

# Parasitism of maternal investment selects for increased clutch size and brood reduction in a host

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The allocation of resources to young that will ultimately be left to die appears counterintuitive. Yet obligate brood reduction has evolved in a number of species, despite the waste of reproductive investment this may incur. Here we test whether brood parasitism could be one factor leading to the evolution of obligate brood reduction because surplus eggs in the nest during incubation offer some protection from the costs of parasitism. Surplus eggs could benefit females in two ways. First, additional eggs may protect against the direct costs of parasitism by facilitating recognition and removal of parasitic eggs with greater accuracy. Second, additional eggs may protect against the indirect costs of parasitism as parasites often damage or remove host eggs when entering the host nest; surplus eggs may be an essential insurance strategy against this damage. We test these possibilities in the Montezuma Oropendola (*Psarocolius Montezuma*), a species experiencing high levels of parasitism by Giant Cowbirds (*Scaphidura oryzivora*) throughout their range. Overall rejection rates of cowbird eggs were high (72%), and experimental addition of parasitic eggs to empty, one-, and two-egg nests demonstrated that recognition success was unaffected by the presence of additional host eggs for comparison. However, the value of surplus eggs when one egg was removed or damaged by a parasite was high; 31.6% of successful two-egg clutches lost a single egg during incubation and would have failed to produce a chick without a second egg. This was directly attributable to parasitism in at least 33% of all cases. Therefore, despite highly developed host defenses against direct costs of parasitism (recognition and removal of parasitic eggs), the associated indirect costs (egg damage and removal) could play an important role in selection for a clutch size that results in more chicks than can be raised. *Key words*: allocation, maternal investment, obligate brood reduction, parasitism. [*Behav Ecol* 17:126–131 (2006)]

The amount a parent invests in offspring production is a crucial factor in determining both parent and offspring fitness. However, while high levels of parental investment may be beneficial to their young, they are likely to be costly to the parent, and any increase in resource allocation in favor of reproduction may result in a trade-off with resources required for long-term survival (Charnov and Krebs, 1974; Williams, 1966). Selection is therefore expected to favor individuals who produce the number of offspring that will maximize production for any given amount of reproductive expenditure. Yet, in many animal species, females often produce more offspring than they are able to raise (Kozłowski and Stearns, 1989; Mock and Forbes, 1995). This may be beneficial when environmental factors are stochastic and local conditions can influence the number of offspring that can be raised in any given breeding attempt (see Forbes and Mock, 2000, for a review). For example, females may overproduce in order to capitalize on changing environmental conditions (the Resource-Tracking Hypothesis) or to have a replacement available should an egg or brood member fail to survive (the Replacement Offspring Hypothesis). Alternatively, females may overproduce if this added investment increases the likelihood of reproductive success, for example, the chances of a particular offspring surviving may be increased by the presence of other members in the brood or nest (the Sib Facilitation Hypothesis).

A further possible explanation as to why females of some species may produce surplus offspring is because the presence of additional eggs in the nest during the laying and incubation period may protect against costs associated with brood parasitism: avian brood parasites lay their eggs in the nests of another species in an attempt to parasitize the maternal allocation of the nest holder. Hosts that are unable to recognize or remove these parasitic eggs then incubate and rear the young as their own, nearly always to the detriment of their own young. This reduction in host fitness imposes a strong selection pressure on hosts to evolve adaptations to avoid the costs associated with being parasitized (Brooke and Davies, 1988; Davies and Brooke, 1988; Dawkins and Krebs, 1979; Mason and Rothstein, 1986; Moksnes et al., 1990; Payne, 1977; Rothstein, 1990). Here we test whether parasitism of maternal investment by brood parasites could select for the production of surplus offspring that the parent then fails to rear because additional eggs in the nest during the egg-laying period reduce the impact of brood parasitism on host fitness.

