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Red-winged blackbird parental investment following brood parasitism by brown-headed cowbirds: is parentage important?

Received: 24 January 1997 / Accepted after revision: 7 June 1997

Abstract Parental investment by red-winged blackbirds (*Agelaius phoeniceus*) in response to natural and experimental parasitism by brown-headed cowbirds (*Molothrus ater*), and in response to freeze-dried, female cowbird mounts presented near redwing nests during the egg-laying period was measured. Two measures of red-wing parental investment were used: nest defense effort toward a model predator, and rate of feeding nestlings. There were no significant differences in levels of parental investment among unparasitized nests, naturally parasitized nests, or experimentally parasitized nests. Similarly, parental investment did not differ between redwings that were exposed to the cowbird mount and those that were not exposed to the mount, or among redwings exposed to the cowbird mount at different distances from the nest. This suggests that red-winged blackbirds do not recognize when they have been parasitized, and hence do not associate parasitism with a decrease in their parentage, or that parentage is not an important predictor of parental investment in this species.

Key words *Agelaius phoeniceus* · Brood parasitism · *Molothrus ater* · Parentage · Parental investment

Introduction

Parental investment occurs in all species of birds (Lack 1968; Silver et al. 1985). Because such behavior is costly (Drent and Daan 1980), it is logical to conclude that birds should avoid investing in unrelated offspring. It has been hypothesized, however, that the effect of parentage on parental investment varies with the predictability of parentage across all matings, the costs of

parental behavior, and the ability of parents to assess their parentage (Maynard Smith 1978; Grafen 1980; Werren et al. 1980; Winkler 1987; Whittingham et al. 1992; Xia 1992; Westneat and Sherman 1993). Applications of molecular techniques to studies of parentage have revealed a considerable degree of extra-pair paternity (females mating with extra-pair males) and extra-pair maternity (conspecific brood parasitism) in many bird species (e.g., Gowaty and Karlin 1984; Birkhead et al. 1990; Lifjeld et al. 1993; Westneat 1993; Mulder et al. 1994; McRae and Burke 1996). Several empirical studies have found positive relationships between parentage and parental investment (Møller 1988, 1991; Davies et al. 1992; Dixon et al. 1994; Weatherhead et al. 1994). Other authors, however, have reported no such relationship (Whittingham et al. 1993; Jamieson et al. 1994; Westneat 1995; Whittingham and Lifjeld 1995; Yezerinac et al. 1996).

Recent studies also have shown that males and females do not discriminate among related and unrelated offspring within a brood (Burke et al. 1989; Lifjeld et al. 1992; Frumkin 1994; Westneat et al. 1995). The absence of individual nestling recognition is likely due to the costs of misidentifying and rejecting related offspring (Beecher 1991). Westneat (1995) suggested that if there were little predictability in the patterns of extra-pair copulations and conspecific brood parasitism, and if behavioral cues did not accurately reflect parentage, then discrimination was unlikely to evolve.

Interspecific brood parasitism provides an extreme example of parental investment in unrelated offspring. Whereas some host species are capable of recognizing and removing parasitic eggs from their nests, many hosts accept foreign eggs even in the absence of egg mimicry (Rothstein 1975). These hosts continue to invest in parasitic eggs and nestlings, often at the expense of their own offspring (Lack 1968; Rothstein 1990). In some acceptor hosts there is evidence that they discriminate against foreign nestlings and that this discrimination has selected for mimicry of host markings and vocalizations by parasitic nestlings (Mundy 1973; Nicolai 1974). The

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vast majority of hosts, however, show no recognition of parasitic nestlings (Davies and Brooke 1989; Rothstein 1990).

There have been few studies examining host parental investment in host-parasite systems in which nestlings of both species coexist to independence (Woodward 1983; Soler et al. 1995a,b). In the current study, I measured parental investment by male and female red-winged blackbirds (*Agelaius phoeniceus*) in response to natural and experimental brood parasitism by the brown-headed cowbird (*Molothrus ater*), and in response to the presentation of freeze-dried, female cowbird mounts near redwing nests during the egg-laying period. Red-winged blackbirds are large enough to eject cowbird eggs (Rohwer and Spaw 1988), but they are not known to do so (Rothstein 1975; Ortega and Cruz 1988; Ward et al. 1996). It has also been demonstrated that redwings can discriminate between brown-headed cowbirds and non-threatening birds (Robertson and Norman 1977; Folkers and Lowther 1985; Neudorf and Sealy 1992). The goals of this study were to determine if (1) red-winged blackbirds can detect brood parasitism by brown-headed cowbirds despite the absence of overt rejection behavior, and if (2) redwings decrease their parental investment at parasitized nests or at nests exposed to a female cowbird mount, where they are likely to suffer decreased parentage.

