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GIANT COWBIRD EGGS IN THE NESTS OF TWO ICTERID HOSTS: THE USE OF MORPHOLOGY AND ELECTROPHORETIC VARIANTS TO IDENTIFY INDIVIDUALS AND SPECIES[1]

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Abstract. The Giant Cowbird (*Scaphidura oryzivora*) is a brood parasite of several icterid hosts in Central and South America. Cowbird eggs can visually resemble those of their hosts. Evidence of egg mimicry requires quantification of the degree of similarity of host and parasite eggs. It is also unclear if nests found with more than one cowbird egg were parasitized by more than one female cowbird. We used electrophoresis of egg proteins and egg morphometric analyses to discriminate among the eggs of two host species (*Cacicus cela* and *Zarhynchus wagleri*) and those of the parasite, and to document the number of females that laid in a single host nest. Electromorphs of transferrin differed between the hosts ("a" alleles only) and the parasite ("b" and "c" alleles only), and thus serve as a species-specific marker. Multivariate assessment of egg measurements and markings indicate significant and non-overlapping differences in morphology between eggs of the three species as well. Electromorph and color morph differences showed that two or more female cowbirds definitely laid in six of 10 nests containing two or more cowbird eggs. In the other four nests, paired cowbird eggs could not be differentiated by color or electromorph and may have been laid by the same female.

Key words: Giant Cowbird; Scaphidura oryzivora; Cacicus cela; Zarhynchus wagleri; *brood parasitism; egg mimicry; protein electrophoresis.*

INTRODUCTION

Studies of avian brood parasitism have often revealed an intricate coevolution (Payne 1977, Rothstein 1990): first, adaptation by the host to counter brood parasitism (e.g., Rothstein 1975, 1982; Robertson and Norman 1977, Smith 1979), and then counteradaptation by the parasite (e.g., Southern 1954, Nicolai 1974, Mason and Rothstein 1986). One of the best examples of the latter is egg mimicry, apparently evolved by the parasite in response to egg recognition and rejection by the host (Chance 1922, Southern 1954, Smith 1968, Brooke and Davies 1988). In some cases the mimicry may be so exact that it is difficult to differentiate parasite eggs from host eggs. One method by which this problem was solved was to compare the karyotypes of embryos of parasitic cuckoos with those of their weaver hosts (Jensen 1980). Other methods, such as egg biochemistry, were suggested (Jensen 1980).

There is evidence for egg mimicry in the Giant Cowbird (*Scaphidura oryzivora*) in Panama (Smith 1968). Mimicry is not absolute, and *Scaphidura* eggs can normally be distinguished by shell thickness and roughness from the eggs of their hosts (based on observations by N. Smith of eggs hatching), but coloration and spotting patterns overlap widely. Smith (1968) visually identified a matching Giant Cowbird egg morph for each of four icterid host species (*Cacicus cela, Zarhynchus wagleri, Psarocolius decumanus,* and *Gymnostinops montezuma*). In addition, an immaculate, white egg, laid by "dumper" females, was not obviously mimetic. This fifth type of egg may have been laid by yearling or inexperienced Giant Cowbirds, or by a separate morph. The morphs were identified by eye as being similar to the eggs of their hosts. However, what is similar or different to human eyes may not be so to hosts. Multivariate morphometrics of egg characteristics (e.g., Fleischer 1985) would quantify egg similarity and might remove some of the subjectivity of visual assessments. Host egg recognition experiments are still necessary to validate that egg similarity represents true egg mimicry (Brooke and Davies 1988; Smith, in prep.).

Multiple parasitism (two or more parasite eggs

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in a nest) was documented in 42.1% of 1,503 host clutches parasitized by *Scaphidura* (Smith 1968). It is generally unknown how many females are responsible for such multiple parasitisms, but observations of banded females have shown as many as three laying in one nest (N. Smith, pers. observ.). Fleischer (1985 and unpubl. data) found that nests containing two or more eggs of the Brown-headed Cowbird (*Molothrus ater*) were usually parasitized by more than one female: in only one of 14 multiply-parasitized nests did the pair or trio of eggs in the nest have the same electromorph combination. Protein electrophoretic markers enable one to determine if two or more eggs found in a nest were laid by more than one female, because electrophoretic variants of proteins from undeveloped eggs have been documented to be genetically-based and maternally derived (e.g., transferrin: Lush 1960, Baker 1967, Brush 1968, Frelinger 1970, Fleischer 1985). If electromorphs vary among eggs, then the number of variants is equal to the minimum number of females responsible for the eggs.

