A META-ANALYSIS OF THE IMPACT OF PARASITISM BY THE BROWN-HEADED COWBIRD ON ITS HOSTS

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Abstract. We used a meta-analytical technique to synthesize the results of studies that have quantified the effect of parasitism by Brown-headed Cowbirds *(Molothrus ater)* on host productivity. The cost of parasitism was defined as the difference in the number of young fledged in parasitized and unparasitized nests because 95% of the empirical studies used this method for calculating the cost of parasitism. We conducted two meta-analyses: one using productivity data based on nests that fledged at least one chick and the other using productivity data based on all nests. The meta-analysis based on successful nests included 40 studies and 19 species, and the meta- analysis based on all nests included 44 studies and 25 species. Across all studies, the number of young fledged per nest was significantly decreased by cowbird parasitism. Larger hosts incurred a smaller cost of parasitism that approached significance when all nests were used in the calculation of parasitism costs. Three granivorous species included in the analyses incurred a significant cost of parasitism. The inclusion of failed nests decreased the overall cost of parasitism, which indicates that predation dilutes the effect of parasitism on a population level. Our analysis is only as good as the studies on which it was based, and we point out several short-comings of many empirical studies that have estimated the cost of parasitism. A better estimate of the cost of parasitism is the difference between the number of young produced by parasitized and unparasitized females during the entire breeding season. Researchers should be aware of the biases that exist when cost is calculated on a per-nest basis.

Key Words: Avian brood parasitism, Brown-headed Cowbird, cost of parasitism, host species, meta-analysis, *Molothrus ater.*

Many studies have quantified the effect of parasitism by the Brown-headed Cowbird (*Molothrus ater*) on host productivity. The question of how cowbird parasitism affects host productivity is particularly interesting because the cowbird has been recorded parasitizing at least 220 species (Friedmann and Kiff 1985) and, therefore, likely affects the reproductive success of different hosts to varying degrees. In this paper, we compiled the results of many of these studies and performed a meta-analysis to confirm whether cowbirds decrease host productivity and, if so, to what extent.

Although meta-analytical techniques were developed in the mid-1970s, only since the early 1990s have these techniques been used in ecology. Since then, several papers have promoted the use of these techniques (Mann 1990, Fernandez-Duque and Valeggia 1994, Arnqvist and Wooster 1995). Meta-analysis is a scientific review in which data are quantitatively synthesized and, as such, provides a better alternative to traditional narrative reviews. Meta-analytical techniques are used to summarize the results of studies in terms of an effect size, calculate a mean effect size for groups of similar studies (referred to as classes), and calculate the overall effect size for all studies. The overall effect size is useful in determining the overall trend in the data, and whether it is significantly different from zero (Gurevitch and Hedges 1993, Arnqvist and Wooster 1995). Often in the past, reviewers combined the results of studies conducted on a subject by comparing the number of studies that rejected the null hypothesis with those that did not reject the null hypothesis. The problem with the latter approach is that studies based on small sample sizes are more likely to result in a Type II error, which is failing to reject the null hypothesis when it is actually false. This is not a problem when meta-analytical techniques are used because the calculated effect size is weighted according to sample size (Gurevitch and Hedges 1993).

Cowbird parasitism lowers the productivity of species that accept cowbird eggs in the following ways: host egg removal by the female cowbird (Sealy 1992), egg breakage during or after parasitism (Marvil and Cruz 1989, Weatherhead 1989, Smith and Arcese 1994), lowered hatching success of host eggs due to inefficient incubation and/or earlier hatching of parasite eggs (Petit 1991, McMaster and Sealy 1997), and lower nestling survival due to crowding and competition for parental care (Marvil and Cruz 1989). Undeniably, cowbirds greatly affect the productivity of some of their hosts. Some small hosts seldom fledge any of their own young when they are parasitized (e.g., Goldwasser et al. 1980), and many reviews have recorded the production of fewer host offspring in parasitized nests versus unparasitized nests (e.g., Payne 1977, May and Robinson 1985). Weatherhead (1989) and Trine (in press) provide data on the productivity of nests of Red-winged Blackbirds (*Agelaius phoeniceus*) and Wood Thrushes (*Hylocichla*

mustelina), respectively, that contain more than one cowbird egg. Herein, we test the hypothesis that multiply parasitized hosts incur a greater cost of parasitism than singly parasitized hosts.

As a generalist brood parasite, Brown-headed Cowbirds parasitize many inappropriate hosts, such as large species, seed-eating species, species that reject parasitic eggs, and even non-passerines. For our study, we predict that inappropriate hosts do not incur as great a cost of parasitism. Large host young should be able to compete with or even outcompete a cowbird chick during the nestling stage (e.g., Common Grackle, *Quiscalus quiscula*; Peer and Bollinger 1997). Hosts that feed seeds to their young should incur little cost associated with parasitism, except possibly for host egg removal and egg damage, because cowbird nestlings are insectivorous and die when fed only seeds (e.g., Middleton 1991, Kozlovic et al. 1996). Species that eject cowbird eggs and desert or bury the contents of parasitized nests should experience less cost than species that raise the cowbird young.

Performing a meta-analysis allowed us to determine how the cost of raising a cowbird differs among host species. We sought answers to the following questions: (1) Do nests fledge fewer young when they are parasitized by the Brown-headed Cowbird? (2) Do small bodied hosts incur a greater cost of parasitism than large bodied hosts? (3) Is brood parasitism less costly for granivorous species that do not usually raise cowbirds than for primarily insectivorous species? (4) Is the calculated cost of parasitism different when fledging success is calculated for all nests or only for successful nests?

METHODS

We reviewed the literature back to 1945 and included studies that presented data on host productivity in parasitized and unparasitized nests. To be included in the meta-analysis, the following data were required for both parasitized and unparasitized nests: (1) some measure of reproductive success for each, (2) an estimate of the variability of these measures (standard deviation or standard error), and (3) sample sizes. Most researchers quantified productivity in terms of the number of host young that fledged from nests, with four exceptions, namely studies by Klaas (1975), Smith (1981), Clark and Robertson (1981), and Roth et al. (1996) (Tables 1, 2).

Some studies that reported the productivity of parasitized and unparasitized nests could not be included in the meta-analysis because standard deviations were not provided. Several authors were contacted for additional information (e.g., standard deviations) not given in their papers.

We urge authors to provide a measure of the variance for all estimated parameters reported because this not only allows others to re-analyze their data, but this is necessary for readers to have an idea of the extent of variation.

Overall, 36 papers and unpublished sources presented information on 29 host species that could be used in our analyses (Tables 1, 2). Some of the papers included more than one host species or broke up the information for the same species by year, time of year, habitat, or number of cowbird eggs in nest. We conducted two meta-analyses, one using productivity data based on nests that fledged at least one host or cowbird chick, and the other using productivity data based on all nests. We conducted the analyses separately because some studies provided productivity data based on both methods and the data were not independent. Studies that presented data on the total number of young produced per female over the entire breeding season were analyzed in the meta-analysis based on all nests. G.T. Braden (pers. comm.) provided raw data for banded California Gnatcatchers (*Polioptila californica*) that allowed us to calculate the cost of parasitism based on all nests, successful nests only, and on a per-female basis. This was the only data-set for which the cost of parasitism was calculated in all three ways.

