1975a, 1975b), whereas accepter species, including other species of corvids, do not reject highly nonmimetic eggs (Yom-Tov 1976, Soler 1990).

Our use of quail eggs matches the procedure Soler and Møller (1990) used to test for egg recognition and rejection in Black-billed Magpies in Europe. Plaster and quail eggs were painted to make them easily distinguishable from magpie eggs because our initial goal was not to test the limits of magpie discrimination but to determine whether they show any discrimination at all. Similarly, introduced eggs were also distinct from magpie eggs in size. Yellow-billed Magpie eggs average 31.5 × 22.5 mm (Reynolds 1995) compared to 28.3 × 20.7 mm for the plaster and 32.6 × 25.7 mm for the quail eggs. We then checked each nest five to six days after addition of the nonmimetic egg to determine whether egg rejection (removal from nest) occurred. Less than 1% of the rejections in related studies occurred after day five, so eggs accepted for five days

TABLE 1. Percent of eggs rejected by Yellow-billed Magpies within five days of addition to clutch.

Type of egg added	Nesting stage	Host egg removed	Host egg not removed	Total	
Nonmimetic	incubation	100 (3/3)	100 (5/5)	100 (8/8)	
	laying	100 (2/2)	—[a]	100 (2/2)	
Mimetic	incubation	0.0 (0/5)	33.3 (1/3)[b]	0.1 (1/8)	
	laying	—[a]	0.0 (0/1)	0.0 (0/1)	

[a] Manipulation not done.
[b] One nest at which there was no rejection had previously been used in a model egg manipulation.

were equated with eggs that had been accepted for the full life of the nest (Rothstein 1975a).

Nonmimetic-egg experiments in 1996 and 1997 indicated that Yellow-billed Magpies show egg discrimination. Thus, we also performed mimetic egg experiments by switching eggs between magpie nests in 1997 to test the degree of discrimination. Experiments with mimetic eggs were initiated by using a permanent marker to place a small number on each magpie egg corresponding to the nest in which it originated. We then placed a single mimetic egg (a magpie egg from a different nest) into nine experimental nests. Nests were checked five days later to determine the response to the manipulation.

All manipulations were done between 06:00 and 18:00. The majority of trials began after egg laying at the nest was finished (incubation phase), however, a few trials began during the laying phase. During each nest check, all eggs were removed from the nest and checked for peck marks or other damage. To control for the possibility that eggs might be rejected due to an increased number of eggs in the nest, one host egg was removed from the host clutch in 5 of 10 nonmimetic trials and 5 of 9 mimetic trials. Unless otherwise stated, no nest was used for more than one trial.

Egg-recognition experiments on Yellow-billed Magpies suggested that the ability to recognize foreign eggs may have been retained from a Black-billed Magpie ancestor. Thus, in 1999, nonmimetic-egg recognition experiments were conducted on North American Black-billed Magpies on the Sterling Wildlife Management Area in southeastern Idaho. We placed a single nonmimetic egg in each of 13 nests. Nonmimetic eggs were made by painting one egg red or white in each nest. Twelve egg replacements occurred during the incubation phase and one during the laying phase. We then checked each nest 24–48 hr after addition of the nonmimetic egg to determine whether egg rejection occurred.

RESULTS

Timing of manipulation (laying vs. incubation), type of nonmimetic egg (plaster vs. quail), and removal vs. nonremoval of a host egg did not significantly affect Yellow-billed Magpie host response (two-tailed Fisher exact test, $P > 0.05$ for all cases; Table 1), thus results were combined for analysis. In two nonmimetic trials, eggs hatched before the 5-day check for rejection, therefore these nests were not used in the analyses. Ejection of the nonmimetic egg occurred by day 5 at each of the 10 remaining nests. In one nest, one host egg as well as the nonmimetic egg was found to be