In species that produce only one or two young, extra egg production could potentially provide an important defense against brood parasitism for two reasons. First, additional eggs in the nest may facilitate recognition of odd parasitic eggs in comparison to their own. For most host species, their ability to recognize and reject foreign eggs is their primary defense against parasitism (Rothstein, 1990). Hosts may either compare foreign eggs to their own using an “odd one out” decision as a general rule of thumb, or, more commonly, hosts may learn to recognize their own eggs and reject anything that is not similar to this template (Lotem et al., 1995; Marchetti, 2001; Moksnes, 1992; Rothstein, 1975, 1990). In both cases,

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Received 16 September 2004; revised 22 February 2005; accepted 2 October 2005.

hosts laying especially small clutch sizes may be at a disadvantage; “odd one out” decision rules may be inadequate (as females would not have a large enough group of their own eggs with which they can compare foreign eggs laid in the same nest), and/or if hosts have to learn what their own eggs look like, small clutches may provide fewer opportunities for females to learn their own egg pattern. Additional eggs may therefore facilitate egg recognition and therefore allow females to avoid paying the direct costs of parasitism, that is, rearing an unrelated chick of a completely different species.

A second reason additional eggs could be beneficial is if they act as an insurance strategy against the indirect costs caused by parasitic events. Parasites often either remove or damage host eggs while attempting to lay their own egg in a host's nest. Even if host-egg recognition is highly developed and parasitic eggs can be recognized and rejected so that the direct cost of rearing an unrelated chick is avoided, additional eggs may play an important role in replacing eggs that are damaged and fail to hatch after parasitic events. These indirect costs of parasitism could remain an important cost of parasitism in systems where host defenses are well developed. Previous studies have demonstrated that the value of producing an extra insurance chick to act as replacement when first-hatched chicks fail to survive can be high (Cash and Evans, 1986); the benefit of a second egg in parasitized species may act much earlier in reproduction ensuring that at least one egg will hatch to produce a chick.

We test these two possibilities in the Montezuma Oropendola (*Psarocolius Montezuma*), a colonially nesting Neotropical blackbird that lays clutches of one or two eggs (Skutch, 1954) but, as this study shows, demonstrates obligate brood reduction and rears only one chick. They generally suffer high levels of parasitism by the Giant Cowbird (*Scaphidura oryzivora*) across their range (Friedmann, 1963; Skutch, 1954; Webster, 1994a), a brood parasite that specializes on oropendola and cacique species in the same Icterid family as themselves (Friedmann, 1963).

## METHODS

### General methodology and background

The study was conducted in several regions of Costa Rica where the Montezuma Oropendola is the primary host of the Giant Cowbird. Montezuma Oropendolas are colonial breeders; individual females build their nests in large clusters, generally in large isolated trees in the middle of more open areas. The breeding system is harem-defense polygyny (Webster, 1994b); males contribute no direct input to nest building, incubation, or parental care but do play a role in alerting the colony to the arrival of Giant cowbirds. There is a strong dominance hierarchy of males that take it in turns to be continuously present in the colony, and the proportion of fertilizations obtained is related to their rank within this hierarchy (Webster, 1994b). Giant cowbirds are regularly seen arriving at the colonies in small groups and attempting to enter the nests of females. Females cluster their nests into groups within the colony, and while nesting tends to be synchronous within a group, nesting between groups is asynchronous, with some females tending chicks while other females are still nest building. While cowbirds may occasionally be seen in close proximity to oropendolas within the colony, they are actively chased away from nests at the egg stage of reproduction by both male and female oropendolas (Webster 1994a; Cunningham EJA, personal observation).

In Costa Rica the breeding season runs from January to July, and between 5 and 120 females may nest together in a single colony with each female producing a long pensile nest in which they generally lay one to two eggs (Skutch, 1954). Eggs

are very similar within an individual (both within and between clutches) but vary greatly between individuals within an individual colony in their background color (ranges of white, blue, and brown), type of pattern (none, scrolls, spots), and intensity of patterns (density: light brown to dark brown) and their shape. First and second eggs of an individual, however, do differ in size, with second eggs being on average 10% smaller than first eggs (Cunningham EJA, Lewis S, and Nunez de la Mora, unpublished data). Cowbird eggs also occur in several morphs (white, white with dark brown markings, and blue with dark brown markings) but are all significantly smaller, rounder, and differ from host eggs in their eggshell texture. The incubation period required for these eggs is several days shorter than for the host egg, and cowbird chicks generally hatch several days before the host young emerges. Parasite and host young were never observed to develop in the nest together in this study. Host chicks that hatch in a parasitized nest die in the same way as any second-hatching oropendola chicks (see later).