In this paper we address two major questions dealing with Giant Cowbirds and their hosts. First, are eggs of the Giant Cowbird differentiated from eggs of two host taxa (*Cacicus* and *Zarhynchus*) on the basis of egg size, coloration, spotting patterns or protein electrophoretic markers? Second, are nests with more than one *Scaphidura* egg the result of parasitism by more than one female?

METHODS AND MATERIALS

FIELDWORK

Eggs were collected from nests within two colonies on U.S. military installations near Panama City, Republic of Panama. One colony was in small palm trees adjacent to the main buildings at the Arraijan Tank Farm (near Arraijan, about 15 km west of Panama City). The second occupied rows of small palms adjacent to the recreation area and swimming pool at Rodman Marine Base. Each palm tree at a site was numbered; each nest was assigned a letter code, mapped within the palm, and its contents and miscellaneous data (e.g., leaves or lining present, nestling number, species and estimated ages) were noted. Leaves in a nest indicate a *Zarhynchus* nest. Both colonies were visited to collect eggs on 10 and 21 March 1986. Five additional visits were made to locate fallen nests with eggs, and to observe host/parasite interactions.

Nests were accessed from hydraulic lifts on trucks provided by the U.S. Air Force (10 March 1986) and U.S. Army (21 March 1986). Most of the nests in each colony could be reached to check nest contents. All the eggs from a nest were collected when they appeared undeveloped or if all were obviously dead. Eggs in nests containing identifiable cowbird eggs were collected, but some nests which did *not* were collected so as to later confirm (i.e., after finding electromorph markers) that we were not mistaking highly mimetic cowbird eggs for host eggs. As noted above, Giant Cowbird eggs generally differ from host eggs by their much thicker and rougher shell.

Eggs were returned to the Smithsonian Tropical Research Institute. Intact eggs were emptied by drilling a hole through the shell, then using a Pasteur pipet to draw out the white and then the yolk. The condition of each egg was noted as spiked (by an unknown, but presumably avian, perpetrator), broken, rotten, undeveloped, or developed with a visible embryo. Yolk and white were placed in separate cryotubes, transported in liquid nitrogen, and then stored at −30°C until electrophoresis.

ELECTROPHORETIC ANALYSES

Egg white and yolk were analyzed with starch (12.5% gels) and polyacrylamide (8%) gel electrophoresis. Several buffer systems were tried for each stain (all buffers but the Ridgeway system described below were from Selander et al. 1970, Shaw and Prasad 1970, or Cole and Parkin 1981). Yolk or white did not react with stains for glutamate dehydrogenase, sorbitol dehydrogenase, malate dehydrogenase, α-glycerophosphate dehydrogenase, alcohol dehydrogenase, isocitrate dehydrogenase, mannose phosphate isomerase, and nucleoside phosphorylase.

Only six systems produced stains from yolk or white, corresponding to 10 putative loci. Not all were resolved well and some rapidly lost activity while frozen. Monomorphic loci include two general proteins, two esterases, phosphogluconate dehydrogenase, and glucose-phosphate isomerase. The loci exhibiting variable electromorphs were dipeptidase (PepD), leucine aminopeptidase (Lap), a third esterase (Est-3), and transferrin (Trf). Est-3 was not satisfactorily resolved after attempts with seven buffer systems on starch and four on polyacrylamide. PepD lost

activity after the first thaw/refreeze of the eggs and thus could not be scored for all eggs.

The Trf and Lap loci were resolved best on the Ridgeway buffer system. The Ridgeway electrode buffer is: 0.06 M lithium hydroxide, 0.30 M boric acid, pH 8.5; the gel buffer is: 0.006 M lithium hydroxide, 0.03 M boric acid, 0.015 M tris, 0.0025 M citric acid, pH 8.0. Both loci were found to be variable only in *Scaphidura*. Electromorphs were interpreted as genotypes, and genotype frequencies from the Trf and Lap loci were used to calculate allele frequencies and were tested for fit to expectations of Hardy-Weinberg equilibrium with χ^2 tests.

MORPHOMETRIC ANALYSES

Empty eggs were placed on a light box under standardized, intense lighting and photographed from a fixed distance with 35 mm color slide film. Each slide contained up to eight eggs, a standard color series, and a millimeter rule. Eggs were fixed in place on bits of clay so that their longest axis was completely parallel to the surface of the light box. Slides were projected and measurements and counts were taken directly from the images on the screen. Lengths or widths were spanned by calipers and then calibrated on a rule traced on paper from the one in the projected slide. One person alone took all the measurements and counts. Four measurements were made on each egg in mm: length, width, width at one-fourth of total length (from the blunt end), and width at three-fourths of total length. Two counts were taken: the number of spots intersecting a line across the width of the egg at one-fourth and at three-fourth of the total length. The background color of each egg was categorized as bluish-green or white.