missing, and an additional host egg showed damage. Rejection occurred in only one of nine mimetic egg trials (11.1%), which is a significantly lower rejection rate than for nonmimetic eggs (two-tailed Fisher exact test, $P < 0.001$). The difference in rejection rate between nonmimetic and mimetic eggs was not due to easier detectability of model eggs as real and plaster nonmimetic eggs were rejected at equal frequencies (2/2 and 8/8, respectively). Note, too, that most birds reject damaged eggs even if they display no egg recognition (Kemal and Rothstein 1988) and that the one mimetic-egg rejection may have occurred due to damage we caused while transferring the egg from one nest to another, rather than to egg recognition. Unfortunately, the 14.2-m mean height of magpie nests in our study made nest access and handling of eggs difficult. Thus, the rejected mimetic egg was possibly, unknowingly, damaged.

In Black-billed Magpie nonmimetic-egg trials, rejection occurred at 100% of nests ($n = 12$). No damage was detected to any other eggs in the nests in which rejection occurred.

DISCUSSION

Yellow-billed Magpies do not now have, nor are they known to have ever had, interspecific nest parasites. However, in this study they rejected 100% of nonmimetic eggs placed into their nests. Because nonmimetic eggs were ejected at a 100% rate regardless of whether they replaced a magpie egg or were simply added to a clutch without removing a magpie egg, the birds clearly discriminated among egg types. We propose that this egg-recognition behavior is best explained as the retention of a trait that provided a selective advantage in the past, possibly inherited from an ancestor, the Black-billed Magpie, which does suffer from brood parasitism in the Old World.

Evidence does not support the alternative hypothesis that intraspecific brood parasitism has resulted in the evolution and/or maintenance of egg recognition in Yellow-billed Magpies. If intraspecific brood parasitism has selected for egg recognition, then birds should regularly reject conspecific eggs placed in their nests. Alternatively, if they do not show such rejection, then the hypothesis that intraspecific parasitism selected for recognition is invalidated. In this study, Yellow-billed Magpies rejected mimetic eggs at a low rate (11.1%), suggesting that they do not have sufficient discrimination ability to reliably recognize foreign conspecific eggs. In addition, multilocus DNA fingerprinting of 10 broods (39 nestlings) revealed no evidence of intra-

specific brood parasitism in the study population (Bolen 1999).

Interspecific brood parasitism also is unlikely to have occurred in the recent past. Yellow-billed (*Coccyzus americanus*) and Black-billed Cuckoos (*C. erythropthalamus*), both New World species, or their ancestors may have been obligate brood parasites (Hughes 1997). However, the Black-billed Cuckoo range does not currently overlap with the Yellow-billed Magpie range and only a small degree of geographic overlap exists between Yellow-billed Magpies and Yellow-billed Cuckoos. Moreover, Yellow-billed Cuckoo eggs are not mimetic to Yellow-billed Magpie eggs (immaculate light blue vs. heavily spotted, respectively) suggesting that they never specialized on Yellow-billed Magpies. In addition, no other obligate brood parasite is known to have been sympatric with the species during the period of historical records.

It might be suggested that magpies eject oddly colored eggs because they have sufficient cognitive ability to allow them to realize that such objects do not belong in their nests. Although corvids such as magpies show remarkable cognitive abilities (Savage 1995, Heinrich 1999), we reject this hypothesis because several species of *Corvus* as well as *Pyrrhocorax* accept strongly nonmimetic eggs (Yom-Tov 1976, Soler 1990). Even the Common Raven, *Corvus corax*, the corvid with the strongest cognitive skills yet demonstrated, accepts nonmimetic eggs (Soler 1990).

