

# THE FREQUENCY OF CONSPECIFIC BROOD PARASITISM AND THE PATTERN OF LAYING DETERMINANCY IN YELLOW-HEADED BLACKBIRDS<sup>1</sup>

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**Abstract.** In altricial birds, conspecific brood parasitism (CBP) is disproportionately common in species that nest in colonies. We investigated the frequency of CBP in a colonial icterid, the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). Using two criteria for detecting parasitism, we found no cases of CBP in a sample of 69 nests monitored for 522 nest-days. To make sense of this finding, we consider why specific forms of CBP may be lacking in this species. Egg removal experiments demonstrated that Yellow-headed Blackbirds are determinate layers, so a nesting female that also laid eggs parasitically would either suffer a reduced clutch size in her own nest or suffer a delay in initiating her own clutch. Neither territories, nor nest-sites, are limiting for female Yellow-headed Blackbirds, so parasitism by floater females is not expected. Although the destruction of clutches during laying was common during the study, we failed to see parasitism associated with this nest loss. Current information suggests that nest loss may not play an important role in promoting conspecific parasitism in most species.

**Key words:** *Conspecific brood parasitism; determinate egg-laying; Yellow-headed Blackbird; Xanthocephalus xanthocephalus; nest predation.*

## INTRODUCTION

Conspecific brood parasitism (CBP) has now been reported in over 100 species of birds, yet remains a poorly understood reproductive behavior (Yom-Tov 1980, Andersson 1984, Rohwer and Freeman 1989). Two approaches have been used to investigate the adaptive significance of this behavior. The most powerful approach has been to determine the identities of parasitic females in populations and investigate the ecological contexts and reproductive trade-offs involved in parasitism. Unfortunately, it has proven difficult to identify parasites in most studies, and the identities and laying tactics of parasitic females are known for only a handful of species (Clawson et al. 1979; Heusmann et al. 1980; Brown 1984; Emlen and Wrege 1986; Gibbons 1986; Møller 1987; Eadie, in press).

A second approach, the comparative method, has been used to identify specific ecological or life-history characters that correlate with the occurrence of CBP (Yom-Tov 1980, Håland 1986, Rohwer and Freeman 1989, Eadie et al. 1988, Eadie 1991). Some preliminary results have emerged from these studies. Parasitism appears to be more common in precocial birds than altricial birds (Yom-Tov 1980, Rohwer and Freeman 1989), largely because parasitism is so common in one precocial group, the waterfowl. Within the waterfowl, nest site limitation appears to be an important factor (Eadie 1991). In altricial birds, a high nesting density appears to be an important prerequisite, as over half of the reported cases involve colonial species (Håland 1986, Rohwer and Freeman 1989).

The data used in these comparative studies suffer from two biases. First, there are biases in our ability to detect CBP (Frederick and Shields 1986) and these may give rise to spurious correlations (MacWhirter 1989). For example, precocial birds have larger clutches than altricial birds and the ability to detect parasitism by some criteria is a function of clutch size (Frederick and Shields 1986). It is possible, therefore, that the

<sup>1</sup> Received 6 November 1991. Accepted 12 February 1992.

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disproportionate number of cases of CBP in precocial species merely reflects this detection bias (MacWhirter 1989).

Compounding these detection biases is a strong reporting bias. Researchers report cases where parasitism was observed, but not cases where parasitism was absent. Rohwer and Freeman's (1989) need to obtain information about species lacking parasitism from personal communications rather than the literature clearly reflects this reporting bias. The combined effects of detection and reporting biases make interpretation of negative evidence difficult. For example, we do not know whether species which lack reports of parasitism simply have not been studied in enough detail to detect parasitism or, alternatively, have been studied adequately but the lack of parasitism was not reported. These problems suggest that studies which clearly document a lack of CBP will be as valuable as those which simply document its occurrence.

We studied Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), a marsh-nesting colonial species, to document the frequency of CBP. We also investigated two aspects of the reproductive ecology of Yellow-headed Blackbirds that could be associated with specific forms of parasitism. First, we conducted egg removal experiments to determine whether Yellow-headed Blackbirds are determinate or indeterminate egg-layers, because indeterminate laying greatly facilitates parasitism by females with nests of their own (Kendra et al. 1988). Second, we monitored the frequency of egg destruction during laying because parasitism in some species is associated with nest loss (e.g., Emlen and Wrege 1986). We also performed egg addition experiments to determine whether female Yellow-headed Blackbirds show behavioral responses to parasitism like egg-rejection or nest-desertion.