The study was conducted in the Guanacaste, Sarapiquí, and Siquirres regions of Costa Rica. These areas are geographically distinct and are separated from each other by approximately 100 and 50 km, respectively. Several colonies at each site were monitored on a regular basis throughout the breeding season, and at the primary study site in Guanacaste, the nests were monitored on a daily basis. Experimental parasitism studies were used to test our first hypothesis: whether larger clutches facilitated recognition of parasitic events. Daily nest monitoring was used to test our second hypothesis that a second egg acts as a protection measure against the indirect costs of parasitism and measure to what extent parasitism was responsible for the partial loss of clutches during the egg stage of reproduction.

### Nest monitoring

Nests were accessed using a Manitou all-terrain vehicle with a hydraulic forklift arm with a reach of 17 m. In 2001 at the Guanacaste site, 90 nests in one colony were accessed at least every other day, and 40 nests in a further five colonies were accessed at intervals during the egg-laying period. In 2002 at the Guanacaste site, the contents of 81 nests in one colony were monitored on a daily basis during the egg-laying period and every second day during the chick-rearing period, and 42 nests in a further three colonies were monitored during the egg-laying period. Monitoring involved checking all nest contents from the nest-lining stage through reproduction and measuring, weighing, and photographing the presence of any new eggs observed in the nest. In 2002, a subsample of 23 nests at the Guanacaste site were also observed continually by a rota of observers from dawn to dusk (approximately 0515 to 1830 h) from at least 3 days before egg laying commenced until egg laying was complete. All oropendola and cowbird nest visits to this subsample of nests and their associated egg-rejection behavior were recorded during observations and confirmed later from constant video recording of the focal nests during the same period.

### Experimental parasitism

In 2002, egg-rejection experiments were conducted at 63 nests in three of the study colonies (one-egg clutches,  $n = 36$ ; two-egg clutches  $n = 27$ ). The 63 nests were divided between two experimental treatments and the remaining nests served as controls. In the first treatment, a model cowbird egg was added to the clutch (addition treatment), and in the second treatment a model cowbird egg was added to the clutch and one of the host eggs was removed (replacement treatment). Cowbirds have been observed to follow both strategies in the wild, though egg addition without removing an egg appears to be the most common strategy (94% of observed cases).

Control nests had their nest contents handled in the same way, but only the host's own eggs were returned to the nest.

Removed eggs were stored at ambient temperature or in an incubator if incubation had begun, turned regularly, and returned to the nest at the end of the 2-day trial. All unrejected experimental eggs were removed on day 2. Model resin eggs were made from molds of real cowbird eggs that had been collected from the same colony the previous year, and rejection rates did not differ from true rejection rates (see Results).

## RESULTS

### Oropendolas show obligate brood reduction

Female Montezuma Oropendolas never raised more than one chick. In 28 attempts, two-egg nests did hatch two chicks; however, in none of these nests did the second chick survive beyond 3 days in the nest. On the other hand, the success rate of first-hatched and single chicks was extremely high, with at least 33 out of 40 host chicks surviving the extended nest-rearing period of 32–40 days in the nest before fledging (82.5%). Two out of these seven failures arose from nests falling just before chicks were due to fledge, and no chick was found in the nest, so it unclear whether these chicks also survived or not; of the five chicks that died in the nest, two were from single-egg clutches and three were from two-egg clutches. Moreover, in a further 19 nests that were found to have chicks before egg data could be obtained at other colonies at other geographically distinct sites, none had two chicks except for one newly hatched brood, despite expecting 62.7% (12) of these nests to have been two-egg clutches. Second-hatched chicks failed to gain any weight and all died within their first 3 days. No signs of injury were observed on dead chicks found in the nest, and they were apparently removed by females as the long pensile nest would prevent removal from the nest by sibs. Montezuma Oropendolas therefore demonstrate obligate brood reduction (defined by convention as more than 90% of second chicks failing to survive) (Mock and Parker, 1997; Simmons, 1988). Any benefit of additional eggs must therefore only be operating at the egg stage of production.