Methods

Study species and study area

Red-winged blackbirds are polygynous icterids (passerine subfamily Icterinae) that show asymmetric biparental care. Females perform all nest construction, incubation, and nestling brooding, as well as the majority of nestling and fledgling feeding (Searcy and Yasukawa 1995). Males are vigilant throughout the nesting cycle (Yasukawa et al. 1992) and may contribute to feeding nestlings and fledglings (Muldal et al. 1986; Whittingham 1989; Yasukawa et al. 1990; Patterson 1991). Males feed nestlings most regularly at the first nest initiated on their territory (Yasukawa et al. 1990; Patterson 1991; but see Muldal et al. 1986; Whittingham 1989; Searcy and Yasukawa 1995). Both sexes defend nests against predators and brown-headed cowbirds (Robertson and Norman 1977; Robertson and Biermann 1979; Folkers and Lowther 1985; Knight and Temple 1988; Neudorf and Sealy 1992).

Brown-headed cowbirds are brood-parasitic icterids, known to parasitize more than 200 species of passerines in North America (Friedmann and Kiff 1985). All parental investment is performed by the host species. Brown-headed cowbirds lay nonmimetic eggs, though the coloration and maculation pattern is similar to many of their hosts' eggs. To human observers, brown-headed cowbird eggs are clearly different in size, shape, color, and maculation pattern from red-winged blackbird eggs (Ortega and Cruz 1988).

I studied red-winged blackbirds and brown-headed cowbirds on Diehls Prairie, an 18-ha grass and sedge meadow in southern Wisconsin, United States (42°32'N, 89°08'W). The behavior of redwings in this area has been extensively studied by K. Yasukawa and his colleagues on neighboring Newark Road Prairie (e.g., Yasukawa et al. 1990, 1992), a site very similar to Diehls Prairie. Data for the current study were collected 1 May–20 June 1995. Diehls Prairie supports 30–35 territorial male redwings each breeding season, and most males attract 2–3 females to their ter-

ritories. The majority (>75%) of territorial and some non-territorial (floater) males were individually color-banded, but fewer than 10% of females were banded. Cowbirds typically parasitize 8–20% of redwing nests in the study area each year (Yasukawa et al. 1990).

Presentation of cowbird mounts

As part of a separate experiment, female cowbird mounts were presented at redwing nests during the egg-laying period. Three mounts were prepared by freeze-drying pre-frozen cowbird specimens at -86 °C for 24 h. All specimens were adult females in breeding plumage. The mount to be used in a given presentation was determined randomly. Live conspecifics courted and displayed to the freeze-dried mounts, which suggests that they were realistic representations of living cowbirds. The freeze-dried mounts were wired to a wooden T-shaped perch approximately 0.75 m tall. Nests were presented with the cowbird mount for 5 min once during the morning (0500–0900 hours CDT) on 2 consecutive days during the 4-day egg-laying period. For each of the two presentations, the mounted cowbird was presented at one of three distances from the redwing nest: <1 m, 5 m, or 10 m (randomly determined). Therefore, some nests were presented with the mounted cowbird at distances of <1 m and 10 m from the nest, others at <1 m and 5 m, and others at 5 m and 10 m. Redwing responses to the cowbird mounts decreased with increasing distance from the nest (E.D. Clotfelter, unpublished work). For each nest presented with a mounted cowbird, a mean mount presentation distance was calculated. For example, a nest presented with the mount at distances of 5 m and 10 m was assigned a mean presentation distance of 7.5 m.

Experimental parasitism of redwing nests

In addition to observing parental investment at naturally parasitized nests, I used brown-headed cowbird eggs collected from Newark Road Prairie to experimentally parasitize redwing nests on Diehls Prairie. I transported eggs by hand 24 h after they were laid and deposited them in nests at the same laying stage. If multiple potential host nests were available, I selected among them randomly. To mimic normal egg removal behavior of brown-headed cowbirds I removed one redwing egg from all experimentally parasitized nests (Weatherhead 1989).