We only briefly summarize the methods here (see Gurevitch and Hedges [1993] for a detailed account of the equations and steps used to perform the meta-analysis). First, we transformed the outcome of each study to an "effect size," which is the difference in the mean number of young fledged in parasitized and unparasitized nests divided by the pooled standard deviation. The effect size for each study was then weighted by the number of parasitized and unparasitized nests. Similar studies were grouped into "classes." In our meta-analyses, studies conducted on the same species were analyzed as one class. Because each class must contain more than one study, species that were studied only once were grouped as insectivorous or granivorous (in the case of the meta-analysis involving successful nests only) or in terms of adult mass (in the case of the meta-analysis involving all nests). Effect sizes for studies that belong to the same class were then combined by taking a weighted average to see whether the class effect size differed from zero. A one-tailed test was used to calculate the 95% confidence limits for class effect size. We used a mixed model that, unlike the fixed model, did not make the stringent assumption that a class of studies shared a common true effect size. In a mixed model, it is assumed that the studies within a class share a common mean effect, but that there is random variation among

studies in a class, in addition to sampling variation. An overall effect size was then found by calculating a weighted average of the class effect sizes (Gurevitch and Hedges 1993). The overall effect size was converted to a Z-score using a standard normal distribution table (as in Tonhasca and Byrne 1994). A test for heterogeneity among the effect sizes of all classes was performed using the between-class heterogeneity statistic, Q_B, which has approximately a chi-square distribution with degrees of freedom equal to the total number of classes minus one. The greater the value of Q_B, the greater the heterogeneity in effect sizes among the classes (Gurevitch and Hedges 1993). For significance, we used $\alpha = 0.05$ in all statistical tests.

The meta-analysis based on successful nests included 40 studies, 19 species and 10 classes. The following eight species were the subject of more than one study and were treated as separate classes: Willow Flycatcher (*Empidonax traillii*), Wood Thrush, Red-eyed Vireo (*Vireo olivaceus*), Prothonotary Warbler (*Protonotaria citrea*), Yellow Warbler (*Dendroica petechia*), Dickcissel (*Spiza americana*), Song Sparrow (*Melospiza melodia*), and Red-winged Blackbird. The remaining 11 species were separated into two classes: granivorous and other insectivorous hosts. The two granivorous hosts were American Goldfinch (*Carduelis tristis*) and House Finch (*Carpodacus mexicanus*). The nine insectivorous hosts included: California Gnatcatcher, Ovenbird (*Seiurus aurocapillus*), Louisiana Waterthrush *(S. motacilla)*, Indigo Bunting (*Passerina cyanea*), Lark Sparrow (*Chondestes grammacus*), Grasshopper Sparrow (*Ammodramus savannarum*), Dark-eyed Junco (*Junco hyemalis*), Chestnut-collared Longspur *(Calcarius ornatus)*, and Western Meadowlark (*Sturnella neglecta*) (Tables 1, 3). These nine insectivorous hosts were not divided into classes according to mass, as in the meta-analysis involving all nests (see below), because natural breaks in the mass data did not exist such that each class would have more than one study. Meta-analytical techniques require more than one study to be included in each class so that the error associated with the class effect size may be estimated.

The meta-analysis based on all nests included 44 studies, 25 species, and 13 classes. The following species were studied more than once and treated as separate classes: Willow Flycatcher, California Gnatcatcher, Wood Thrush, Plumbeous Vireo (*V. plumbeous*), Red-eyed Vireo, Yellow Warbler, Indigo Bunting, Song Sparrow, and Red-winged Blackbird. The remaining 16 species were grouped into four additional classes according to adult mass. The following four classes were formed using natural breaks in the

mass data with the restriction that each class had to contain more than one study: (1) Blue-gray Gnatcatcher (*Polioptila caerulea*, 6.0 g), Clay-colored Sparrow (*Spizella pallida*, 12.0 g), Western Wood-Pewee (*Contopus sordidulus*, 12.8 g), Warbling Vireo (*Vireo gilvus*, 14.8 g); (2) Grasshopper Sparrow (17.0 g), Baird's Sparrow (17.5 g), Chestnut-collared Longspur (18.9 g), Eastern Phoebe (*Sayornis phoebe*, 19.8 g), Savannah Sparrow (20.0 g), Louisiana Waterthrush (20.3 g); (3) Purple Finch (*Carpodacus purpureus*, 24.9 g), Sprague's Pipit (*Anthus spragueii*, 25.3 g), Western Tanager (*Piranga ludoviciana*, 28.1 g), Lark Sparrow (29.0 g); and (4) Bobolink *(Dolichonyx oryzivorus*, 42.0 g), Western Meadowlark (100.7 g) (Tables 2, 4). Mean adult masses were obtained from Dunning (1993). We used the average mass of both sexes combined for dimorphic species. Note that the Purple Finch was the only granivorous species included in this meta-analysis and, therefore, could not be analyzed in a separate class.

Trine (in press) provided data on fledging success for Wood Thrush nests containing up to six cowbird eggs. Simple linear regression was used to determine whether the number of cowbird eggs in Wood Thrush nests affected the effect size of parasitism. Linear regression was also used to determine whether host mass affected the effect size of parasitism. When more than one study was conducted on a species, a pooled effect size for the species was used as a single observation in the regression analysis to avoid pseudoreplication.

Although our analysis included species that often desert or bury parasitized nests (e.g., Yellow Warbler, Clark and Roberston 1981; Willow Flycatcher, Sedgwick and Knopf 1988; Red-eyed Vireo and Song Sparrow, Graham 1988), the effect of nest desertion or burial on the cost of parasitism could not be determined accurately because most studies provided productivity data on a per-nest basis rather than on a per-female basis. Our meta-analysis does not include ejector species because no one has compared the productivity of naturally parasitized and unparasitized nests of ejector species. It is difficult to study naturally parasitized nests of ejector species because a cowbird egg may be ejected before the foreign egg can be detected (Scott 1977, Sealy and Bazin 1995).