### Parasitism and overproduction

If obligate brood reduction operates within the first few days of a 6-week chick-rearing stage, it is likely that the production and maintenance of an extra egg may occur due to the advantage it confers at the egg stage of reproduction. We first tested whether two-egg nests are significantly more likely to hatch a chick than one-egg nests. We then investigated whether any difference could be explained by (1) additional eggs facilitating recognition of parasitic events or (2) additional eggs acting as an insurance egg if the other egg is destroyed or removed by the parasite.

#### *The fate of one- and two-egg nests*

Of 171 nests monitored intensively from egg laying to hatching during the 2 years, 44 produced one-egg clutches and 78 produced two-egg clutches, 1 produced a three-egg clutch, and 13 produced two clutches; double brooders were not consistent in their clutch size (10 out of 13 females produced both a one-egg clutch and a two-egg clutch). The remaining nests either failed to reach the egg stage, or they were very early nests that already contained a chick at the start of observations, so the egg number was unknown. Thirty-nine of the one-egg attempts ( $n = 54$ ) failed before hatching, and 38 of the two-egg attempts ( $n = 91$ ) failed before hatching, and

hence two-egg attempts are significantly less likely to fail to produce a chick ( $\chi^2 = 11.04$ ,  $df = 1$ ,  $p = .001$ ).

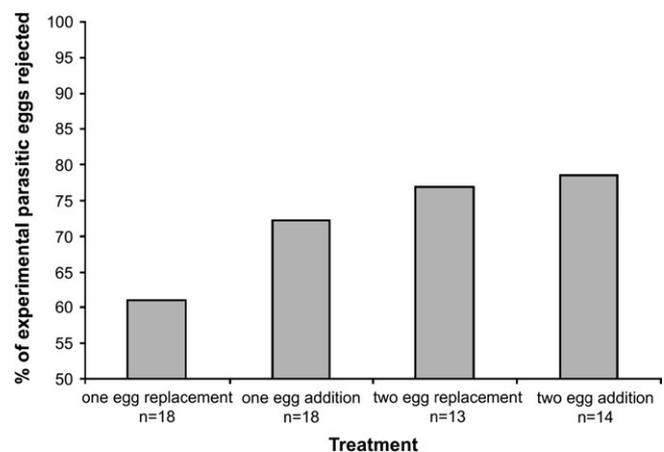
#### *Does overproduction facilitate cowbird egg recognition?*

Continual nest monitoring for natural parasitic events demonstrated that although cowbirds removed a host egg in only 6% of cases when parasitism was directly observed (1/15 attempts), 80% of parasitism attempts (12/15) occurred before the oropendola had laid a second egg. Hence in the majority of cases, hosts had only a single cowbird egg or a cowbird egg plus one of their own eggs on which to base a rejection decision.

We first compared egg-rejection rates over the four experimental treatments—(1) one-egg clutch replacement: the oropendola had only the single experimental cowbird egg in the nest on which to base a rejection decision, (2) one-egg clutch addition: the oropendola had only ever had one egg and had its own egg and one experimental cowbird egg in the nest on which to base a rejection decision, (3) two-egg clutch replacement: the oropendola has had two of its own eggs but again only had one of its own eggs and one experimental cowbird egg in the nest on which to base a rejection decision (4) two-egg nest addition: the oropendola had her own two eggs and an experimental cowbird egg in the nest on which to base a rejection decision. We would therefore expect it to become progressively easier for the oropendola to make the correct decision with each treatment. However, the overall rejection rate was high (72%) and unaffected by whether females had another egg in the nest with which to compare the model cowbird egg; there was no effect of clutch size (nominal logistic model,  $\chi^2 = 1.31$ ,  $df = 2$ ,  $p = .51$ ) or replacement and addition strategies on rejection rates ( $\chi^2 = 0.25$ ,  $df = 2$ ,  $p = .88$ , Figure 1). No egg rejection from control nests was observed.