Redwing nest defense effort

In order to measure red-winged blackbird nest defense effort, I recorded responses made toward a plastic crow (*Corvus brachyrhynchos*) model. Crows are common in the study area and a known predator of redwing eggs and nestlings (Knight and Temple 1988; Searcy and Yasukawa 1995). The model was placed on a 1-m metal pole 5 m from the focal nest. I presented the crow model once at each nest during the incubation stage, 4–12 days after clutch completion. The crow model was presented at redwing nests for 5 min, with observation periods divided into 10-s intervals. In each interval, the following responses were recorded for both sexes: approaches, alarm calls, passes, and strikes. I began recording responses when either the male or female redwing oriented toward the model. I recorded an approach whenever the male or female came within 2 m of the model. Alarm calls included the vocalizations described in Knight and Temple (1988). I recorded a pass whenever a redwing dove within 1 m of the model and a strike whenever a redwing made physical contact with the model. In a 10-s interval as many as three responses could be recorded for both males and females; only passes and strikes were mutually exclusive response categories. I observed redwings from inside an observation blind or from behind concealing vegetation at a distance of approximately 30 m from the nest and dictated observations into a microcassette recorder for later transcription. In none of the trials

did either the female or male direct their responses toward me rather than toward the crow model. If there was no response to the model after 10 min, the trial was terminated. I examined the importance of the following variables in determining male and female nest defense effort: date of crow presentation, time of presentation, clutch age (number of days after clutch completion), total clutch size (including cowbird egg, if any), and nest status (based on chronological sequence of nests initiated on a territory).

Redwing feeding of nestlings

I observed males and females feeding nestlings from inside an observation blind placed approximately 30 m from focal nests. I began observing nests once all nestlings hatched and continued until the first nestling fledged (10–14 days posthatching) or until the nest failed. The order of nest observations was determined randomly each day. I observed nests for 30 min/day, with the 30-min period beginning with the first trip to the nest by either parent. I made this stipulation because it indicated that the redwings no longer were disturbed by the observer entering the blind. Only nests that I was able to observe for at least 5 days were included in the analysis. To control for variance in the number of observation days, I calculated mean feeding rates over all observation days for each nest observed. I examined the importance of the following variables in determining male and female feeding rates: mean date of observations, mean time of observations, mean nestling age (number of days posthatching), mean brood size (including cowbird nestling, if any), nest status, and presence or absence of a cowbird nestling.

Statistical analysis

Multiple regressions, Kruskal-Wallis ANOVA, Mann-Whitney *U*-tests, and Wilcoxon matched-pairs signed-ranks tests were performed using SYSTAT (Wilkinson 1990). To control for potentially confounding effects (e.g., date, time, nestling age) on redwing feeding of nestlings, I obtained standardized residuals from multiple regressions of those variables on male and female feeding rates. These residuals were then used to examine the importance of nest parasitism (unparasitized, naturally parasitized, and experimentally parasitized), exposure to cowbird mount (exposed and unexposed), and the mean distance of cowbird mount exposure (<3 m, <5 m, 7.5 m) using Kruskal-Wallis ANOVA or Mann-Whitney *U*-tests. This approach allowed me to compare parental investment among pairs of redwings that were subjected to multiple experimental treatments, and therefore had varying degrees of exposure to cowbirds. Results from multiple regressions showed no effects of presentation date, presentation time, clutch age, and clutch size on any of the four measures of redwing nest defense effort (see below). Therefore, I used the raw response data rather than the standardized residuals to compare among experimental treatments. Means are presented ± 1 SE. All tests are two-tailed, and differences were considered significant at $P < 0.05$. To determine the power of nonparametric tests I used a \log_{10} transformation, analyzed the transformed data with the appropriate parametric test (ANOVA, two sample *t*-test), and performed a *post-hoc* power analysis (Zar 1996). For tests where residuals were used in place of raw data, I used a $\log_{10}[x + (a + 1)]$ transformation, where *a* is the absolute value of the largest residual in the analysis.

Results

I found 86 red-winged blackbirds nests on Diehls Prairie in 1995. Of these, 13 (15.1%) were parasitized by brown-headed cowbirds. An additional 17 (19.7%) were experimentally parasitized with cowbird eggs from New-

ark Road Prairie. All parasitized nests contained only one cowbird egg each. I presented the freeze-dried, female cowbird mounts twice at each of 34 redwing nests. Redwings responded aggressively to the cowbird mount in 64 (94.1%) of the 68 trials.