## METHODS

We conducted this study on two marshes 15 km SE of Hanceville, British Columbia, Canada, from 13 May to 6 June 1989. The marshes are part of a system of wetlands managed by Ducks Unlimited Canada, so water levels were controlled and maintained at high levels during this study. The blackbirds nested in beds of *Scirpus lacustris* growing along the edges of the ponds and foraged on the prairie surrounding the marshes.

We used two standard criteria to determine whether CBP had occurred (Yom-Tov 1980,

Brown 1984, Gibbons 1986, Møller 1987), (1) the appearance of two or more new eggs in a single day during laying and (2) the appearance of new eggs after the host had completed laying her own clutch. We usually visited nests once a day, but did not visit the study area on five different days and some nests were visited less frequently after clutch completion. On each visit, all new eggs were numbered with a fine-point, indelible felt pen. We report two sample sizes. First, we report the total number of nests monitored during laying and incubation. However, we did not follow all nests through to hatching so simply reporting the number of nests followed does not accurately reflect our ability to detect parasitism by each criterion. Therefore, we also report the total number of nest-days that nests were monitored *where we could have detected parasitism* by each criterion (see Frederick and Shields 1986). For example, we didn't count the first day of incubation as a nest-day of observation because we could not have detected parasitism on this day. Of the 64 nests to which we applied the two egg per day criterion, 54 were found on, or before, the day the first egg was laid, and 10 were found when they contained two eggs. The cases found with two eggs occurred when we did not visit the study area for two days so we assume that these birds initiated on the day we missed.

To determine whether Yellow-headed Blackbirds are indeterminate or determinate egg-layers, we removed one egg from each of 25 nests during laying (Removals). Considering only the 19 Removal nests that successfully reached clutch completion, we removed the first egg on the day it was laid at seven nests (First Day Removals), and removed one egg on the day the second egg was laid at 12 nests (Second Day Removals). For both experimental and non-experimental nests we recorded whether eggs were destroyed or abandoned. We concluded that nest contents were destroyed if the nest was known to be active on the last visit before the eggs were lost or damaged. Since we did not conduct behavioral observations at nests, we could not distinguish among conspecific egg destruction, predation, or egg destruction by Marsh Wrens (*Cistothorus palustris*, Picman 1977). Nests were considered abandoned if the eggs were cold in the nest prior to destruction, or if an incomplete clutch (one or two eggs) remained in the nest for more than one day.

TABLE 1. The frequency of conspecific brood parasitism in Yellow-headed Blackbirds. Results for incubation and laying are presented separately because different criteria were used for each of these phases of reproduction (see text). Two measures of sample size are given: the number of nests monitored during each phase of reproduction, and the total number of nest-days of observation for each phase.

	Nests	Nest-days	Parasitized nests
Non-experimental nests			
Laying	46	158	0
Incubation	28	142	0
Experimental nests			
Laying	18	68	0
Incubation	22	154	0
All nests			
Laying	64	226	0
Incubation	50	296	0

We used egg addition experiments to determine whether Yellow-headed Blackbirds respond to parasitism with behaviors like egg-rejection or nest-desertion. To determine whether females reject eggs added to their nest before they have begun to lay their own clutch, we added single eggs to seven nests before the "host" female had initiated her own clutch (Early Additions). We removed all experimental eggs in Early Addition nests that had not been rejected by the time the female laid her own first egg. To determine whether females are capable of recognizing eggs from other females we added single real blackbird eggs to seven nests after clutch completion (Late Additions).

## RESULTS

### FREQUENCY OF CONSPECIFIC BROOD PARASITISM

We detected no cases of CBP in our census of 69 nests for a total of 522 nest-days (Table 1). The first criterion for detecting parasitism, the appearance of more than one egg per day, was applied to 64 nests followed during laying for a total of 226 nest-days. The second criterion, new eggs appearing after the owner of the nest had completed laying, was applied to 50 nests monitored during incubation for a total of 296 nest-days. Experimental nests were included in these totals as we could see no reason why our experimental egg removals or additions would alter the natural rates of parasitism. However, for completeness, we partition sample size totals for experimental

TABLE 2. Results of an egg removal experiment to reveal the pattern of egg-laying determinacy. Single eggs were removed at Removal nests; at First Day Removals, the first egg was removed on the day it was laid, while at Second Day Removals, an egg was taken on the day the second egg was laid. Removal final clutch size is the number of eggs remaining in the Removal nests after clutch completion, while removal total is the final clutch size plus the single egg we removed.