In 26 of the nests where we had removed an oropendola egg and replaced it with an experimental cowbird egg, we were able to monitor the females reaction to her own egg being returned at the end of the experiment. Females were significantly more likely to accept their own egg than they were to accept a foreign cowbird egg (18 out of 26 cases,  $\chi^2 = 7.692$ ,  $n = 26$  nests,  $p = .006$ ). This is an acceptance rate of 69% as opposed to an acceptance rate of 28% when parasitic eggs were encountered.

Finally, we compared how well experimental parasitism matched patterns of natural parasitism. In the subset of 23 continually observed nests, the combination of daily nest monitoring and continual observation of all nest entries by cowbirds and hosts and of egg removal by hosts on returning to



**Figure 1**

The percent frequency of rejection of experimental parasitic eggs. The overall rejection rate was high (72%), but there was no difference in rejection rate between treatments or clutch sizes.

**Table 1**  
**The fate of one- and two-egg nests**

	% Nests with egg loss	% Nests with one-egg failure	% Nests with two-egg failure	% Nests that failed due to loss
One-egg nests	70.2% (33/47)	70.2% (33/47)	—	70.2% (33/47)
Two-egg nests	54.0% (47/87)	17.2% (15/87)	36.8% (32/87)	36.8% (32/87)

After excluding nests that fell during the incubation stage (seven nests with one egg and four nests with two eggs), the proportion of nests that experienced some form of egg loss did not differ significantly between one- and two-egg nests. However, as the loss of an egg led to complete nest loss in one-egg nests but not in two-egg nests, two-egg nests were significantly more likely to be successful. All partial clutch loss arose from direct replacement by parasites, damage by parasites, or missing eggs. No hatching failure was recorded in any nest that suffered partial loss.

nests revealed that 12 (52%) were naturally parasitized at least once, and females accepted cowbird eggs in 3 out of 12 nests (25%) (5/15 parasitic attempts). All egg-rejection behavior was by egg removal from the nest by the female. Experimental investigation by artificial parasitism demonstrated that artificial eggs were accepted in 18 out of 63 trials (28.6%). Only one misrejection where the female rejected her own egg and kept and incubated the experimental egg was recorded. Hence, experimental and natural rejection rates did not differ significantly ( $\chi^2 = 0.132$ ,  $df = 1$ ,  $p = .72$ ). Overall, 13% (3/23) of all the continually observed nests remained parasitized, closely matching the natural parasitism rates found from our daily nest checks of 13.1% (19/145 attempts).

In summary, parasitism rates are high, but egg-rejection behavior is well developed, and the rejection rate of foreign eggs by hosts is not significantly affected by the number of eggs present in the nest.

#### *Does parasitism induce the need for an insurance egg?*

The nest-monitoring data demonstrated that two-egg nests do significantly better than single-egg nests. How much of this difference can be attributed to cases where a second egg results in a chick after the first is lost due to a parasitic event? Cowbirds targeted both one- and two-egg nests to the same extent; during our period of continual observation on a subsample of nests, we directly observed 15 parasitic attempts in our focal nests and a further 3 parasitism attempts in adjacent nests. Of these 18 direct observations of successful parasitism by cowbirds, 5 were one-egg clutches and 13 were two-egg clutches. One ( $n = 54$ ) and two ( $n = 91$ ) egg clutches did not differ significantly in their likelihood of being parasitized ( $\chi^2 = 0.78$ ,  $df = 1$ ,  $p = .37$ ).

Overall, the likelihood that any given nest would successfully avoid any egg loss did not differ between one-egg and two-egg clutches ( $\chi^2 = 3.32$ ,  $df = 1$ ,  $p = .07$ ). However, while the loss of a single egg always resulted in nest failure of one-egg nests, this was not true of two-egg nests (Table 1), and therefore two-egg nests were significantly more likely to hatch a chick ( $\chi^2 = 33.65$ ,  $df = 1$ ,  $p < .001$ ).