Redwing nest defense effort

I presented the crow model at 53 red-winged blackbird nests, and redwings at all nests responded aggressively to the model. Eight of these nests were naturally parasitized, 12 were experimentally parasitized, and 33 were unparasitized; 20 nests were exposed to the cowbird mount and 33 were not exposed to the cowbird mount. Approaches toward the model and alarm calling at the model were the most common responses, while passes and strikes were relatively rare (Fig. 1). Males performed significantly more approaches toward the model than did females ($\bar{x}_{\text{males}} = 16.96 \pm 1.32$ approaches/5 min, $\bar{x}_{\text{females}} = 11.02 \pm 1.60$ approaches/5 min, Wilcoxon matched-pairs signed-ranks test, $z = -3.090$, $P = 0.002$). Similarly, males performed more alarm calls, passes, and strikes toward the model than did females (alarm calls: $\bar{x}_{\text{males}} = 24.94 \pm 1.03$, $\bar{x}_{\text{females}} = 17.55 \pm 1.53$, $z = -4.217$, $P < 0.001$; passes: $\bar{x}_{\text{males}} = 7.21 \pm 0.76$, $\bar{x}_{\text{females}} = 1.70 \pm 0.56$, $z = -5.039$, $P < 0.001$; strikes: $\bar{x}_{\text{males}} = 3.94 \pm 0.63$, $\bar{x}_{\text{females}} = 0.094 \pm 0.77$, $z = -5.163$, $P < 0.001$). Results from a multiple regression show that presentation date, presentation time, clutch age, and total clutch size were not significant

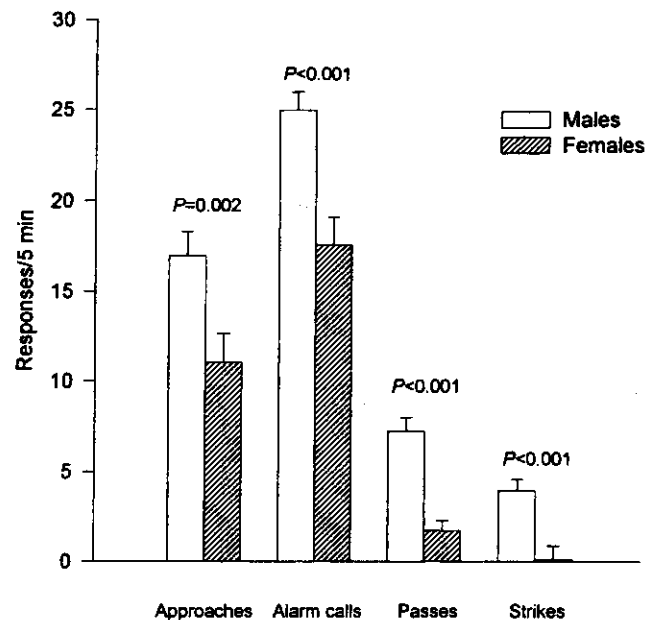


Fig. 1 Comparison of nest defense effort by male and female redwinged blackbirds toward a model crow ($n = 53$ nests). Responses (approaches, alarm calls, passes, and strikes) were recorded for each 10-s interval of a 5 min observation period. *P* values represent the results of Wilcoxon matched-pairs signed-ranks tests

predictors of nest defense by either males (Table 1) or females (Table 2), with the exception of a significant positive relationship between presentation time and the number of passes performed by males. Nest status was not included in the full analysis because the status was not known for many of the nests in the sample; however, I ran a separate regression on this subsample ($n = 34$),

and nest status had no significant effect on any measure of nest defense (Tables 1, 2).

Differences in nest defense effort by pairs of redwings with varying degrees of exposure to cowbirds is summarized in Table 3. There were no differences among naturally parasitized, experimentally parasitized, or unparasitized nests in any measure of male nest defense

Table 1 Effects of presentation date, presentation time, clutch age, and total clutch size on nest defense effort by male redwings toward the model crow ($n = 53$). The effect of nest status was calculated

from a subsample of the data set ($n = 34$). Data presented include the unstandardized regression coefficients (SE) and the P value

	Approaches	Alarm calls	Passes	Strikes
Constant	30.36 (32.16) $P = 0.35$	27.88 (25.23) $P = 0.28$	-27.91 (16.45) $P = 0.10$	15.85 (15.16) $P = 0.30$
Date	-0.13 (0.17) $P = 0.43$	-0.01 (0.13) $P = 0.94$	0.053 (0.086) $P = 0.54$	-0.013 (0.080) $P = 0.87$
Time	0.002 (0.008) $P = 0.83$	-0.006 (0.007) $P = 0.40$	0.015 (0.004) $P = 0.001$	-0.003 (0.004) $P = 0.41$
Clutch age	0.37 (0.53) $P = 0.48$	0.15 (0.41) $P = 0.72$	0.22 (0.27) $P = 0.42$	-0.26 (0.25) $P = 0.30$
Total clutch size	0.20 (2.26) $P = 0.93$	0.79 (1.77) $P = 0.66$	2.27 (1.16) $P = 0.06$	-1.00 (1.07) $P = 0.35$
Nest status	-2.37 [†] (4.71) $P = 0.62$	1.32 (2.91) $P = 0.65$	3.68 (2.41) $P = 0.14$	-3.02 (2.49) $P = 0.24$