A criticism of meta-analytical studies is that the results may be affected by a publication bias because papers that demonstrate no effect are less likely to be published than those with statistically significant effects. Referred to as the "file-drawer" problem, there is a possibility that the number of unpublished statistically insignificant results is high enough to invalidate the re-

TABLE 1. MEAN NUMBER OF HOST YOUNG FLEDGED SUCCESSFUL FROM PARASITIZED AND UNPARASITIZED NESTS IN 40 STUDIES OF 19 HOST SPECIES

Host	Unparasitized mean ± SD (N)	Parasitized mean ± SD (N)	Effect size	Reference
Willow flycatcher	2.20 ± 0.3 (9)	2.00 ± 0.0 (2)	-0.65	Sedgwick and Knopf 1985
	2.00 ± 1.00 (3)	0.80 ± 1.30 (5)	-0.86	Harris 1991[a]
California Gnatcatcher	2.75 ± 0.93 (102)	2.16 ± 0.96 (19)	-0.63	M.J. Whitfield, pers. comm.
Wood Thrush	2.90 ± 1.13 (80)	0.00 ± 0.00 (9)	-2.67	G.T. Braden, pers. comm.[a]
	2.94 ± 1.03 (47)	2.07 ± 0.73 (14)	-0.88	Donovan et al. 1995[b]
	2.70 ± 1.03 (6)	1.90 ± 1.29 (10)	-0.63	Trine, in press (nests with 1 cowbird egg)[b]
	2.70 ± 1.03 (6)	1.00 ± 0.71 (9)	-1.89	Trine, in press (2 cowbird eggs)[b]
	2.70 ± 1.03 (6)	1.10 ± 0.90 (13)	-1.63	Trine, in press (3 cowbird eggs)[b]
	2.70 ± 1.03 (6)	1.40 ± 1.52 (6)	-0.92	Trine, in press (4 cowbird eggs)[b]
	2.70 ± 1.03 (6)	0.83 ± 0.75 (8)	-1.99	Trine, in press (5 cowbird eggs)[b]
	2.70 ± 1.03 (6)	0.33 ± 0.58 (5)	-2.52	Trine, in press (6 cowbird eggs)[b]
Red-eyed Vireo	2.94 ± 0.87 (18)	0.90 ± 1.05 (29)	-2.04	Southern 1958[a]
	3.00 ± 1.00 (19)	2.40 ± 1.34 (5)	-0.54	Donovan et al. 1995[b]
Prothonotary Warbler	4.50 ± 0.90 (42)	3.50 ± 1.40 (14)	-0.95	Petit 1991 (early nests)
	3.90 ± 1.00 (42)	2.90 ± 1.20 (7)	-0.96	Petit 1991 (late nests)
Yellow Warbler	0.80 ± 0.16 (35)	0.44 ± 0.33 (31)	-1.4	Clark and Robertson 1981[c]
	3.23 ± 1.12 (125)	2.50 ± 1.38 (30)	-0.62	Goossen and Sealy 1982[d]
	3.76 ± 0.77 (21)	2.67 ± 1.12 (9)	-1.2	Burgham and Picman 1989
	3.56 ± 1.11 (48)	1.90 ± 0.91 (20)	-1.55	Weatherhead 1989
	2.56 ± 1.26 (25)	2.31 ± 1.44 (13)	-0.19	J.C. Ortega, C.P. Ortega, S. Allerton, S.A. Backensto, C.A. Rapp, and S. Vorisek, unpubl. abstract
Ovenbird	4.16 ± 0.94 (63)	2.00 ± 0.95 (8)	-2.27	Donovan et al. 1995[b]
Louisiana Waterthrush	5.20 ± 1.30 (5)	2.29 ± 1.60 (7)	-1.8	Eaton 1958
Indigo Bunting	3.44 ± 0.88 (9)	1.46 ± 1.20 (13)	-1.76	Twomey 1945[a]
Dickcissel	3.70 ± 0.72 (9)	1.80 ± 1.22 (41)	-1.63	Zimmerman 1983 (prairie habitat)[e]
	3.20 ± 1.03 (54)	2.00 ± 1.28 (57)	-1.02	Zimmerman 1983 (old field habitat)[e]
Lark Sparrow	3.20 ± 0.79 (10)	2.25 ± 0.96 (4)	-1.07	Newman 1970[a]
Grasshopper Sparrow	3.72 ± 0.24 (18)	2.40 ± 0.60 (5)	-3.75	Davis and Sealy, in press
Song Sparrow	4.13 ± 0.88 (16)	2.64 ± 1.57 (11)	-1.2	Cavalcanti 1981 (early season)
	3.60 ± 1.30 (15)	2.71 ± 1.38 (7)	-0.65	Cavalcanti 1981 (late season)
Dark-eyed Junco	2.70 ± 1.10 (12)	1.50 ± 1.10 (8)	-1.04	Wolf 1987
Chestnut-collared Longspur	3.61 ± 0.22 (23)	3.50 ± 0.50 (4)	-0.4	Davis and Sealy, in press
Red-winged Blackbird	2.40 ± 0.97 (39)	1.30 ± 0.50 (4)	-1.14	Ortega and Cruz 1988 (1984 data)
	2.90 ± 0.93 (60)	2.40 ± 0.90 (19)	-0.54	Ortega and Cruz 1988 (1985 data)
	2.90 ± 0.99 (111)	1.40 ± 0.54 (7)	-1.53	Ortega and Cruz 1988 (1986 data)
	3.15 ± 1.01 (46)	2.92 ± 1.06 (24)	-0.22	Weatherhead 1989 (singly parasitized)
	3.15 ± 1.01 (46)	2.28 ± 1.11 (7)	-0.84	Weatherhead 1989 (multiply parasitized)
	2.72 ± 1.00 (654)	1.78 ± 1.50 (55)	-0.9	Røskaft et al. 1990

TABLE 1. CONTINUED

Host	Unparasitized mean ± SD (N)	Parasitized mean ± SD (N)	Effect size	Reference
Western Meadowlark	3.00 ± 0.38 (14)	2.25 ± 0.49 (8)	−1.71	Davis and Sealy, in press
American Goldfinch	2.90 ± 2.37 (77)	2.30 ± 2.12 (18)	−0.26	Middleton 1977, pers. comm.[e]
House Finch	3.80 ± 0.79 (10)	2.64 ± 1.21 (11)	−1.08	Kozlovic, in press

[a] The mean number of young fledged in parasitized and unparasitized nests, standard deviations, and sample sizes were calculated from raw data.
[b] Donovan et al. (1995) and Trine (in press) were contacted for exact values of the means and standard deviations that were presented in graphical form in their papers.
[c] Productivity is in terms of number of host young fledged per egg laid, including buried eggs.
[d] Goossen and Sealy's (1982) data were re-analyzed to obtain standard deviations.
[e] Standard errors were converted to standard deviations.

sults of the meta-analysis by bringing the significance level up to $P \geq 0.05$ (Fernandez-Duque and Valeggia 1994, Arnqvist and Wooster 1995). We used the formula provided in Fernandez-Duque and Valeggia (1994) to calculate the number of unpublished studies with insignificant results that would be required to invalidate the results of our meta-analysis. We set the minimum meaningful value for the mean effect size at 0.2. To evaluate effect size, Cohen (1988:25) suggested that $d = 0.2$ is small, $d = 0.5$ is medium, and $d = 0.8$ is large. Presumably an effect size greater than 1.0 is "very large" (Gurevitch and Hedges 1993).