Twelve out of 38 two-egg clutches (31.6%) that successfully made it through incubation lost a single egg during incubation and would have failed completely if a second egg was not present. In four cases, this partial clutch loss were attributable directly to parasitism in that spiking of an egg was observed (the parasite puts a small hole in the egg but leaves it in the nest, preventing it from hatching) or an egg was directly replaced by a parasitic egg (10.5% of successful nests). In the remaining eight cases of partial clutch loss, an egg went missing from the nest during the first 5 days of laying. These were potentially attributable to parasitism that had not been detected because damaged or parasitic eggs were likely to be rejected before they were encountered during monitoring. In none of these cases

was a second egg beneficial simply because one egg failed to hatch. Hence, at least 10.5%, but potentially as much as 31.6%, of two-egg nests were successful because the second egg ensured that at least one offspring was produced after damage to a female's clutch due to parasitism (Table 2).

## DISCUSSION

Montezuma oropendolas appear to benefit from producing two-egg clutches, but successful second eggs never result in fledged offspring due to obligate brood reduction (defined by convention as cases in which more than 90% of broods lose a nestling) (Mock and Parker, 1997; Simmons, 1988). In our study we had 100% death of second chicks during their first few days after hatching. If overproduction is playing an insurance role to increase the likelihood of success, it would appear that any beneficial effects of overproduction occurs at the egg stage as opposed to the chick-rearing stage.

We first examined whether extra eggs may confer an advantage to females by facilitating recognition of parasitic events. The ability of female oropendolas to recognize and reject a foreign egg did not appear to be influenced by the number of oropendola eggs present in the nest with which females could compare a parasitic egg. Furthermore, successful rejection rates were high (72%), suggesting that the majority of females were able to recognize that the egg was different from their own. Further evidence for this comes from the reaction of females to their own eggs when they are returned to the nest after experimental parasitism. Females were significantly more likely to accept their own egg than they were to accept the parasitic egg that had originally replaced it, despite the fact that the female's own egg had reappeared in her

**Table 2**  
**The reproductive value of additional eggs**

Reproductive value of additional egg	31.6%
Reproductive value of additional egg directly attributable to parasitism	10.5–31.6%
Reproductive value of additional egg due to egg loss (potentially due to parasitism)	0–20.1%
Reproductive value of additional egg due to hatching failure	0%

The reproductive value of additional eggs can be calculated by subtracting the proportion of broods in which a second chick survives in a nest when core eggs or chicks fail (12/38) from the proportion of broods in which a second chick survives when no core egg or chick has failed (0/38) (see Forbes and Mock, 2000). The additional reproductive value was attributable to egg damage arising from parasitism in 4/12 cases, from eggs that went missing in the first few days of laying in 8/12 cases, and from hatching failure in 0/12 cases.

previously empty nest. These findings suggest that selection may act on a number of cognitive processes to ensure that females are able to recognize costly parasitic events and that oropendolas are capable of true recognition as has been suggested for a number of other species that regularly face brood parasitism (e.g., Lahti DC and Lahti AR, 2002; Moksnes, 1992; Rothstein, 1990; Victoria, 1972).

We then examined how often the presence of a second egg in the nest resulted in the production of a single chick due to egg losses attributable to parasitism. The likelihood of experiencing egg loss did not differ between one- and two-egg nests. Instead, two-egg nests were significantly more likely to produce a chick simply due to the numerical advantage of having double the opportunity to escape the detrimental effects of egg loss. Nearly half of these could be attributed directly to parasitism, and given that all other cases were due to the loss of a single egg in the first few days of laying, it is likely that parasitism was the cause of egg loss in these cases as well, either because a parasite had removed an egg when placing its own egg in the nest, which was subsequently rejected by the host (rejection generally occurs with 10 min of the female returning to the nest (Cunningham EJA, personal observation), or because the parasite had damaged an egg, which was rejected by the female on her return. The majority of egg predators that take the eggs of this species tend to be large predatory species that would normally take both eggs at a time and leave signs of having entered the nest as they are unable to enter through the small nest entrance. Hatching failure explained the loss of some nests that failed to produce any chicks; eggs were often found covered in egg yolk after ejections of cowbird eggs, which would interfere with their hatching success in some cases. Egg damage and desertion of disturbed nests may also be a cause. However, in none of the cases in which a second egg ensured the production of at least one chick was the benefit of the second egg attributable to hatching failure. Overall, the estimates of the reproductive value of an additional egg were high and in line with previous estimates of the value of producing an additional chick as an insurance strategy against failure at later stages of the chick-rearing phase (Cash and Evans, 1986). However, in all cases, the benefit of the extra egg was in ensuring at least one egg hatched to produce a chick and never in ensuring that at least one of two chicks survived to fledge.