Table 2 Effects of presentation date, presentation time, clutch age, and total clutch size on nest defense effort by female redwings toward the model crow ($n = 53$). The effect of nest status was

calculated from a subsample of the data set ($n = 34$). Data presented include the unstandardized regression coefficients (SE) and the P value

	Approaches	Alarm calls	Passes	Strikes
Constant	16.06 (38.49) $P = 0.68$	17.46 (36.47) $P = 0.63$	1.76 (13.79) $P = 0.90$	-0.47 (1.89) $P = 0.80$
Date	-0.15 (0.20) $P = 0.48$	0.038 (0.19) $P = 0.84$	-0.015 (0.072) $P = 0.84$	0.000 (0.01) $P = 0.98$
Time	0.004 (0.010) $P = 0.71$	-0.014 (0.009) $P = 0.14$	0.001 (0.004) $P = 0.73$	0.001 (0.000) $P = 0.26$
Clutch age	0.81 (0.63) $P = 0.20$	0.67 (0.60) $P = 0.27$	0.15 (0.23) $P = 0.51$	-0.013 (0.031) $P = 0.67$
Total clutch size	1.13 (2.71) $P = 0.68$	0.83 (2.56) $P = 0.75$	-0.18 (0.96) $P = 0.85$	0.012 (0.13) $P = 0.93$
Nest status	3.92 (6.22) $P = 0.53$	2.83 (5.31) $P = 0.60$	-1.25 (2.66) $P = 0.64$	-0.39 (0.37) $P = 0.30$

Table 3 Effects of parasitism (natural, experimental, unparasitized), exposure to a freeze-dried cowbird mount (exposed, unexposed), and cowbird mount distance (<3 m, <5 m, 7.5 m) on four mea-

asures of nest defense effort for male and female redwings. P values represent the results of Kruskal-Wallis ANOVA and Mann-Whitney U -tests

Response	Parasitism ($n = 8, 12, 33$)	Cowbird exposure ($n = 20, 33$)	Cowbird distance ($n = 6, 5, 9$)
Male approaches	$H = 1.26, P = 0.53$	$U = 246, P = 0.12$	$H = 3.42, P = 0.18$
Female approaches	$H = 0.19, P = 0.91$	$U = 268, P = 0.24$	$H = 1.21, P = 0.55$
Male alarm calls	$H = 2.69, P = 0.26$	$U = 232, P = 0.06$	$H = 3.00, P = 0.22$
Female alarm calls	$H = 0.096, P = 0.95$	$U = 350, P = 0.71$	$H = 4.01, P = 0.14$
Male passes	$H = 2.06, P = 0.36$	$U = 306, P = 0.66$	$H = 0.37, P = 0.83$
Female passes	$H = 7.44, P = 0.02$	$U = 370, P = 0.42$	$H = 3.47, P = 0.18$
Male strikes	$H = 0.45, P = 0.80$	$U = 314.5, P = 0.77$	$H = 0.45, P = 0.80$
Female strikes	$H = 0.98, P = 0.61$	$U = 350, P = 0.27$	$H = 0.00, P = 1.00$

Table 4 Effects of mean observation date, mean observation time, mean nestling age, mean brood size, nest status, and the presence or absence of a cowbird nestling on male and female redwing feeding rates ($n = 38$). Data presented include unstandardized regression coefficients (SE) and P -values

Variable	Male feeding rate	Female feeding rate
Constant	0.41 (6.24), $P = 0.95$	-6.70 (11.35), $P = 0.56$
Mean date	0.014 (0.032), $P = 0.66$	0.002 (0.058), $P = 0.97$
Mean time	-0.004 (0.002), $P = 0.03$	0.006 (0.003), $P = 0.05$
Mean brood size	0.42 (0.16), $P = 0.01$	0.35 (0.28), $P = 0.23$
Cowbird nestling	0.066 (0.18), $P = 0.72$	0.084 (0.33), $P = 0.80$
Mean nestling age	0.14 (0.081), $P = 0.09$	0.39 (0.15), $P = 0.01$
Nest status	-0.60 (0.23), $P = 0.01$	0.92 (0.42), $P = 0.04$

effort. Females, however, were significantly more likely to pass at the crow model when defending naturally or experimentally parasitized clutches. Neither exposure to the cowbird mount nor distance of the mount presentation had significant effects on male or female nest defense effort.