RESULTS

OVERALL EFFECT SIZE

Regardless of whether the calculation of fledging success was based on all nests or on successful nests only, brood parasitism by the Brown-headed Cowbird significantly decreased host productivity across all studies. The overall effect size across all of the classes was −1.09 (± 0.01) when the meta-analysis was based on successful nests, and −0.81 (± 0.01) when the analysis was based on all nests. Therefore, in our analyses, the mean effect size of parasitism on the productivity of its hosts was "large" when productivity was based on all nests and "very large" when productivity was based on successful nests only, according to Cohen's (1988) and Gurevitch and Hedge's (1993) guidelines. Calculating fledging success based on successful nests resulted in a greater cost of parasitism compared with calculating fledging success using all nests. For example, 15 of the 17 studies for which productivity data were calculated using both methods had a smaller effect size when fledging success was based on all nests (Table 5).

Another way of interpreting the value of effect sizes is in terms of the difference in standard deviation units between the experimental and control groups (Gurevitch and Hedges 1993). Cowbird parasitism caused a mean decrease of 0.79 standard deviations in the number of young that fledged from a nest, and a mean decrease of 1.09 standard deviations when based on successful nests only. Converting the effect size to a Z-score revealed that an average parasitized nest fledged fewer young than 79% of the unparasitized nests, and an average parasitized successful nest fledged fewer young than 86% of the unparasitized successful nests.

Using the formula provided in Fernandez-Duque and Valeggia (1994), 134 unpublished studies that estimated productivity based on all nests with statistically insignificant results and 178

TABLE 2. MEAN NUMBER OF HOST YOUNG FLEDGED FROM ALL PARASITIZED AND UNPARASITIZED NESTS IN 44 STUDIES OF 25 HOST SPECIES

Host	Unparasitized mean ± SD (N)	Parasitized mean ± SD (N)	Effect size	Reference
Western Wood-Pewee	1.69 ± 1.41 (111)	0.29 ± 0.85 (17)	−1.02	D.R. Curson, pers. comm.
Willow Flycatcher	1.50 ± 1.29 (4)	0.31 ± 0.85 (13)	−1.18	Harris 1991[a]
	1.51 ± 1.54 (186)	0.31 ± 0.84 (133)	−0.92	M.J. Whitfield, pers. comm.
Eastern Phoebe	4.39 ± 3.62 (97)	1.97 ± 2.48 (79)	−0.76	E.E. Klaas, pers. comm.[b]
California Gnatcatcher	3.30 ± 2.85 (23)	0.63 ± 1.18 (27)	−1.24	G.T. Braden, pers. comm. (1992–1993 data)[a,b]
	2.11 ± 2.39 (64)	0.50 ± 1.07 (8)	−0.69	G.T. Braden, pers. comm. (1994–1995 data)[a,b]
Blue-grey Gnatcatcher	1.44 ± 1.68 (36)	0.11 ± 0.58 (129)	−1.43	D.R. Curson, pers. comm.
Wood Thrush	4.00 ± 0.00 (3)	2.00 ± 1.73 (3)	−1.31	Twomey 1945[a]
	3.10 ± 2.00 (128)	3.10 ± 2.20 (90)	0.00	Roth et al. 1996[b]
Sprague's Pipit	1.36 ± 0.43 (14)	0.00 ± 0.00 (3)	−3.22	Davis and Sealy, in press
Warbling Vireo	0.40 ± 0.54 (5)	0.06 ± 0.25 (16)	−0.98	C.P. Ortega, pers. comm.[c]
Plumbeous Vireo	2.09 ± 1.66 (80)	0.49 ± 1.04 (81)	−1.15	Chace et al., *this volume*
	1.39 ± 1.69 (18)	0.25 ± 0.80 (76)	−1.1	D.R. Curson, pers. comm.
Red-eyed Vireo	2.00 ± 2.83 (2)	1.60 ± 1.07 (10)	−0.27	Twomey 1945[a]
	2.41 ± 1.40 (22)	0.46 ± 0.87 (56)	−1.84	Southern 1958[a]
Yellow Warbler	1.89 ± 1.82 (227)	0.96 ± 1.49 (78)	−0.53	Goossen and Sealy 1982[d]
	2.00 ± 1.94 (15)	0.32 ± 1.10 (25)	−1.12	DellaSala 1985[e]
	2.28 ± 1.94 (75)	0.88 ± 1.14 (43)	−0.82	Weatherhead 1989
Louisiana Waterthrush	3.71 ± 2.75 (7)	2.00 ± 1.69 (8)	−0.72	Eaton 1958
Western Tanager	2.00 ± 1.65 (26)	1.00 ± 1.06 (42)	−0.75	D.R. Curson, pers. comm.
Indigo Bunting	1.24 ± 1.76 (25)	1.19 ± 1.22 (16)	−0.03	Twomey 1945[a]
	2.25 ± 1.75 (8)	0.00 ± 0.00 (5)	−1.5	Phillips 1951[a]
	1.54 ± 1.46 (763)	0.37 ± 0.81 (277)	−0.89	Payne and Payne 1998 (Niles)
	1.62 ± 1.51 (556)	0.40 ± 0.90 (140)	−0.86	Payne and Payne 1998 (George Reserve)
Clay-colored Sparrow	1.49 ± 0.74 (148)	0.04 ± 0.20 (26)	−2.10	Knapton 1978, pers. comm.
Lark Sparrow	1.88 ± 1.73 (17)	0.64 ± 1.15 (14)	−0.81	Newman 1970[a]
Savannah Sparrow	1.09 ± 0.33 (21)	0.11 ± 0.11 (9)	−3.35	Davis and Sealy, in press
Baird's Sparrow	1.55 ± 0.29 (42)	1.21 ± 0.31 (24)	−1.13	Davis and Sealy, in press
Grasshopper Sparrow	2.03 ± 0.35 (33)	0.92 ± 0.39 (13)	−3.02	Davis and Sealy, in press
Song Sparrow	3.27 ± 1.73 (26)	3.28 ± 2.01 (45)	0.01	Smith 1981 (adult)[e,f]
	2.06 ± 2.21 (32)	2.13 ± 2.01 (24)	0.03	Smith 1981 (juvenile)[e,f]
	1.77 ± 1.13 (30)	0.63 ± 0.83 (19)	−1.09	Smith and Arcese 1994 (1983 data)[e,g]
	1.92 ± 1.40 (37)	0.92 ± 1.02 (24)	−0.78	Smith and Arcese 1994 (1984 data)[e,g]
	1.05 ± 1.25 (94)	0.58 ± 0.76 (31)	−0.41	Smith and Arcese 1994 (1986 data)[e,g]
	1.04 ± 1.25 (51)	0.49 ± 0.86 (43)	−0.50	Smith and Arcese 1994 (1987 data)[e,g]
Chestnut-collared Longspur	1.73 ± 0.28 (48)	1.75 ± 0.70 (8)	0.05	Davis and Sealy, in press
Bobolink	1.33 ± 1.33 (3)	1.33 ± 1.33 (3)	0.00	Davis and Sealy, in press
Red-winged Blackbird	0.80 ± 1.26 (121)	0.60 ± 0.73 (9)	−0.16	Ortega and Cruz 1988 (1984 data)