	Mean clutch size	SE	<i>n</i>
Control	3.9	0.06	46
Removal total	3.7	0.13	19
Removal final			
All removals	2.7	0.13	19
1st day removals	2.6	0.20	7
2nd day removals	2.8	0.17	12

versus non-experimental nests separately (Table 1).

The proportion of cases of parasitism that would be detected by the criteria we used can be affected by two factors. If parasites removed a host egg before laying (e.g., Lombardo et al. 1989), then neither criterion would detect parasitism. However, since we numbered all eggs on each visit, egg removal by parasites would have resulted in the disappearance of previously numbered eggs. We did not observe the disappearance of any previously numbered eggs. Second, the rate of egg-laying by nesting females can also affect the efficiency of detecting parasitism based on the appearance of two or more new eggs in a single day. For example, if nesting females did not lay eggs every day but skipped days between laying, many cases of parasitism would go undetected. However, almost all females laid their own eggs in a continuous laying sequence and only two females skipped days during laying—one and two days between eggs, respectively. Thus, we would have successfully detected virtually all cases of parasitism that occurred during the hosts' laying periods and more than a day after clutch completion. Our failure to detect parasitism therefore reflects a true lack of parasitism rather than an inability to detect parasitism.

### DETERMINATE OR INDETERMINATE LAYERS?

The total number of eggs laid by Removals (final clutch size plus the one removed egg) did not differ significantly from the clutch size of Controls (Table 2;  $t = 1.20$ , 2-tailed  $P = 0.24$ ,  $df =$

TABLE 3. Egg addition experiments to assess whether female Yellow-headed Blackbirds can recognize foreign eggs, or whether they will reject eggs added before they lay their first egg. For Early Additions, time when experimental egg was added is the number of days before the host's first egg, for Late Additions, it is the number of days after clutch completion.

Nest	When added	Days followed	Fate
Early Additions			
E1	-3		Desert?
E2	-3		Reject
E3	-3		Reject
E4	-7		Reject
E5	-1		Accept
E6	-1		Accept
E7	-1		Accept
Late Additions			
L1	2	6	Accept
L2	4	6	Accept
L3	2	8	Accept
L4	4	7	Accept
L5	3	10	Accept
L6	3	6	Accept
L7	2	8	Accept

63). However, the final clutch sizes of Removal females were significantly smaller than the clutch sizes of Control females (Table 2;  $t = 8.94$ , 1-tailed  $P < 0.001$ ,  $df = 63$ ). The means for these two groups differ by 1.2 eggs which is very close to a difference of one egg predicted by determinate laying.

In some determinate laying species, females lay replacement eggs if the first egg is removed on the day it is laid, but will not replace eggs that are removed later (Parsons 1976). Since two thirds of our removals were done on the day females laid their second egg, our support for determinate laying could be biased. However, excluding Second Day Removals from the analysis does not alter the result; the clutch sizes of First Day Removals were significantly smaller than the clutch sizes of Controls (Table 2;  $t = 7.29$ ,  $P < 0.001$ ,

$df = 51$ ). In addition, the clutch sizes of First and Second Day Removals did not differ (Table 2;  $t = 0.98$ ,  $P = 0.34$ ,  $df = 17$ ). Together, these observations indicate that Yellow-headed Blackbirds are determinate layers, at least with respect to egg removal (Kennedy 1991).

#### RESPONSE TO EGG ADDITIONS

None of the experimental eggs in the Late Addition group were rejected and none of the females deserted (Table 3). In contrast, three of the seven Early Addition eggs disappeared from the nest before the female laid her own first egg (Table 3). We found two of the experimental eggs in the water under the nests, with peck holes in them, indicating that they had been removed, rather than taken by an egg predator. However, we cannot distinguish between removal by the host female and removal by Marsh Wrens. One other female may have abandoned her nest in response to the egg we added. Only one egg was laid in this nest so it was either abandoned after the experimental addition or it was an inactive nest that received a single egg from a parasite.