Redwing feeding of nestlings

I observed red-winged blackbirds feeding nestlings at 38 nests. Of these nests 6 were naturally parasitized, 10 were experimentally parasitized, and 22 were unparasitized; 15 were exposed to the cowbird mount and 23 were not exposed to the mount. Female redwings fed at all the nests I observed, and males fed at 27 of the 38 (71%) nests. Female feeding rates were significantly higher than male feeding rates ($\bar{x}_{\text{males}} = 2.13 \pm 0.11$ feeding trips/30 min, $\bar{x}_{\text{females}} = 4.54 \pm 0.19$ feeding trips/30 min, Wilcoxon matched-pairs signed-ranks test, $z = -5.373$, $P < 0.001$). Mean male feeding rate was calculated from all males, including those not observed feeding. Generally, male and female feeding rates were positively related to brood size and nestling age, though some of these relationships were not significant (Table 4). Mean observation time and nest status had opposite effects on male and female nestling feeding rates. Male feeding rate was negatively related to both observation time and nest status whereas female feeding rates were positively associated with these variables (Table 4). Neither mean observation date nor the presence of a cowbird nestling in the nest had an effect on male or female feeding rates (Tables 4, 5).

Discussion

There was no evidence that brood parasitism by brown-headed cowbirds or the presentation of cowbird mounts

at nests during the egg-laying period affected parental investment by red-winged blackbirds. A mechanistic explanation for this negative result could be that red-winged blackbirds are unable to detect parasitism, and therefore do not associate adult cowbirds, cowbird eggs, or cowbird nestlings with a decrease in their parentage. A selective explanation could be that red-winged blackbirds recognize when they have been exposed to cowbirds or been parasitized, but do not reduce their parental investment in response to decreased parentage.

Detection of brood parasitism

There is considerable evidence that hosts of interspecific brood parasites, including red-winged blackbirds, respond to mounts or models of adult parasites differently than they do to nonthreatening controls (Robertson and Norman 1977; Folkers and Lowther 1985; Davies and Brooke 1988; Hobson and Sealy 1989; Moksnes and Røskaft 1989; Neudorf and Sealy 1992). These studies suggest that red-winged blackbirds can recognize adult cowbirds and associate their presence with brood parasitism. In addition, some researchers report that presenting a common cuckoo, *Cuculus canorus*, mount at host nests increases the frequency of rejection of cuckoo eggs by those hosts (Davies and Brooke 1988; Moksnes and Røskaft 1989; Moksnes et al. 1993), though similar work with brown-headed cowbird mounts found no effect (Hill and Sealy 1994; Sealy 1995).

Red-winged blackbirds, like many other hosts, show no rejection of parasitic eggs (Rothstein 1975; Ortega and Cruz 1988; Ward et al. 1996). They abandon nests parasitized before their own first egg is laid, but abandonment is not due to the cowbird egg *per se* (Ortega and Cruz 1988). Some host species may recognize parasitic eggs but appear not to because they are physically unable to remove them from the nest. This is unlikely to be true for red-winged blackbirds, as they are large enough to remove plaster redwing eggs and non-egg ob-

Table 5 Effects of nest parasitism (natural, experimental, unparasitized), exposure to the freeze-dried cowbird mount (exposed, unexposed), and cowbird mount distance (< 3 m, < 5 m, 7.5 m) on female and male redwing feeding rates. P values represent results of

	Parasitism ($n = 6, 10, 22$)	Cowbird exposure ($n = 25, 23$)	Cowbird distance ($n = 4, 5, 6$)
Male feeding rate	$H = 0.08, P = 0.96$	$U = 148, P = 0.46$	$H = 1.69, P = 0.43$
Female feeding rate	$H = 0.26, P = 0.88$	$U = 191, P = 0.58$	$H = 5.04, P = 0.08$

Kruskal-Wallis ANOVA and Mann-Whitney U -tests on residuals (from regression controlling for date, time, nestling age, brood size, and nest status)

jects of similar dimensions (Kemal and Rothstein 1988; Ortega and Cruz 1988; Rohwer and Spaw 1988). In addition to such proximate constraints, there may be fitness consequences that prevent rejection from becoming established. Rejector hosts may damage their own eggs in the process of removing parasitic eggs (Rothstein 1977; Rohwer et al. 1989), be unable to find new nest sites (Petit 1991), or suffer nest predation by adult parasites (Soler et al. 1995c). There is no evidence, however, that these constraints explain the lack of egg recognition in red-winged blackbirds; recognition failure in this species is likely due to evolutionary lag (Rothstein 1982; Ward et al. 1996).