TABLE 2. CONTINUED

Host	Unparasitized mean ± SD (N)	Parasitized mean ± SD (N)	Effect size	Reference
Red-winged Blackbird (continued)	1.00 ± 1.48 (176)	1.50 ± 1.36 (30)	0.34	Ortega and Cruz 1988 (1985 data)
	1.19 ± 1.51 (299)	0.70 ± 0.82 (15)	-0.27	Ortega and Cruz 1988 (1986 data)
	1.24 ± 1.68 (118)	1.33 ± 1.63 (57)	0.05	Weatherhead 1989 (singly parasitized)
	1.24 ± 1.68 (118)	1.23 ± 1.42 (13)	-0.01	Weatherhead 1989 (multiply parasitized)
Western Meadowlark	1.13 ± 0.28 (37)	0.64 ± 0.64 (28)	-1.03	Davis and Sealy, in press
Purple Finch	1.88 ± 1.87 (186)	1.00 ± 1.85 (8)	-0.47	Wootton 1996

[a] The mean number of young fledged in parasitized and unparasitized nests, standard deviations, and sample sizes were calculated from raw data.
[b] Productivity is in terms of number of young that fledged per female or pair per breeding season.
[c] C. P. Ortega (pers. comm.) recorded the number of young that fledged per nest, but she remarked that this value was probably not any different from the number of young fledged per female because at her study site in southwestern Colorado, the nesting season is short and second nesting attempts are rare.
[d] Goossen and Sealy's (1982) data were re-analyzed to obtain standard deviations.
[e] Standard errors were converted to standard deviations.
[f] Productivity is in terms of number of young that reached independence per female (i.e., number of young that survived to four weeks after hatching).
[g] Data from 1985 and 1988 were not included in meta-analysis because food experimentally added to territories in these years decreased the cost of parasitism.

unpublished studies that estimated productivity based on successful nests with statistically insignificant results would be required to conclude that cowbird parasitism had no effect on the hosts.

META-ANALYSIS BASED ON SUCCESSFUL NESTS

There was a significant difference in the effect of cowbird parasitism among all classes in the meta-analysis based on successful nests ($Q_B = 63.7$, df = 9, P < 0.001). Fledging success was reduced by cowbird parasitism in all species, as indicated by uniformly negative effect sizes (Table 3). Furthermore, the 95% confidence limits for effect sizes did not overlap zero in any of the classes in the meta-analysis based on successful nests, which indicated that the effect sizes for all species were significantly less than zero. Thus, cowbird parasitism significantly decreased the productivity of successful nests in Willow Flycatchers, Wood Thrushes, Red-eyed Vireos, Prothonotary Warblers, Yellow Warblers, Dickcissels, and Red-winged Blackbirds (Table 3). Cowbird parasitism also significantly decreased the productivity of successful nests of the nine species in the "other insectivorous hosts" class and the two species in the "granivorous hosts" class. This finding was confirmed because all individual effect sizes for the studies in the two latter classes were negative.

META-ANALYSIS BASED ON ALL NESTS

There was a significant difference in the effect of cowbird parasitism among all of the species ($Q_B = 36.2$, df = 12, P < 0.001; Table 4). The 95% confidence interval for effect sizes overlapped zero for Wood Thrushes and Red-winged Blackbirds, indicating that the effect sizes for these two species were not significantly different from zero, and that cowbird parasitism did not significantly affect the productivity of these species. The class effect sizes for all other species were significantly less than zero, indicating that cowbird parasitism significantly decreased the productivity of these species.

COMPARISON OF THE COST OF PARASITISM WHEN CALCULATED USING DIFFERENT METHODS

G.T. Braden's (pers. comm.) data on California Gnatcatchers were the only data for which the cost of parasitism could be calculated in all three ways. The effect size of parasitism based on the productivity of females was -0.81 (Table 6). The use of successful nests only grossly overestimated the cost of parasitism (effect size = -2.27), whereas the use of all nests underestimated the cost of parasitism (effect size = -0.54).

TABLE 3. THE MASS AND EFFECT SIZES FOR EIGHT SPECIES STUDIED MORE THAN ONCE, AND FOR THE NINE INSEC-
TIVOROUS AND TWO GRANIVOROUS SPECIES STUDIED ONCE; PRODUCTIVITY IS BASED ON SUCCESSFUL NESTS

| | Mean adult mass (g) | Effect size (no. studies in class) | 95% confidence limits | |
			Lower	Upper
≥2 studies per species:				
Willow Flycatcher	13.4	−0.67 (3)	−0.87	−0.47
Wood Thrush	47.4	−1.32 (7)	−1.42	−1.22
Red-eyed Vireo	16.7	−1.44 (2)	−1.69	−1.19
Prothonotary Warbler	14.3	−0.95 (2)	−1.16	−0.74
Yellow Warbler	9.5	−0.95 (5)	−1.03	−0.88
Dickcissel	27	−1.24 (2)	−1.41	−1.07
Song Sparrow	20	−0.94 (2)	−1.2	−0.68
Red-winged Blackbird	52.6	−0.79 (6)	−0.85	−0.73
1 study per insectivorous host:				
California Gnatcatcher	6	−2.67		
Ovenbird	19.4	−2.27		
Louisiana Waterthrush	20.3	−1.8		
Indigo Bunting	14.1	−1.76		
Lark Sparrow	29	−1.07		
Grasshopper Sparrow	17	−3.75		
Dark-eyed Junco	20	−1.04		
Chestnut-collared Longspur	18.9	−0.4		
Western Meadowlark	100.7	−1.71		
		−1.81 (9)	−1.88	−1.74
1 study per granivorous host:				
American Goldfinch	12.9	−0.26		
House Finch	21.4	−1.08		
		−0.55 (2)	−0.75	−0.35

EFFECT OF MULTIPLE PARASITISM ON COST OF PARASITISM

The effect size of parasitism tended to increase as the number of cowbird eggs laid in Wood Thrush nests increased; however, this trend was not significant (effect size = − 0.258 [number of cowbird eggs] − 0.693; t = −1.88, P = 0.13, r^2 = 0.25). Successful multiply parasitized Red-winged Blackbird nests had a greater effect size of parasitism than successful singly parasitized nests (-0.84 and −0.22, respectively).