The third assumption, that the Yellow-billed Magpie is descended from the Black-billed Magpie, is supported by the extensive almost circumpolar range of the latter species and the small range of the Yellow-billed Magpie, which is limited to the Central Valley and adjacent areas of coastal California. If our hypothesis that the Yellow-billed Magpie inherited egg recognition from the Black-billed Magpie is correct, then North American Black-billed Magpies also should show rejection behavior despite an absence of interspecific parasitism. Furthermore, such rejection behavior would be evidence for retention of egg recognition in the absence of selection and gene flow as mitochondrial DNA data show a high degree of differentiation (3.9% divergence) between Black-billed Magpies in northeast Asia and North America (Zink et al. 1995). This level of divergence suggests that the two populations have been separated for at least two million years (Moore and DeFilippis 1997).

Evidence from this study shows that at least one population of North American Black-billed Magpies do exhibit rejection behavior, 100% of nonmimetic eggs were rejected from experimental nests. The possibility, however, that such rejection behavior in this species is currently under selection pressure due to intraspecific brood parasitism cannot be ruled out (X. Wang, pers. comm.).

Because we are unable to identify any current or past selection pressure favoring egg recognition in Yellow-billed Magpies, and recognition cannot be due to introgression from Black-billed Magpies because the two species are allopatric, the Yellow-billed Magpie's recognition is best interpreted as a plesiomorphic trait inherited from an ancestral taxon. We cannot rule out the possibility that egg recognition in Yellow-billed

Magpies has some current adaptive value in a context unknown to us, but retention from an ancestral taxon is the most parsimonious explanation.

Here we have presented evidence that Yellow-billed Magpies have retained egg recognition in the absence of brood parasites for thousands of years, possibly even through a speciation event. The long-term retention indicated by our study implies that egg recognition of strongly nonmimetic eggs inflicts few or no costs, which is consistent with data on catbirds and most other North American rejecter species (Rothstein 1976). Thus, the Yellow-billed and Black-billed Magpie differ from most North American passerines, which show no indication of egg recognition even when given eggs strongly divergent from their own (Rothstein 1982a).

Unlike the magpies we tested, European Black-billed Magpies are either sympatric with Great-spotted Cuckoos, which specialize on parasitizing them, or allopatric with this cuckoo but receiving gene flow from populations that are sympatric (Soler and Møller 1990, Soler et al. 1999). Because of selection or gene flow, these European populations should have higher rejection rates of nonmimetic eggs than the North American magpies we tested. Instead, the latter had higher rejection rates, and this is true even for European magpies experiencing cuckoo parasitism (Soler et al. 1999). Contrasting the nonmimetic egg rejection rates of European magpie populations (mean = 70.6%, median = 69.2%, Soler et al. 1999) with the two North American populations we tested (mean and median = 100%) results in a nearly significant result (P = 0.062, two-tailed Mann-Whitney U-test). It is unclear why our results failed to show the expected lower rates of rejection in North American magpies, much less higher rejection rates. Eight of 10 of our Yellow-billed Magpies were tested with plaster eggs, which were slightly smaller than magpie eggs, whereas Soler et al. (1999) used painted quail eggs, which are slightly larger than magpie eggs. But Soler et al. (1998) reported no difference between magpie responses to plaster and quail eggs. In addition, Black-billed Magpies in our study were given painted conspecific eggs, so for them introduced eggs differed little or not at all from their own eggs. Magpies in most regions have domed nests (Birkhead 1991), which may reduce light levels inside nests. For ease of access, we opened holes into nests so greater visibility of eggs may have been a factor in our study. Soler et al. (1998, 1999) did not address the issue of visibility in nests at which they conducted experiments. In addition, avian vision differs from human vision in a number of ways, including the ability of birds to detect ultraviolet light (Parrish et al. 1984). Thus, although both we and Soler et al. (1999) painted eggs red, there may have been spectral differences in the red paints used in the two studies. Regardless of whether the higher rejection rates in our study represent a real difference between European and North American magpies, or a difference in methodology, the salient result of our study is that the latter magpies have high rates of rejection, contrary to the hypothesis that egg recognition is lost in the absence of interspecific parasitism. Soler et al. (1999) showed that European magpies allopatric and sympatric with the Great