#### EGG PREDATION AND DESTRUCTION

Destruction of clutches was common. Of the 65 non-experimental nests monitored, 25 nests (38%) had their contents disappear or destroyed, and 18 nests (28%) were destroyed during laying (Table 4). Loss or destruction of nests containing single eggs was particularly common; 10 nests, or 40% of all cases of egg loss occurred in nests that contained a single egg.

To determine whether egg destruction was distributed non-randomly among different stages of the nesting cycle we calculated the expected number of cases of egg loss for: (1) laying versus incubation and (2) nests on the first day of laying versus all other nests. To calculate expected values we multiplied the total number of destroyed clutches (25 nests) by the fraction of total nest-days of observations for each period (Table 4).

TABLE 4. The number of nests that suffered nest predation during three stages of reproduction: on the first day of laying, during the rest of the laying period, and during incubation. Expected values were calculated by multiplying the total number of depredated nests times the proportion of the total nest-days that active nests spent in each stage.

	Stage of reproduction			Total
	First egg	Rest of laying	Incubation	
No. nests depredated	10	8	7	25
Expected no. depredated nests	3.3	9.9	11.8	25
% of total nest-days	13.3	39.4	47.3	100

Comparison of the expected versus observed cases of nest predation during laying versus incubation suggests that nest predation was higher during laying (Table 4;  $G$ -test for goodness of fit, with William's correction,  $G = 3.81$ , 1 df,  $P < 0.06$ ). Comparison of the expected versus observed cases of nest predation for nests containing the first egg versus nests at all other stages indicates that nest predation is disproportionately common at nests containing one egg ( $G = 10.95$ , 1 df,  $P < 0.001$ ).

## DISCUSSION

We found no evidence for CBP in the population we studied in British Columbia. It is possible that either the year of the study or the population we studied was not typical for Yellow-headed Blackbirds. However, there is some evidence that parasitism is rare in other populations as well. In a five year study in eastern Washington, Harms et al. (1991) found that about one percent of over 1,000 nests were parasitized. This suggests that our findings are representative.

It is also possible that parasitism occurred, but in a pattern impossible to detect by the criteria we used. For example, it is conceivable that the disproportionate loss of eggs from nests containing a single egg (Table 4) were instances where parasites laid two or more days prior to the host's first egg, followed by egg removal. However, this scenario is unlikely because parasitism would then be restricted to the period prior to hosts' laying periods, since we found no evidence for parasitism during laying or incubation (Table 1). Such a restricted temporal pattern of laying by parasites has not been reported for other species (Clawson et al. 1979; Møller 1987; Brown 1984; Emlen and Wrege 1986; Gibbons 1986; Evans 1988; Eadie, in press; Lyon 1991), and it is difficult to understand why it would occur in Yellow-headed Blackbirds. In addition, if the disappearance of first eggs were cases where hosts received and removed a parasite egg prior to laying their own eggs, then we would expect these nests to have been subsequently used by the owners. However, only one nest received additional eggs after the loss of the first egg, and since the clutch size in this nest was the smallest observed (2 eggs), the egg that disappeared was likely the nest owner's own egg. Thus, some explanation other than parasitism, such as a high rate of predation on first eggs, likely accounts for the disproportionate loss of eggs from nests containing single eggs.

The removal of some of the eggs added to nests prior to laying could also be interpreted as evidence that conspecific parasitism sometimes occurs, especially since interspecific brood parasitism is absent in Yellow-headed Blackbirds (Ortega and Cruz 1990). For example, in several species with CBP, hosts will remove eggs added prior to the host's first egg, but not after (Brown 1984, Emlen and Wrege 1986, Møller 1987, Stouffer et al. 1987). However, explanations other than defense against parasitism could also account for the egg removal we observed. Egg removal prior to laying is not necessarily an evolved response to conspecific parasitism but, instead, could represent generalized nest-cleaning behavior (Brown and Brown 1989). Alternatively, the eggs could have been removed by Marsh Wrens as they were common at the site and are known to destroy and remove the eggs of blackbirds (Verner 1975, Picman 1977). Thus, observations of egg removal do not necessarily contradict the observed lack of parasitism.