EFFECT OF HOST MASS ON COST OF PARASITISM

When the meta-analysis was based on all nests, the cost of parasitism decreased as host mass increased for species that were studied more than once (effect size = −1.21−0.022 [mass]; F = 8.8, df = 1, 7; P = 0.02, r^2 = 0.49) (Fig. 1). The relationship only approached significance (F = 4.44, df = 1, 11; P = 0.06, r^2 = 0.22) when the four classes grouped by mass were included in the regression analysis. When all 25 species were included in the regression analysis, the trend was still apparent but the relationship was no longer statistically significant (F = 1.16, df = 1, 23; P = 0.29, r^2 = 0.007). When the meta-analysis was based on successful nests only, no association was found between

the cost of parasitism and host mass, regardless of whether all species were included or when only species studied more than once were included (F < 0.005, df = 1, 17; P = 0.95, r^2 = 0; and F = 0.08, df = 1, 6; P = 0.78, r^2 = 0, respectively).

DISCUSSION

Overall, brood parasitism significantly affected host productivity. The results of our meta-analyses were resistant to the file-drawer problem (see Fernandez-Duque and Valeggia 1994, Arnqvist and Wooster 1995) because a sufficiently high number of unpublished studies with statistically insignificant results would have been required for us to conclude that cowbird parasitism had no effect on the hosts: 134 studies that estimated productivity based on all nests and 178 studies that estimated productivity only on successful nests.

Calculation of the cost of parasitism based on all nests resulted in a more moderate estimate of the cost of parasitism than using successful nests only (Table 5). Whether to calculate the cost of parasitism using all nests or only successful nests is debatable. The difference in fledging success of successful parasitized and unparasitized nests reflects the combination of both

TABLE 4.   MASS AND EFFECT SIZES FOR NINE SPECIES STUDIED MORE THAN ONCE, AND FOR THE 16 SPECIES STUDIED ONLY ONCE; PRODUCTIVITY IS BASED ON ALL NESTS

	Mean adult mass (g)	Effect size (no. studies in class)	95% confidence limits	
			Lower	Upper
≥2 studies per species:				
Willow Flycatcher	13.4	−1.00 (2)	−1.33	−0.68
California Gnatcatcher	6	−0.99 (2)	−1.31	−0.67
Wood Thrush	47.4	−0.17 (2)	−0.37	0.03
Plumbeous Vireo	16.6	−1.13 (2)	−1.27	−0.99
Red-eyed Vireo	16.7	−1.50 (2)	−1.76	−1.23
Yellow Warbler	9.5	−0.84 (3)	−0.99	−0.69
Indigo bunting	14.1	−0.55 (2)	−0.95	−0.15
Song Sparrow	20	−0.35 (6)	−0.42	−0.28
Red-winged Blackbird	52.6	0.004 (5)	−0.11	0.11
1 study per species:				
Blue-grey Gnatcatcher	6	−1.43		
Clay-colored Sparrow	12	−2.1		
Western Wood-Pewee	12.8	−1.02		
Warbling Vireo	14.8	−0.98		
		−1.47 (4)	−1.56	−1.38
Grasshopper Sparrow	17	−3.02		
Baird's Sparrow	17.5	−1.13		
Chestnut-collared Longspur	18.9	0.05		
Eastern Phoebe	19.8	−0.76		
Savannah Sparrow	20	−3.35		
Louisiana Waterthrush	20.3	−0.72		
		−1.21 (6)	−1.29	−1.13
Purple Finch	24.9	−0.47		
Sprague's Pipit	25.3	−3.22		
Western Tanager	28.1	−0.75		
Lark Sparrow	29	−0.81		
		−0.87 (4)	−0.99	−0.76
Bobolink	42	0		
Western Meadowlark	100.7	−1.03		
		−0.78 (2)	−1.13	−0.42

clutch and brood reduction caused by cowbirds, whereas the overall difference in fledging success of parasitized and unparasitized nests includes differences in nest-survival frequencies in the two groups (Weatherhead 1989). If the intention is to isolate the effect of brood parasitism, then it is most appropriate to consider successful nests only. If one is interested in determining the effect of parasitism on the entire population, then it is necessary to consider all nests. Roth et al. (1996) remarked that only studies that consider both parasitism and predation truly evaluate the effect of parasitism on host productivity. When predation frequencies are high, the effects of parasitism will be swamped (Stutchbury 1997). A criticism, however, of using all nests is that failed nests are less likely to be found than successful ones (Mayfield 1961). Below, we suggest a method of calculating the cost of parasitism that is better than using nest productivity data.

EFFECT OF HOST MASS ON COST OF PARASITISM

We predicted that host mass would have a significant effect on the cost of parasitism when cost was based on successful nests because the cost of parasitism would not be confounded by predation. Interestingly, we found the opposite. Host mass significantly affected the cost of parasitism when cost was based on all nests; larger species experienced a lower cost of parasitism (Fig. 1). Scott and Lemon (1996) suggested that a cowbird nestling is less able to compete with nestlings of large host species, therefore, hosts larger than a certain mass experience negligible costs due to nestling competition. Much of the cost of parasitism for species larger than 20 g (Song Sparrow, Dark-eyed Junco, Dickcissel, Wood Thrush, and Red-winged Blackbird) is manifested through egg removal by the female cowbird (Smith 1981, Zimmerman 1983, Wolf 1987, Røskaft et al. 1990, Trine in press). The

TABLE 5. EFFECT SIZE OF PARASITISM FOR STUDIES THAT CALCULATED PRODUCTIVITY OF HOSTS IN PARASITIZED AND UNPARASITIZED NESTS BASED ON SUCCESSFUL NESTS AND ALL NEST

| Species | Effect size | | Reference |
	Successful nests	All nests	
Willow Flycatcher	−0.86	−1.18	Harris 1991
Willow Flycatcher	−0.63	−0.92	M.J. Whitfield, unpubl. data
California Gnatcatcher	−2.67	−0.98	G.T. Braden, pers. comm.[a]
Red-eyed Vireo	−2.04	−1.84	Southern 1958
Yellow Warbler	−0.62	−0.53	Goossen and Sealy 1982[b]
Yellow Warbler	−1.55	−0.82	Weatherhead 1989
Louisiana Waterthrush	−1.8	−0.72	Eaton 1958
Indigo Bunting	−1.76	−0.03	Twomey 1945
Lark Sparrow	−1.07	−0.81	Newman 1970
Grasshopper Sparrow	−3.75	−3.02	Davis and Sealy, in press
Chestnut-collared Longspur	−0.40	0.05	Davis and Sealy, in press
Red-winged Blackbird	−1.14	−0.16	Ortega and Cruz 1988 (1984 data)
Red-winged Blackbird	−0.54	0.34	Ortega and Cruz 1988 (1985 data)
Red-winged Blackbird	−1.53	−0.27	Ortega and Cruz 1988 (1986 data)
Red-winged Blackbird	−0.22	0.05	Weatherhead 1989 (singly parasitized)
Red-winged Blackbird	−0.84	−0.01	Weatherhead 1989 (multiply parasitized)
Western Meadowlark	−1.71	−1.03	Davis and Sealy, in press

Note: A negative sign indicates a cost of parasitism, and an effect size of 0.2 is small, 0.5 is medium, and ≥0.8 is large (see text for details).
[a] Pooled effect size for 1992–1995. Productivity is in terms of number of young fledged per female.
[b] Goossen and Sealy's (1982) data were re-analyzed to obtain standard deviations.

next logical question is how does host mass affect the number of host eggs that are removed?