The morphometric data were analyzed with both univariate and multivariate statistical methods in the SAS statistical analysis package (SAS Institute 1982). Means of each egg variable were compared among the three taxa by one-way analysis of variance (ANOVA) and over all six variables by one-way multivariate analysis of variance (MANOVA). Principal components were extracted from a correlation matrix of the six variables and the factor score coefficients were examined to interpret the "meaning" of the axis. Principal component scores were calculated for each egg for the first two axes and compared among taxa, genotypes, and egg morphs by ANOVA. In addition, Pearson product-moment correlation coefficients were calculated between PC scores from cowbird eggs found in the same nest.

RESULTS AND DISCUSSION

COLONY COMPOSITION

A total of 203 nests were examined during the two days at each site (15 nests were seen but could not be reached). Of these 203, three had been usurped by the piratic flycatcher, *Legatus leucophaius*. Of the remaining 200 nests, 107 were nests of *Zarhynchus* and 93 were nests of *Cacicus*. *Cacicus* were less common than *Zarhynchus* at one of the sites: 52.3% of 149 nests examined at Arraijan were *Cacicus* versus 29.4% of 51 nests examined at Rodman. Only 41 (38.3%) of the *Zarhynchus* nests had eggs or young (31 had eggs, 10 had young) and only 24 (25.8%) of the *Cacicus* nests had eggs (none had young).

Parasitism was higher in *Cacicus* than in *Zarhynchus* nests (54.2% of 24 nests versus 25.8% of 31 nests; $\chi^2 = 4.6$, $P < 0.05$). In addition, multiple parasitism (>1 parasite egg per nest) was significantly higher in *Cacicus* (37.5% of 24 versus 3.2% of 31 in *Zarhynchus*; $\chi^2 = 10.7$, $P < 0.005$). This difference is also reflected by the higher mean number of *Scaphidura* eggs per *Cacicus* nest (1.00 ± 1.09) versus per *Zarhynchus* nest (0.29 ± 0.53; $t = 3.16$, $P < 0.01$).

EGG COLLECTIONS

A total of 74 host or Giant Cowbird eggs were removed from 19 nests of *Cacicus cela* and 16 nests of *Zarhynchus wagleri* (mean of 2.11 eggs/nest). A total of 56 eggs from 24 nests were collected from the Arraijan site, while 18 eggs from 11 nests were collected from the Rodman site. Of the 31 *Scaphidura* eggs collected, three had been spiked, two had rotted and one had a well-developed embryo. Thus 25 *Scaphidura* eggs were available for electrophoresis. Only four of the 31 were "immaculate" eggs. Of 24 *Cacicus* eggs collected, seven had been spiked and two were rotten. A total of 18 *Cacicus* eggs could be used for electrophoresis because three of the spiked eggs still had egg white. Of 19 *Zarhynchus* eggs collected, eight had been spiked and one was rotten, leaving nine eggs for electrophoresis. What species spiked the eggs is unknown.

EGG ELECTROPHORESIS

Thus, of 74 collected eggs, 52 could be used for electrophoresis. Transferrin (Trf) resolved three

TABLE 1. Allele frequencies and χ^2 values assessing the fit of observed genotype frequencies to expectations of Hardy-Weinberg equilibrium for *n* eggs of each taxa for the transferrin (Trf) and leucine aminopeptidase (Lap) loci.

	Trf					Lap			
	n	a	b	c	χ^2	*n*	a	b	χ^2
Scaphidura	23	0.00	0.89	0.11	0.36	24	0.94	0.06	0.11
Cacicus	18	1.00	0.00	0.00	—	18	1.00	0.00	—
Zarhynchus	9	1.00	0.00	0.00	—	8	1.00	0.00	—

phenotypes, corresponding to genotypes "aa," "bb" and "bc." Trf was fixed for the "a" allele in *Zarhynchus* and *Cacicus,* and was polymorphic ("b" and "c" alleles) in *Scaphidura* (Table 1). Leucine aminopeptidase (Lap) resolved two phenotypes, corresponding to genotypes "aa" and "ab." Lap was fixed for the "a" allele in *Zarhynchus* and *Cacicus,* and polymorphic for the "a" and "b" allele in *Scaphidura* (Table 1). Genotype frequencies for *Scaphidura* at both loci did not differ from expectations of Hardy-Weinberg equilibrium ($\chi^2 = 0.36$, $P > 0.5$, for Trf; $\chi^2 = 0.11$, $P > 0.9$, for Lap). Thus, Trf appears fixed for alternative alleles in host and parasite taxa, and could be used to discriminate visually similar host and parasite eggs as Jensen (1980) used karyotypes.