Spotted Cuckoo differ more in rejection rate of mimetic eggs than of nonmimetic eggs. This result is expected because the fine discrimination needed to reject mimetic eggs is more likely to result in occasional mistaken rejections of a magpie's own eggs, so selection should decrease the tendency to reject mimetic eggs if a host population is no longer parasitized. Given this consideration, North American magpies should show less discrimination of mimetic eggs than do European magpies parasitized with cuckoos. Unfortunately, we cannot test this prediction adequately with our data. Compared to mimetic egg ejection rates of 11.1–63.6% for European magpies sympatric with the Great Spotted Cuckoo (mean = 38.7%, median = 38.1%), only one of nine (11.1%) Yellow-billed Magpies rejected a conspecific egg, which can be viewed as a mimetic foreign egg. But the mimetic eggs used by Soler et al. (1999) differed more from the host magpie eggs than the ones we used because they were smaller and were painted as opposed to having natural colors. Thus it is unclear whether Yellow-billed Magpies and European magpies differ in rejection rates of mimetic eggs.

Various cases of putative loss and retention of recognition (Rothstein 1977, Cruz and Wiley 1989, Davies and Brooke 1990) indicate that this behavior is retained as least as often as it is lost. The level of costs associated with an adaptation is likely to be a major factor determining the rate at which the adaptation is lost in the absence of selection. As described above, the discrimination needed to detect mimetic parasitic eggs is more likely to result in mistaken rejections of a host's own egg than is the discrimination needed to reject nonmimetic eggs. Because most cuckoo hosts are parasitized with mimetic eggs, unlike cowbird hosts (Rothstein 1990), cuckoo hosts should be more likely to show differences between populations sympatric and allopatric with parasites or even differences in recognition that are related to the level of cuckoo parasitism (Brooke et al. 1998). In accord with this expectation, studies of actual or potential cuckoo hosts (Cruz and Wiley 1989, Brown et al. 1990, Davies and Brooke 1990) are more likely to show variation in egg recognition behavior that correlates with the risk of parasitism than is the case for cowbird hosts (Cruz et al. 1985, Peer and Bollinger 1997) which in general show little or no geographic variation in response to foreign eggs (Rothstein 1975a, 1977, Peer and Bollinger 1997). However, there are exceptions to this trend. Great Reed Warblers (*Acrocephalus arundinaceus*) are parasitized by Common Cuckoos (*Cuculus canorus*) in parts of Japan, but a warbler population not in contact with cuckoos at Lake Biwa rejected eggs at as high a rate as a parasitized population 270 km away in Nagano (Nakamura et al. 1998). Briskie et al. (1992) reported that American Robins (*Turdus migratorius*) allopatric with cowbirds had a significantly lower rejection rate of cowbird eggs than a population sympatric with cowbirds. Thus, a number of other factors besides costs of rejection may be important in determining whether egg recognition is lost in the absence of parasitism. Despite evidence that egg recognition is sometimes lost in the absence of parasitism, it is clear from results presented here and elsewhere that it is often retained. Such retention of egg recognition has profound implications for the coevolutionary interactions between obligate brood parasites and their hosts. If hosts rapidly lose recognition in the absence of parasitism, parasites could go through cycles in which they shift from hosts with good defenses to ones with poor defenses, only to eventually shift back to their old hosts once these have lost their defenses (Davies and Brooke 1989b, Soler et al. 1998). Similarly, parasites will be able to utilize successfully all or most potential hosts when they colonize new regions that lack parasites, if recognition is rapidly lost in the absence of selection.

Alternatively, if recognition is retained for long periods in the absence of selection, cycles may be absent or may be so prolonged that their durations exceed the life spans of the species involved. Thus, long term retention could result in more and more potential host species acquiring and retaining egg recognition with parasites eventually becoming constrained to using a narrow subset of host species whose eggs can be mimicked with near perfection or whose biological features make acceptance of parasitic eggs a more adaptive option than rejection. Acceptance could be more adaptive than rejection for all members of a host species if the cost of parasitism is low or for a portion of a species, such as first time breeders that have not yet learned the range of variation of their own eggs (Lotem et al. 1995). Because evidence exists for both the retention and loss of recognition in the absence of parasitism, we suggest that this in part explains some of the considerable diversity that exists in the coevolutionary interactions between parasitic birds and their hosts.