Preliminary results based on 21 studies on 18 species suggest that the size of the host does not affect the average number of host eggs that are removed from parasitized nests (y = 0.991−0.005 [host mass]; t = −0.46, P = 0.65, r² = 0). The mean number of host eggs removed at parasitized nests by female cowbirds was 0.88 ± 0.51 (N = 18 species; Lorenzana and Sealy, unpubl. data). Therefore, the significant relationship between host mass and cost of parasitism apparently exists because fewer host young are outcompeted by cowbird nestling(s) as hosts increase in size, rather than an increased number of host eggs removed by cowbirds.

There was no significant relationship between host mass and the cost of parasitism when cost was based on successful nests only. This is puzzling; we cannot adequately explain these results. Other factors besides host mass probably affect the difference in the number of young that fledge from parasitized and unparasitized nests.

For example, the relative availability of food in different habitats affects the cost of parasitism. Smith and Arcese (1994) found that the cost of parasitism was less in years when food supplies were artificially supplemented. Consideration of species characteristics may also help explain the lack of effect of host mass on cost of parasitism when cost was calculated on the basis of successful nests only. Yellow Warblers (9.5 g) probably incurred a smaller cost of parasitism than expected for their size because they often bury cowbird eggs; Clark and Roberston (1991) demonstrated that buried and unparasitized Yellow Warbler nests fledged the same number of young. Wood Thrushes (47.4 g) probably incurred a larger cost of parasitism than expected for their size because their nests received up to 6 cowbird eggs (Trine in press).

Parasitized nests of Red-winged Blackbirds and Wood Thrushes did not fledge significantly fewer young than their unparasitized counterparts when cost was calculated using all nests. However, for successful nests only, Ortega and

TABLE 6. THE EFFECT SIZE OF THE COST OF PARASITISM FOR CALIFORNIA GNATCATCHERS (G.T. BRADEN, PERS. COMM.)

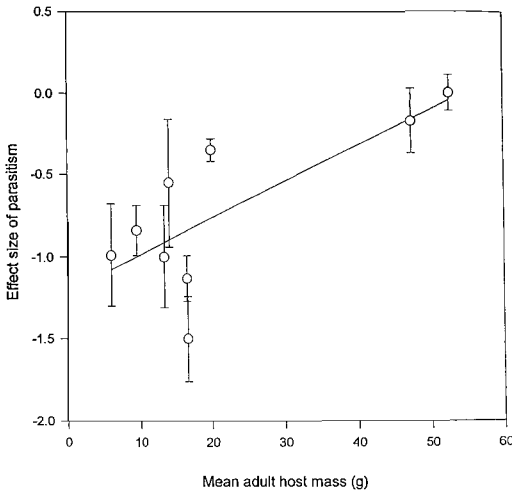| Method used to calculate effect size | Unparasitized | | | Parasitized | | | Effect size |
	N	Mean no. fledged young	SD	N	Mean no. fledged young	SD	
All nests	346	0.67	1.34	58	0	0	−0.54
Successful nests	80	2.9	1.13	9	0	0	−2.27
Females only	87	2.43	2.56	35	0.6	1.14	−0.81

FIGURE 1. The effect of host mass on the cost of raising a Brown-headed Cowbird chick when host productivity is calculated based on all nests, including only species on which more than one study was conducted. Each data point represents the mean effect size for one host species, and error bars are 95% confidence intervals. Negative scale on y-axis indicates a cost of parasitism.

Cruz (1988) and Weatherhead (1989) demonstrated that parasitized individuals suffered reproductive loss due to cowbird parasitism, but that ejection behavior for the population as a whole was not selected because of the relatively low parasitism frequency. This may explain why Red-winged Blackbirds accept cowbird eggs despite being able to eject objects as large as cowbird eggs (Ortega and Cruz 1988).

GRANIVOROUS HOSTS

We hypothesized that granivorous hosts should incur fewer costs associated with parasitism because the insectivorous cowbird nestlings are unable to survive on a diet of seeds (Middleton 1991, Kozlovic et al. 1996, Wootton 1996). Our hypothesis was supported because the granivorous hosts class had the lowest effect size among all classes. Nonetheless, parasitized nests of American Goldfinches and House Finches fledged significantly fewer young than unparasitized nests because of host egg removal by the cowbird. Hatchability of the remaining host eggs was not affected by the cowbird eggs (Middleton 1977, Kozlovic in press).

LIMITATIONS OF USING NEST PRODUCTIVITY TO CALCULATE THE COST OF PARASITISM

A meta-analysis is only as good as the studies on which it is based. A limitation of our analysis is that 95% of the studies calculated the cost of parasitism on a per-nest basis. It is important to note that nest productivity does not accurately reflect seasonal fecundity because birds may renest after successfully fledging a brood or after nest failure due to parasitism, predation, severe weather or nest desertion (May and Robinson 1985, Pease and Grzybowski 1995). Therefore, females that renest after nesting failure due to cowbird parasitism may still successfully fledge young in the same breeding season (e.g., Roth et al. 1996). For this reason, a better method of calculating the cost of parasitism is to determine the effect of parasitism on the productivity of parasitized individuals over the entire breeding season rather than on an individual's nesting success (Pease and Grzybowski 1995). Calculation of the costs based on seasonal fecundity more accurately reflects the selective pressure of cowbird parasitism on a host population.

To our knowledge, only four studies have attempted to follow parasitized and unparasitized females over the course of the entire nesting season. Considering only nesting attempts during the time that cowbirds actively lay may overestimate the cost of parasitism. Smith (1981) found that parasitism depressed the breeding success of female Song Sparrows in a given breeding attempt, but females raised the same total number of young to independence in a breeding season, regardless of whether they were parasitized because they made more breeding attempts per year. Similarly, in a 16-year study Roth et al. (1996) found that parasitized and unparasitized Wood Thrush females fledged the same number of young per year because females renested when the frequency of cowbird parasitism was lower. On the other hand, Klaas (1975) and G.T. Braden (pers. comm.) found that Eastern Phoebes and California Gnatcatchers, respectively, incurred a significant cost of parasitism when breeding success was based on the entire nesting season. However, Klaas (1975) did not work with a marked population and he assumed that pairs renested in their original territories.