EGG MORPHOMETRICS

Both ANOVA and MANOVA indicate that the species differ significantly in all measures of egg size and spotting (Table 2). The Wilk's lambda calculated from the MANOVA on all six variables indicated a highly significant difference among the centroids for each species ($F = 9.9$, $P < 0.0001$). Variances did not differ significantly, but tended to be smaller for *Scaphidura* than for the other taxa (Table 2). This runs counter to expectation if *Scaphidura* eggs truly mimic a range of hosts.

The principal components analysis created two axes or principal components with eigenvalues greater than 1.0 (PC1 and PC2; Table 3). PC1 was interpreted as a measure of egg size with a minor contribution from the number of spots on the blunt end of the egg. Thus, large, spotless eggs have high scores; small eggs with spotted bottoms have low, negative scores. PC2 was interpreted as an axis of overall spottedness: high scores indicate heavy spotting, low scores indicate immaculate eggs.

Mean PC1 and PC2 scores differed significantly among species by ANOVA (Table 2). When the ANOVA was limited to the 44 eggs that had been identified as *Zarhynchus* or *Cacicus* on the basis of an "aa" Trf genotype, or as *Scaphidura* on the basis of a "bb" or "bc" Trf genotype the results were more significant for PC1 ($F = 174.1$, $P < 0.0001$), but were no longer significant for PC2 ($F = 2.1$, $P = 0.13$). A plot of PC1 versus PC2 scores using only the genotyped eggs reveals the nearly complete separation of the three taxa in multidimensional space (Fig. 1). Thus each of these three species may be easily identifiable on

TABLE 2. Sample sizes (*n*), means and standard deviations (in parentheses) for each variable for the three taxa. Means were compared with one-way ANOVA and significance of the difference is indicated by *F* statistic and asterisk.

Variable	*Cacicus*	*Scaphidura*	*Zarhynchus*	*F*
n	18	31	16	
Length	30.17 (1.69)	35.79 (1.87)	33.74 (1.63)	42.9***
Width	20.17 (1.10)	24.86 (0.86)	22.69 (1.52)	73.9***
No. top spots	1.67 (1.61)	1.00 (1.09)	2.44 (1.90)	3.8*
No. bottom spots	3.67 (2.11)	1.77 (1.48)	4.38 (1.50)	11.0***
¼ width	18.73 (1.10)	22.02 (0.74)	20.88 (1.03)	54.5***
¾ width	15.94 (1.56)	20.16 (2.53)	17.69 (2.78)	13.0***
PC1	−2.33 (1.07)	1.50 (0.76)	−0.46 (1.06)	96.0***
PC2	−0.56 (1.06)	−0.10 (0.94)	0.84 (1.19)	7.6**

* $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$.

TABLE 3. Eigenvalues and proportion of the variance explained for PC1 and PC2, and eigenvectors for each variable on the principal components.

	PC1	PC2
Eigenvalue	3.50	1.30
% variance explained	58.3	21.7
Length	0.45	0.23
Width	0.51	0.12
No. top spots	−0.16	0.75
No. bottom spots	−0.31	0.57
¼ width	0.50	0.17
¾ width	0.40	0.10

the basis of egg morphometry. However, there may not be similar differences among eggs of *Scaphidura* and the eggs of other icterids that they parasitize (e.g., *Psarocolius* or *Gymnostinops*). Thus these results cannot be generalized beyond the cases of the two host species and colonies discussed herein. In addition, these results, and those of a canonical correlation analysis between host and cowbird eggs (Wilk's lambda = 0.018, $P = 0.17$), are not in support of egg mimicry by *Scaphidura* on these two hosts. Larger samples may be required to further resolve this question.

EGG PLACEMENT AND MULTIPLE PARASITISM

We categorized *Scaphidura* eggs as either white or colored (bluish-green). Because it is likely that individual females lay eggs of only one color morph we used color *and* electromorphs to determine the minimum number of females at a site. We found only five from among 18 possible combinations of egg morph (white or colored), Trf electromorph (bb, bc, or cc), and Lap electromorph (aa, ab, bb) at the Arraijan colony (Table 4). Thus a *minimum* of five female *Scaphidura* parasitized nests at this site (if females are able to lay both colored and white eggs this would reduce the minimum number to four females). The number that actually used the colony is likely higher than four or five: e.g., probably more than one female was responsible for the 12 eggs of the phenotype "colored-bb-aa."