Given there is a strong benefit of producing a second egg in this species (increasing the chance of producing successful offspring by 31.6%), why do some females only lay one egg? The costs of producing this extra egg are unknown (egg size is approximately 4–6% of female body weight). However, in other species, both egg production and the incubation of additional eggs have been shown to be costly to the parent (Heaney and Monaghan, 1997; Monaghan et al., 1998) and estimates of energy expenditure derived from comparing metabolic rates of laying females versus nonlaying females vary from a 22% to 64% increase in basal metabolic rate (Vezina and Williams, 2002). Hence, not all females might be able to afford the costs associated with this insurance strategy. If maternal quality covaries with clutch size because higher quality individuals can afford to produce a beneficial additional egg, female quality could be an additional factor contributing to the success of two-egg nests (see, e.g., Clifford and Anderson, 2001; Forbes et al., 2002), though this obviously would not explain the functional benefit of producing two eggs in the first place given that second chicks are never raised.

Why not rear the extra chick? Oropendolas have an extended chick-rearing period of 6 weeks, and females continue to feed their offspring during the postfledging period (Cunningham EJA, personal observation). Providing food for two chicks during this extended period may simply be too costly

for females. While adults are omnivorous, and able to capitalize on locally abundant fruit, chicks are not and hence invertebrate availability may be a limiting factor on the number of chicks that can be raised. At one of our sites, food availability has been artificially increased as adults are able to access provided sources of fruit, freeing some of the constraint on time they have to spend foraging for themselves. However, no attempt to rear a second chick was observed in this colony, providing indirect support that additional chicks do not appear to provide any benefit after the egg stage of reproduction.

The effect of parasitism on the evolution of female allocation decisions has previously suggested that brood parasitism should select for a reduction in clutch size. Initial work on intraspecific parasites suggested that females may benefit by investing less in their own clutch because increases in clutch size due to parasitism push the clutch above the limit that would ensure that the usual number of the young in the nest receive enough food to survive (Power et al., 1989). A smaller clutch size may also reduce the amount of competition in the nest (Lyon, 1998) (but see Ruxton and Broom, 2002). In interspecific host-parasite systems where host young are reared alongside parasitic young, similar benefits of decreasing the number of eggs produced could also be important if parasitism pushes clutch size above the threshold level for rearing the optimum number of chicks (Hauber, 2003). However, this study demonstrates that a larger clutch size could also be beneficial when the indirect costs of parasitism are high by decreasing the likelihood of total nest failure when parasitism does occur and that obligate brood reduction can be a mechanism whereby competition between too many nestlings is prevented.

Egg recognition has been an important trait in host defense against parasitism and is well developed in the Montezuma Oropendola. However, even when incidences of parasitism can be recognized and removed, the loss or damage to eggs can be high (Massoni and Rebores, 2002). Additional eggs that confer an advantage at the egg stage of reproduction, but that ultimately result only in dead chicks, may be beneficial in this context.

Alejandra Nuñez de la Mora, Miguel Rubio, Damon Bridge, Ailsa Reid, and Francis Daunt provided considerable help and support throughout the project. The Viquez family, the Murillo Family, Alex Martínez, Finca Yafa, and Finca Del Oro provided much appreciated help and permission to work on their land. Julio Sanchez at the Museo Nacional, the Organización para Estudios Tropicales, and ESCO in Costa Rica provided help and logistical support. Scott Forbes, Nick Davies, and Steve Rothstein provided helpful comments. The work was funded by The Royal Society, The British Ecological Society, and the Association for the Study of Animal Behaviour.

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