Despite sometimes obvious size differences, no hosts are known to reject parasitic nestlings (Davies and Brooke 1989; Rothstein 1990). One explanation for the lack of nestling discrimination is that brood parasites enforce acceptance by hosts by presenting them with a supernormal stimulus (Dawkins and Krebs 1979). The supernormal stimulus hypothesis may also explain higher feeding rates to parasitized broods compared with unparasitized controls (Gill 1982; Woodward 1983; Soler et al. 1995b; but see Davies and Brooke 1988; Brooke and Davies 1989). In the current study, the presence of a cowbird nestling was not a significant predictor of male or female redwing feeding rates to nestlings, and feeding rates did not differ among unparasitized nests, experimentally parasitized nests, and naturally parasitized nests. This finding is not surprising considering the similarities in size and growth trajectory between redwing and cowbird nestlings (Weatherhead 1989). While I cannot reject the hypothesis that redwing acceptance of cowbird nestlings is somehow due to a supernormal stimulus, there was no evidence that this stimulus had a significant effect on redwing parental investment.

Hosts may not discriminate against parasitic nestlings because the costs of recognition errors are too great (Beecher 1991). Lotem (1993) predicted that hosts of the common cuckoo could suffer significant fitness costs if they imprinted on a cuckoo egg (i.e., identified it as their own) in their first nesting attempt, and that this cost could be sufficient to negate any potential benefits of nestling recognition. He also predicted that nestling recognition by hosts would occur in systems in which host and parasitic nestlings are raised together. In support of his prediction, visual and vocal mimicry of host nestlings by some parasitic species suggests that their respective hosts do discriminate (Mundy 1973; Nicolai 1974). The model of Lotem's (1993) cannot explain, however, the absence of discrimination in many hosts of New World cowbirds (*Molothrus*, *Scaphidura* spp.). It has been suggested that birds show no recognition of their individual offspring because they recognize only nest locations, and that individual recognition does not occur until nestlings leave the nest (Peek et al. 1972; Burt 1977). This site-dependent recognition is likely to reduce the potential risks of misidentifying and rejecting related offspring, although it is open to exploitation by

brood parasites and by extra-pair copulators. Red-winged blackbirds show no recognition of their nestlings (Peek et al. 1972), which helps to explain their acceptance of brown-headed cowbird nestlings.

Importance of parentage

The relationship between parentage and parental investment has received considerable attention in the recent literature. Early theoretical work suggested that if parentage is similar for all matings, then it should have no effect on parental investment (Maynard Smith 1978; Grafen 1980). More recent models show that the effect of parentage on parental investment varies with the ability of parents to assess their parentage and the costs of parental behavior (Werren et al. 1980; Winkler 1987; Whittingham et al. 1992; Xia 1992; Westneat and Sherman 1993). The shape of the optimal parental effort-parentage function, however, remains unclear (Houston 1995). Results from some empirical studies have shown positive relationships between parentage and parental investment (Møller 1988, 1991; Davies et al. 1992; Dixon et al. 1994), while others show no relationship (Whittingham et al. 1993; Jamieson et al. 1994; Whittingham and Liffeld 1995; Yezerinac et al. 1996).

Studies of parentage and parental investment in red-winged blackbirds have yielded similarly inconclusive results. Weatherhead et al. (1994) showed that male redwings decreased their nest defense effort at nests with high levels of extra-pair paternity. In contrast, two studies by Westneat and his colleagues (Westneat 1995; Westneat et al. 1995) showed no evidence that male redwings decreased their feeding rates to broods in which extra-pair paternity was high, or to unrelated nestlings, respectively. Their results suggest that parentage may be a relatively weak predictor of red-winged blackbird parental investment, at least compared with factors such as brood size and nestling age. The selective pressure exerted by cowbird parasitism is likely to be even weaker than that exerted by extra-pair parentage. Studies of redwings have revealed that typically 20–40% of all offspring are sired by an extra-pair male (Gibbs et al. 1990; Westneat 1993; Weatherhead et al. 1994; Gray 1997), though the proportion of nestlings in my redwing population that are actually cowbirds is usually less than 5% (E.D. Clotfelter, unpublished work). Therefore, it is not surprising that the redwings in the current study did not decrease their parental investment to parasitized broods, despite the decrease in parentage.