The allozyme and color morph data were also used to assess whether multiply-parasitized nests contained eggs from different females. In *Cacicus,* there were eight nests with two and one nest with four *Scaphidura* eggs; in *Zarhynchus* there was only one nest with two *Scaphidura* eggs. We thus had a total of 15 "pairings" of *Scaphidura*

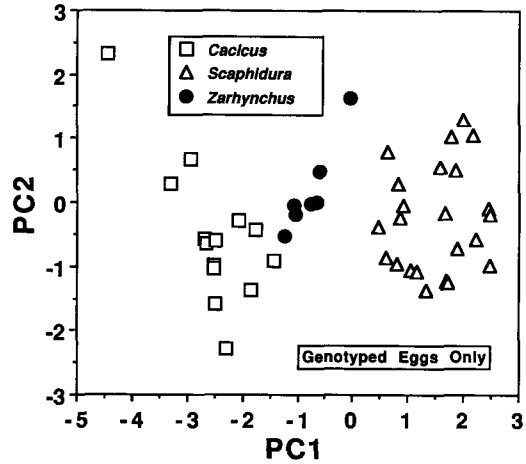

FIGURE 1. Plot of PC1 scores versus PC2 scores of individual eggs of the two host (*Cacicus* and *Zarhynchus*) and parasite (*Scaphidura*) species. Only eggs for which we had transferrin genotypes to confirm their species designation (see text) were included in this figure. Note lack of overlap between the taxa.

eggs: nine pairs from the nests with one pair of eggs, and six pairs from the single nest with four eggs. If the color morph or genotype differed among eggs from a nest we presumed that the eggs came from different females. Of the 10 multiply-parasitized nests, six had an egg that could be excluded by color morph or electromorph as having been laid by the female that laid the other egg(s). Of 15 two egg pairs, eight (53.3%) could be discriminated. Only one cowbird egg in the nest with four *Scaphidura* eggs differed (by Lap genotype) from the other three.

The PC1 scores for each egg of a pair were plotted against each other to demonstrate how morphologically similar were two *Scaphidura* eggs laid in the same nest (Fig. 2). The pairs were separated into two categories: those that had been discriminated by color morph or electromorph

TABLE 4. The number of *Scaphidura* eggs of particular color morphs and protein variant phenotypes collected from host nests at the Arraijan site. See text for details.

Morph	Trf	Lap	No.
Colored	bb	aa	12
Colored	bc	aa	4
Colored	bc	ab	1
White	bb	aa	2
White	bb	ab	2

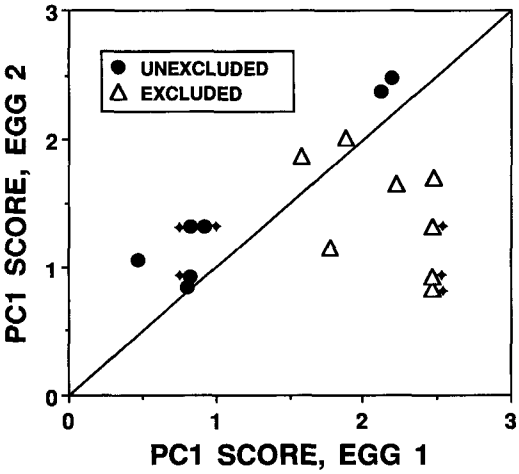

FIGURE 2. Plot of the PC1 scores of 15 pairs of *Scaphidura* eggs found in the same nest (i.e., multiply parasitized). Designation of eggs of a pair as "egg 1" or "egg 2" was arbitrary. Eggs that differed in genotype or color morph were laid by different females and are considered "excluded." Eggs that could not be discriminated on the basis of genotype or color morph were considered to be "unexcluded." The unexcluded pairs tend to lie closer to the line indicating a one-to-one correspondence between PC1 scores than the excluded pairs. This suggests that both eggs were more likely to have been laid by the same female. The six comparisons of eggs from the single four-egg clutch are starred.

as having been laid by two different females, "discriminated," and those that had not, "undiscriminated." The discriminated pairs mostly fell further away from the line of one-to-one correspondence between PC1 scores than did the undiscriminated pairs. These data support the suggestion that most of the undiscriminated pairs of eggs had been laid by only one female.

These findings differ from the case for Brown-headed Cowbirds (Fleischer 1985 and unpubl. data) in which 13 of 14 nests with two or more parasitic eggs were found to have been parasitized by two or more females. In that study, however, greater discrimination of individuals was possible because four loci (including a 4-allele esterase) were used rather than two. But Figure 2 suggests that those paired *Scaphidura* eggs that were not discriminated were indeed laid by only one female because of their morphological similarity.

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