Our failure to document cases of brood parasitism is therefore likely to reflect a genuine lack of parasitism in Yellow-headed Blackbirds. Why would a species lack parasitism? One possibility is that genetic variation for parasitic behavior is lacking, despite a potential selective advantage, as was argued to account for the lack of egg rejection in some species parasitized by the Brown-headed Cowbird (*Molothrus ater*; Rothstein 1982). The fact that parasitism does occur rarely in Yellow-headed Blackbirds (Harms et al. 1991) suggests that genetic variation does occur, but we cannot rule out the possibility that these rare cases of parasitism are simply mistakes without a genetic basis.

It is also possible that parasitism is completely prevented by effective host nest-defense (Rohwer and Freeman 1989). In blackbird species, nest defense by males reduces the risk of nest destruction (Weatherhead 1990), and it could also reduce the occurrence of parasitism. In addition, interactions among females could also deter parasites. Female Yellow-headed Blackbirds do show aggression toward conspecific females (Lightbody and Weatherhead 1987), and this could further reduce the opportunities for parasites. However, it is unlikely that host defenses can completely account for the lack of parasitism in Yellow-headed Blackbirds. The occurrence of parasitism at moderate to high frequencies in several species that exhibit nest defense against

parasites (Gowaty et al. 1989, Emlen and Wrege 1986, Møller 1987, Brown and Brown 1989), as well as in aggressively territorial species (Gibbons 1986, Lyon 1991), suggests that defense against parasites cannot be completely effective.

Finally, parasitism may be absent in Yellow-headed Blackbirds because it does not provide a selective advantage. To assess this possibility we consider the ecological or social contexts that are known to correlate with specific types of parasitism in other species and ask whether these contexts occur in Yellow-headed Blackbirds. A few studies have clearly shown that some of the parasitism in populations is by floater females without nests of their own in a given year (Clawson et al. 1979; Huesmann et al. 1980; Eadie, in press; Lyon 1991). In some taxa, floater females appear to be a consequence of nest-site limitation (Stutchbury and Robertson 1985), and indirect evidence suggests that much of the parasitism in cavity-nesting waterfowl (Eadie 1991) and arctic-nesting geese (Lank et al. 1989) may be due to floaters. Territory saturation in monogamous species may also give rise to a floater population of parasitic, floater females (Lyon 1991). Yellow-headed Blackbirds are colonial, polygynous, and only appear to use a fraction of the available nesting habitat. Thus, nest site limitation and territory saturation should not be important. In support of this, Orians (1980) found no evidence for floater females in his long-term study of Yellow-headed Blackbirds. Our failure to find parasitism by floater females is therefore not surprising.

Some authors have suggested that destruction of partially complete clutches may force females to resort to parasitism (Yom-Tov 1980, Andersson 1984). Egg destruction during laying appears to be common in Yellow-headed Blackbirds, particularly at nests containing a single egg (Table 4), so this selective factor could be important. However, the importance of nest loss as a factor promoting parasitism remains unclear. There is strong evidence that nest loss plays an important role in promoting parasitism for only one species, the White-fronted Bee-Eater (*Merops bullockoides*, Emlen and Wrege 1986). In the European Starling (*Sturnus vulgaris*), two studies have experimentally induced parasitism with nest destruction during laying (Feare 1991, Stouffer and Power 1991), but one of these then concluded that most naturally occurring parasitism was not associated with nest loss (Stouffer and

Power 1991). In studies of other species where parasitic individuals were identified, nest loss was not involved (Clawson et al. 1979; Heusmann et al. 1980; Brown 1984; Gibbons 1986; Møller 1987; Eadie, in press). Moreover, nest loss during laying is common for many species of altricial birds (Ricklefs 1969, Clark and Wilson 1981), yet conspecific parasitism appears to be relatively uncommon (Rohwer and Freeman 1989).

Overall, CBP rarely appears to be associated with nest loss. The reasons for this are not clear but it suggests that females that suffer nest loss have better options to which they can resort. For indeterminate egg-layers, females could simply reneest (Parsons 1976), as long as replacement nests can be rebuilt quickly. For determinate layers, females could resorb the remaining eggs in the clutch and reneest with a full-sized clutch after a lag period. If resorption is not possible, then females could lay the remaining eggs in the clutch and regain the energy by eating the eggs (Payne 1977). Given these various options, it seems unreasonable to expect all species that suffer nest loss during laying to exhibit conspecific parasitism.