LITERATURE CITED

BENT, A. C. 1940. Life histories of North American cuckoos, goatsucker, hummingbirds, and their allies. U.S. Natl. Mus. Bull. No. 176.

BOLEN, G. M. 1999. Extra-pair behavior in Yellow-billed Magpies (*Pica nuttalli*). Ph.D. diss., Univ. California, Berkeley, CA.

BIRKHEAD, T. R. 1991. The magpies. Academic Press, San Diego, CA.

BRISKIE, J. V., S. G. SEALY, AND K. A. HOBSON. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. Evolution 46:334–340.

BROOKE, M DE L., N. B. DAVIES, AND D. G. NOBLE. 1998. Rapid decline of host defenses in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. Proc. R. Soc. Lond. B 265:1277–1282.

BROWN, R. J., M. N. BROWN, M. DE L. BROOKE, AND N. B. DAVIES. 1990. Reactions of parasitized and unparasitized populations of *Acrocephalus* warblers to model cuckoo eggs. Ibis 132:109–111.

CRUZ, A., AND J. W. WILEY. 1989. The decline of an

adaptation in the absence of a presumed selection pressure. Evolution 43:55–62.

CRUZ, A., T. D. MANOLIS, AND J. W. WILEY. 1985. The Shiny Cowbird: a brood parasite expanding its range in the Caribbean region. Ornithol. Monogr. 36.

DAVIES, N. B., AND M. DE L. BROOKE. 1989a. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J. Anim. Ecol. 58:207–222.

DAVIES, N. B., AND M. DE L. BROOKE. 1989b. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination and general discussion. J. Anim. Ecol. 58:225–236.

DAVIES, N. B., AND M. DE L. BROOKE. 1990. Coevolution of the cuckoo and its hosts. Sci. Am. 264: 92–98.

FRIEDMANN, H., AND L. F. KIFF. 1985. The parasitic cowbirds and their hosts. Proc. West. Found. Vert. Zool. 2:225–304.

HARRISON, H. H. 1979. A field guide to western birds nests. Houghton Mifflin, Boston.

HEINRICH, B. 1999. Mind of the raven: investigations and adventures with wolf-birds. Cliff Street Books, New York.

HUGHES, J. M. 1997. Taxonomic significance of host-egg mimicry by facultative brood parasites of the avian genus *Coccyzus* (*Cucilidae*). Can. J. Zool. 75:1380–1386.

JOHNSGARD, P. A. 1997. The avian brood parasites, deception at the nest. Oxford Univ. Press, New York.

KEMAL, R. E., AND S. I. ROTHSTEIN. 1988. Mechanisms of avian egg recognition: adaptive responses to eggs with broken shells. Anim. Behav. 36:175–183.

LOTEM, A., H. NAKAMURA, AND A. ZAHAVI. 1995. Constraints on egg discrimination and cuckoo-host coevolution. Anim. Behav. 49:1185–1209.

MOKSNES, A., E. ROSKAFT, AND A. T. BRAA. 1991. Rejection behavior by Common Cuckoo hosts towards artificial brood parasite eggs. Auk 108:348–354.

MOKSNES, A., E. ROSKAFT, A. T. BRAA, L. KORSNES, H. M. LAMPE, AND H. C. PEDERSEN. 1991. Behavioral responses of potential hosts towards artificial cuckoo eggs and dummies. Behaviour 116:64–89.

MOORE, W. S., AND V. R. DEFILIPPIS. 1997. The window of taxonomic resolution for phylogenies based on mitochondrial cytochrome b, p. 83–119. *In* D. P. Mindell [ED.], Avian molecular evolution and systematics. Academic Press, San Diego, CA.