The analysis of G.T. Braden's (pers. comm.) data on the fledging success of California Gnatcatchers indicated that the use of successful nests only in the calculation of cost of parasitism grossly overestimated the cost. The use of all nests, however, underestimated the cost relative to cost calculated on the basis of female productivity over the entire breeding season (Table 6). The difference in the calculated costs of parasitism is likely due to the high frequency of nest failure of gnatcatcher nests. Indeed, 74% of unparasitized gnatcatcher nests failed due to predation, nest desertion, weather, or infertility (Braden et al. 1997b). Because a high proportion

of gnatcatcher nests failed for reasons other than cowbird parasitism, the calculated cost of parasitism was quite low when all nests were considered in the cost of parasitism. Although these data may be extreme because of frequent failure, a comparison of the results obtained when the cost of parasitism is calculated in different ways confirms that the way in which the cost of parasitism is calculated influences strongly the value for the cost. Researchers should be cautious when interpreting costs of parasitism calculated using nest productivity data.

Pease and Grzybowski (1995) developed a model that may be used to estimate the seasonal fecundity of a population based on several life history parameters that are more easily measured in the field. They tested their model using Prairie Warbler (*Dendroica discolor*) and Black-capped Vireo (*Vireo atricapillus*) data and found that their theoretical estimates of seasonal fecundity matched closely values measured directly (empirical observation = 2.2 and prediction from model = 2.2 Prairie Warblers raised per female; empirical observation = 0.9 or 1.0 and prediction from model = 1.0 Black-capped Vireos raised per female). Researchers who cannot measure the seasonal fecundity of their host population in question should consider using the Pease and Grzybowski (1995) model. Furthermore, studies that measure the seasonal fecundity of a host population directly may be used to test the validity of the model.

A second problem with most studies that quantified the cost of parasitism is that young produced in a season were monitored only until they fledged. Much more effort is required to monitor fledged young because it requires color-marked individuals that generally are very difficult to relocate once they have left the nest. To our knowledge, only Smith's (1981) study determined the survivorship of host young to independence (four weeks after hatching). Basing host productivity on the number of young that fledge from a nest underestimates the cost of parasitism if disproportionately fewer host young survive to independence because their parents are also caring for fledgling cowbirds. Robinson (1992) found that hosts often cared only for cowbird fledglings. Clearly, studies of the productivity of cowbird hosts should look beyond the nestling stage.

Further studies are also needed to determine whether there is a difference in the number of young fledged by parasitized and unparasitized hosts and recruited into a breeding population. Even when the number of young fledged by parasitized and unparasitized females does not differ (see Smith 1981, Roth et al. 1996), the number of young recruited to future breeding sea-

sons may be different. Payne and Payne (1998) found that Indigo Buntings that fledged from nests that also fledged a cowbird were only 18% as likely to return the next year compared to buntings from nests that did not fledge cowbirds. Whitfield and Sogge (*this volume*) also found that young fledged by parasitized pairs were less likely to return than young fledged from unparasitized pairs. This was due to the fact that parasitized pairs were forced to renest before successfully fledging young, and young that fledged later had lower return rates than earlier-fledged young (see also Perrins 1970, Hochachka 1990).

Another possible cost of parasitism that was not addressed by our study is the reduction in a host's future reproductive success. Caring for an additional chick may reduce a host's future productivity by reducing adult survival (May and Robinson 1985). Parasitized adults may work harder to feed additional cowbird young (Furrer in Friedmann et al. 1977). This cost is likely to be more important for small hosts. Only one study has attempted to assess the long-term cost of parasitism. Payne and Payne (1998) did not find that survival or reproductive success of Indigo Buntings was affected by parasitism in the previous year, and concluded that nearly all costs of parasitism are manifested in the parasitized brood. However, results from Gustafsson and Sutherland's (1988) study, in which a conspecific egg was added to Collared Flycatcher (*Ficedula albicollis*) nests, demonstrated that raising additional young may decrease an adult's future fecundity. Gustafsson and Sutherland (1988) reported that more chicks fledged from nests with enlarged clutches, but juveniles survived less well and those that did survive had reduced fecundity as measured by the number of their offspring that survived to breed. Furthermore, females with experimentally enlarged clutches laid fewer eggs the following year. The difference between Gustafsson and Sutherland's (1988) experiment and cases involving cowbird parasitism is that female cowbirds often remove one host egg from nests they parasitize (e.g., Sealy 1992). Host egg removal may reduce some of the negative effects of brood parasitism on future fecundity (McMaster and Sealy 1997); however, one cowbird egg may represent the equivalent of more than one small host egg. It is conceivable, therefore, that some of the effects of enlarged Collared Flycatchers clutches are analogous to the effect of cowbird parasitism on the future fecundity of hosts. A limitation of the studies of Payne and Payne (1998) and Gustafsson and Sutherland (1998) is that they assessed long-term costs by considering the survivorship and fecundity of females in the next year; they did not consider the lifetime cumu-

lative effects of parasitism. Assessing the lifetime cumulative effects of parasitism is difficult because breeding individuals must be tracked over their lifetime with an accounting of all of their breeding attempts.

RECOMMENDATIONS FOR FUTURE STUDIES OF PRODUCTIVITY

Our meta-analysis summarized empirical studies that quantified the cost of cowbird parasitism. Across all studies, the number of young fledged per nest was significantly decreased by cowbird parasitism, and larger species incurred a smaller cost of parasitism that approached significance when all nests were used in the calculation of parasitism costs. It is important to assess the costs of parasitism accurately to understand better host responses to cowbird parasitism. If the cost of parasitism is not as great as the cost of evolving anti-parasite strategies such as egg ejection behavior, then it makes sense that some species raise cowbird young. For example, our meta-analysis revealed that Red-winged Blackbirds and Wood Thrushes did not incur a significant cost when the cost of parasitism was calculated on the basis of all nests (Table 4). It is also necessary to understand the impact of cowbird parasitism because of its conservation implications. If cowbird parasitism is not as costly as traditionally believed, there will be less support for the control of female cowbirds. Calculating the cost of parasitism based on successful nests only overestimated the cost of parasitism relative to the cost of parasitism based on all nests (Table 5) or on female seasonal fecundity (Table 6).

Ninety-five percent of the studies defined the cost of parasitism in terms of the difference in the number of young fledged from parasitized and unparasitized nests. This estimation does not necessarily reflect the selection pressure that parasitized individuals face because some parasitized individuals that renest raise the same number of young as unparasitized individuals (Smith 1981, Roth et al. 1996). Fledglings of parasitized pairs may have a lower probability of surviving to the next year than young of unparasitized pairs (e.g., Whitfield and Sogge *this volume*). We strongly encourage researchers to quantify the productivity of females over the entire breeding season. If this is not possible, the Pease-Grzybowski model may be used to estimate the seasonal fecundity of the host in question. Following young beyond the nestling stage and determining how parasitism affects the lifetime reproductive success of hosts are necessary to obtain a more accurate representation of the cost of parasitism. These questions are difficult to assess through empirical studies; hence, mathematical models may be required to determine the cost of parasitism.