Power of statistical tests

It must also be considered that the lack of an effect of parasitism on parental investment in the current study could have been due to statistical tests of insufficient power to reject the null hypothesis in cases where it was actually false. To address this possibility, I performed

post hoc power analyses on tests of the effects of parasitism on parental investment. These analyses revealed that all tests had a power of less than 0.60 and that in some tests the power was less than 0.40. Therefore, the probability of committing a type II statistical error was greater than 50% in most cases. This illustrates the importance of obtaining additional data from other host-parasite systems to determine whether these negative results could be statistical artefacts.

Factors affecting redwing parental investment

I found that male red-winged blackbirds gave significantly more responses toward the crow model than did female redwings. Male-biased nest defense effort has been reported previously for red-winged blackbirds and other passerine species (e.g., Regelman and Curio 1986; Breitwisch 1988; Knight and Temple 1988). More than 70% of the male redwings I observed fed their nestlings, and those that fed did so approximately half as frequently as females. These results are consistent with those reported for many populations of red-winged blackbirds (Muldal et al. 1986; Whittingham 1989; Yasukawa et al. 1990; Patterson 1991; Searcy and Yasukawa 1995).

Parental investment theory predicts that the reproductive value of a clutch or brood increases with age and clutch or brood size, and therefore so should parental investment (Dawkins and Carlisle 1976; Lazarus and Inglis 1986; Winkler 1987). Many empirical studies have found such a relationship for nest defense effort (Robertson and Biermann 1979; Searcy 1979; Greig-Smith 1980; Windt and Curio 1986; Breitwisch 1988) and nestling feeding rate (Smith et al. 1988; Muldal et al. 1986; Whittingham 1989; Carey 1990; Yasukawa et al. 1990; Conrad and Robertson 1993). The current study offers limited support for these general predictions. I observed no relationship between the ages of redwing clutches and nest defense effort by either sex. This suggests that clutch age is not a significant predictor of nest defense because parents do not respond to changes in the reproductive value of a clutch until it hatches, when predation rates typically increase. There was also no significant effect of total clutch size on male or female nest defense effort. Feeding rates by male redwings were positively related to brood size, and females increased their feeding rates to older broods.

I found no evidence that nest status had an effect on any measure of male or female nest defense, consistent with work by Weatherhead (1990) and Searcy and Yasukawa (1995). However, males fed nestlings in primary nests significantly more frequently than those in secondary or tertiary nests. This result indicates that females who mate with already-mated males pay a cost in terms of reduced paternal investment. Studies of red-winged blackbirds and other polygynous bird species have demonstrated that males preferentially feed nestlings in primary nests (Alatalo et al. 1982; Yasukawa

et al. 1990; Patterson 1991; Johnson et al. 1993). However, other studies show no apparent cost to secondary or even tertiary females in terms of reduced male feeding rates (Muldal et al. 1986; Whittingham 1989; Searcy and Yasukawa 1995).

In conclusion, red-winged blackbirds did not adjust their parental investment in response to brood parasitism by brown-headed cowbirds or in response to exposure to freeze-dried, female cowbird mounts. I found no evidence that red-winged blackbirds were able to detect parasitism, despite their ability to recognize adult cowbirds as potential threats to their nests. It is also possible that redwings did not change their nest defense effort or their feeding rates to nestlings following brood parasitism because parentage is a relatively unimportant factor in determining parental investment decisions in this species. More data are needed on host parental investment responses to brood parasitism, particularly in socially monogamous, biparental species.

Acknowledgements I would like to thank L. Diehls and his family for allowing me to work on their land. J. Baylis, A. Coulthard, L. Keller, W. Searcy, D. Westneat, L. Whittingham, K. Yasukawa, and an anonymous reviewer made helpful comments on previous versions of this paper. H. O'Brien contributed valuable assistance in the field, and K. Yasukawa loaned equipment and provided logistical support. M. DeCapita was kind enough to send me cowbird specimens, and J. Kirsch allowed me the use of his equipment to freeze-dry them. This work was supported by the National Science Foundation (IBN95-28346), Sigma Xi, and the Netzer/Brouchoud Foundation of the University of Wisconsin.

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Communicated by W.A. Searcy