NAKAMURA, H., S. KUBOTA, AND R. SUZUKI. 1998. Coevolution between the Common Cuckoo and its major hosts in Japan: stable versus dynamic specialization on hosts, p. 94–112. *In* S. I. Rothstein and S. K. Robinson [EDS.], Parasitic birds and their hosts: studies in coevolution. Oxford Univ. Press, New York.

PARRISH, J. W., J. A. PTACEK, AND K. L. WILL. 1984. The detection of near-ultraviolet light by nonmigratory and migratory birds. Auk 101:53–58.

PEER, B. D., AND E. K. BOLLINGER. 1997. Explanation for the infrequent cowbird parasitism on Common Grackles. Condor 99:151–161.

REYNOLDS, M. D. 1995. Yellow-billed Magpie. *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 180. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.

ROHWER, S., AND C. D. SPAW. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. Evol. Ecol. 2:27–36.

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

ROTHSTEIN, S. I. 1975b. Evolutionary rates and host defenses against avian brood parasitism. Am. Nat. 109:161–176.

ROTHSTEIN, S. I. 1976. Experiments on defenses Cedar Waxwings use against cowbird parasitism. Auk 93:675–691.

ROTHSTEIN S. I. 1977. Cowbird parasitism and egg recognition of the Northern Oriole. Wilson Bull. 89: 21–32.

ROTHSTEIN, S. I. 1982a. Mechanisms of avian egg recognition: which egg parameters elicit responses by rejecter species? Behav. Ecol. Sociobiol. 11:229–239.

ROTHSTEIN, S. I. 1982b. Successes and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. Am. Zool. 22: 547–560.

ROTHSTEIN, S. I. 1990. A model system for coevolution: avian brood parasitism. Annu. Rev. Ecol. Syst. 21:481–508.

ROTHSTEIN, S. I. 1994. A century of avifaunal change in western North America. Stud. Avian Biol. 15: 301–315.

SAVAGE, C. 1995. Bird brains: the intelligence of crows, ravens, magpies, and jays. Sierra Club, San Francisco.

SOLER, J. J., J. G. MARTINEZ, M. SOLER, AND A. P. MØLLER. 1999. Genetic and geographic variation in rejection behavior of cuckoo eggs by European magpie populations: an experimental test of rejecter-gene flow. Evolution 53:947–956.

SOLER, M. 1990. Relationships between the Great Spotted Cuckoo (*Clamator glandarius*) and its corvid hosts in a recently colonized area. Ornis Scand. 21:212–223.

SOLER, M., AND A. P. MØLLER. 1990. Duration of sympatry and coevolution between the Great Spotted Cuckoo and its magpie host. Nature 343:748–750.

SOLER, M., J. J. SOLER, J. G. MARTINEZ, T. PEREZ-CONTRERAS, AND A. P. Møller. 1998. Micro-evolutionary change and population dynamics of a brood parasite and its primary host: the intermittent arms race hypothesis. Oecologia 117:381–390.

TAKASU, F. 1988. Why do all host species not show defense against avian brood parasitism: evolutionary lag or equilibrium? Am. Nat. 151:193–205.

VICTORIA, J. K. 1972. Clutch characteristics and egg discriminative ability of the African Village Weaverbird (*Ploceus cucculatus*). Ibis 114:367–376.

YOM-TOV, Y. 1976. Recognition of eggs and young by the Carrion Crow (*Corvus corone*). Behaviour 59: 247–251.

ZINK, R. M., S. ROHWER, A. V. ANDREEV, AND D. L.

DITTMAN. 1995. Trans-beringia comparisons of mitochondrial DNA differentiation in birds. Condor 97:639–649.