In altricial and semi-precocial birds, most parasitism appears to be by females that also have nests of their own (Brown 1984, Gibbons 1986, Møller 1987, Lyon 1991), a form of parasitism that has been called a mixed strategy. A mixed parasitic strategy is facilitated by indeterminate laying because it permits a female to lay parasitically in a continuous sequence with the eggs she lays in her own nest without sacrificing the clutch size in her own nest (Kendra et al. 1988). By contrast, a determinate-laying female must reduce her own clutch size by the number of eggs she lays parasitically, if she is to lay in a continuous sequence. Alternatively, she could lay a full clutch of eggs parasitically and, after a lag period, lay a second clutch in her own nest, a strategy which has been called a dual reproductive strategy (Sorenson 1991). Thus, parasitism in determinate-laying species entails two potential costs not incurred by indeterminate layers: a reduced clutch size in the parasite's own nest or a substantial delay in initiation of her own nest.

Yellow-headed Blackbirds are determinate layers and parasites would therefore suffer either the costs of a reduced clutch size or the costs of delayed nesting. The costs of a reduced clutch size are obvious but the costs of a delay in nesting are less clear. One potential cost is a lower success

for nests initiated later in the season, a cost that appears to be particularly severe for Yellow-headed Blackbirds (Ortega and Cruz 1990). Delaying nesting could also jeopardize assistance by the male in this polygynous species because males only feed the nestlings of the first one or two females to nest on their territory (Willson 1966, Patterson et al. 1980). A dual strategy may also yield a lower benefit per parasitic egg because females must commit an entire clutch to parasitism even when suitable hosts are not available for the entire clutch. This lack of flexibility, coupled with the high costs of delay, probably explains why a dual strategy is lacking in Yellow-headed Blackbirds. However, clutch removal experiments with individually-marked females would indicate the amount of delay in nesting that a dual strategy would require, and would allow a more precise evaluation of the costs of a delay.

We have attempted to understand the absence of CBP in Yellow-headed Blackbirds by considering why specific types of parasitism are absent. It is also worth using this approach to ask why parasitism occurs in the European Starling, a species that shares many of the reproductive characteristics of Yellow-headed Blackbirds. Like Yellow-headed Blackbirds, starlings have altricial young, are determinate egg-layers (Kennedy and Power 1990), and often breed in colonies (Evans 1988). Unlike Yellow-headed Blackbirds, CBP is very common in starlings (Evans 1988, Lombardo et al. 1989, Romagnano et al. 1990).

Why do these species differ so dramatically in the frequency of parasitism? There is virtually no direct evidence as to which specific types of parasitism occur in starlings (Evans 1988, Lombardo et al. 1989, Romagnano et al. 1990). Determinate egg-laying in starlings suggests that parasitism as a mixed strategy is unlikely. Although experimental nest destruction can trigger parasitic behavior in starlings (Feare 1991, Stouffer and Power 1991), nest loss is rare and thought to be unimportant in naturally-occurring cases of parasitism (Stouffer and Power 1991). One important ecological difference between the two species is that starlings are secondary cavity nesters and, unlike Yellow-headed Blackbirds, are probably nest-site limited (Evans 1988, Lombardo et al. 1989). This suggests that nest-site limitation is the critical ecological factor promoting CBP in starlings, and therefore predicts that most parasitism should be by floater females

without nests of their own. Interestingly, circumstantial evidence suggests this is true (Evans 1988, Romagnano et al. 1990, Pinxten et al. 1991).

We have shown that it can be useful to ask why a species lacks brood parasitism, especially when done in a comparative context. The comparison of blackbirds and starlings illustrates how the comparative method can help identify ecological attributes that may promote or constrain parasitism. However, comparisons like these can only provide indirect evidence for the importance of specific ecological factors, and should therefore be considered as only the first step in understanding the occurrence of parasitism. To confirm that the ecological factors identified by comparisons do in fact promote parasitism, it will be critical to identify individual parasites in populations, to determine the constraints they face, and to elucidate the reproductive tradeoffs that parasitism entails.

#### ACKNOWLEDGMENTS

We thank John Eadie, Scott Freeman, Kyle Harms and an anonymous reviewer for comments on the manuscript. This research was supported by funding by the Frank M. Chapman Fund of the American Museum of Natural History, National Geographic Society, United States National Science Foundation, Princeton University and Sigma Xi Society.

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