AN UNUSUAL TYPE OF SIBLING AGGRESSION IN BLACK-CROWNED NIGHT HERONS[1]

MATTHEW J. MEDEIROS, EMILY E. EMOND AND BONNIE J. PLOGER
Department of Biology, Hamline University, 1536 Hewitt Ave., St. Paul, MN 55104, e-mail:
bjploger@piper.hamline.edu

Abstract. Sibling aggression varies with brood size, nestling age disparities, and food characteristics. We observed feeding and fighting within two broods of Black-crowned Night Herons (*Nycticorax nycticorax*) in Minnesota. In one nest, on two different days, a senior chick swallowed the head of its smallest sibling, immobilizing it until it seemed near death. Occasional fights also occurred in this nest only. Senior chicks in both nests gained more food than juniors. We discuss possible functions of head-swallows, including how this behavior, as well as fighting and other factors, may have enhanced the feeding advantage of seniors.

Key words: Black-crowned Night Heron, head swallows, Nycticorax nycticorax, *prey size, sibling aggression, sibling competition.*

Sibling aggression varies considerably among the handful of ardeid species that have been studied, from frequently fatal (siblicidal) to virtually no fights (Mock and Parker 1997). Proximate and ultimate influences on fighting in these species include brood size, disparities in sizes/ages of siblings, food scarcity, and prey size (Mock and Parker 1997). This latter, prey-size, hypothesis (Mock 1985) predicts that nestlings should fight when fed items small enough to be economically defensible, but not when fed larger items.

We report an unusual and potentially injurious form of sibling aggression in one brood of Black-crowned Night Herons (*Nycticorax nycticorax*). In two broods, we also investigated feeding frequency, quantity and size of prey, and whether seniors gained a feeding advantage over their junior siblings.

METHODS

Our observations took place on Egret Island Scientific and Natural Area, in Pelican Lake, near Ashby, Grant County, Minnesota, on 8 days between 6–23 June 1998, during a larger study of sibling aggression in

Great Egrets (*Ardea alba*). A mix of Great Egrets, Double Crested Cormorants (*Phalacrocorax auritus*), Great Blue Herons (*A. herodias*), and Black-crowned Night Herons nested in stands of mostly boxelder (*Acer negundo*), which were separated by meadows. Night herons nested from approximately 2.5–5 m high in the trees.

We erected a 2.5-m tall blind within 12 m of two night heron nests, which we observed with binoculars and a spotting scope. We observed nest 1 when chicks were ages 6, 11–15, and 18 days, for a total of 81 hr. We observed nest 2 for 76 hr when chicks were ages 12–16, 19, and 24. On 3 days, we observed both nests continuously from about 05:00 to 22:00, breaking this period into approximately 8 hr shifts by changing observers at 14:00. On other days, we observed for only one 4–8 hr shift. Both nests contained four chicks initially, but in nest 1 a Red-tailed Hawk (*Buteo jamaicensis*) killed the C-chick when the brood was about 14.5 days old and the D-chick had disappeared when the brood was 18 days old.

We classified chicks as seniors ("Srs") and juniors ("Jrs") by plumage development and easily distinguishable size differences. Often we could further distinguish the youngest (D-chick) from the other ("C") Jr. Brood age was the age of the oldest ("A") chick. For nest 1, we estimated the A-chick's hatching date as the day before we saw the first feed (Palmer 1962), 4 days after last seeing eggs only. We estimated A's age in nest 2 as 1 day older than in nest 1 by comparing plumage and motor-skills of the A-chicks.

Each "feed" consisted of a parent regurgitating a series of discrete boluses, no two of which were more than 10 min apart (Mock 1985). We estimated bolus lengths as percentages, to the nearest 10%, of the parents' bill length from tip to eye. We standardized bolus lengths against a scale drawing of boluses relative to adult head dimensions (Ploger and Mock 1986). We used study skins at the University of Minnesota's Bell Museum to determine the bill length of seven adult Black-crowned Night Herons from Minnesota. Bill length averaged 9.6 ± 2.6 cm from tip to eye. We thus