

# CLUTCH SIZE AND REPRODUCTIVE SUCCESS OF HOUSE WRENS REARING NATURAL AND MANIPULATED BROODS

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**ABSTRACT.**—We assessed reproductive success of House Wrens (*Troglodytes aedon*) with natural or experimentally manipulated broods to determine if females produced as many offspring as they could rear successfully in each attempt. The number of nestlings fledged and nestling mass at 12 days old measured success. In nonmanipulated nests, the number of nestlings fledged increased with clutch size. The larger clutches fledged more young. Nestling mass and fledging success did not differ among natural brood sizes. However, the most common clutch size was smaller than the most productive clutch size.

Experimentally enlarged broods fledged more offspring than control or reduced broods, but the nestlings weighed significantly less. Reduced broods fledged fewer offspring than control or enlarged broods, but the nestlings weighed significantly more. Thus, parents with a smaller clutch size were able to fledge additional offspring, but at the cost of reduced fledgling mass. Further, nestlings from enlarged broods were significantly lighter than nestlings from natural broods of the same size. Nestlings from reduced broods were significantly heavier than those from natural broods of the same size. Second broods of double-brooded females were not manipulated. However, nestlings from second broods of females that reared enlarged first broods were significantly lighter than nestlings from second broods of females that reared control first broods. Nestlings from second broods of females that reared reduced first broods were significantly heavier than nestlings from second broods of females that reared control first broods. Received 5 January 1989, accepted 2 October 1990.

FACTORS that may influence clutch size have been the focus of many studies. Lack (1947, 1954, 1966) hypothesized that passerines should produce clutch sizes equal to the maximum number of young that they can, on average, feed successfully. He suggested that if clutch size is heritable, then the most productive clutch size in a population will equal the most common clutch size. Clutches larger than the most common size will produce fewer surviving offspring either by fledging fewer young than average clutches, because of a higher proportion of nestling mortality, or by fledging lighter nestlings, assuming a correlation between fledging mass and subsequent survival (e.g. Perrins 1965, Lack 1966, von Haartman 1971, Loman 1977, Schifferli 1978, Garnett 1981).

Some studies that used either natural (non-manipulated) populations or populations in which natural brood sizes had been altered have supported Lack's hypothesis (e.g. Lack 1948, Perrins 1964, Crossner 1977, Hogstedt

1980, Murphy 1983; and for reviews, see Klomp 1970, Lessells 1986, and Martin 1987). Others have shown that in some species or populations the number fledged increases with clutch size even for clutches larger than average (Lack 1949, 1950; Tutor 1962; Kluver 1963; Seel 1970; Bryant 1979; Bijlsma 1982; Hogstedt 1980; Ross and McLaren 1981; Smith 1981); that nestling mass may be independent of brood size (Lack and Silva 1949, Seel 1970, Askenmo 1973, Murphy 1978, Zach 1982) or even increase with brood size (Snow 1958); or that enlarged broods fledge more young, and the nestlings do not differ significantly in mass from nestlings in control broods (Bryant 1975, DeSteven 1980, Slagsvold 1982, Finke et al. 1987).

Subsequent modification of Lack's basic ideas have followed several different paths. In one, other components of the life history are taken into account, particularly parental survival and lifetime reproductive success. Such life-history models predict that individual optimal clutch size may be smaller than the most productive, as defined on a population level, if reducing parental investment in the current breeding attempt increases the probability of parental survival and lifetime reproductive success (Cody

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1966, Williams 1966, Mountford 1973, Charnov and Krebs 1974, Trivers 1978). In such cases, parents could rear additional young, and nestlings from experimentally enlarged broods would have survival rates and masses similar to nestlings in nonmanipulated broods, although future parental survival or reproductive output would decrease.

A second approach takes into account more proximal factors and argues that clutch size during any one attempt may be related to territory quality (Kluyver 1963; Askenmo 1979, 1982; Hogstedt 1980) or parental ability to forage for the young (Lack 1966, Perrins and Moss 1975, Bryant 1979, Askenmo 1982, Slagsvold 1982, Westerterp et al. 1982, Slagsvold and Lifjeld 1988). An optimal clutch size may be the maximum number of offspring that an individual can rear on its territory rather than the maximum number an average individual can rear on an average territory (Hogstedt 1980). In such cases, nestling survival and nestling mass are likely to be independent of natural clutch or brood size (Perrins and Moss 1975). However, if individuals produce as many young as they can rear successfully in each breeding attempt, experimental alteration of brood size should be reflected in nestling survival, nestling mass, or both.

We attempted to determine if females in a population of House Wrens (*Troglodytes aedon*) produced as many young as they could rear successfully in each attempt. We observed natural (nonmanipulated) nests, to establish if the most productive clutch size was the most common clutch size in the population and if nestling mass and nestling survival (i.e. fledgling production) were independent of clutch or brood size. In addition, broods were increased and decreased experimentally to determine if nestling mass and nestling survival were similar for enlarged, natural, and reduced broods. We attempted to compare nestling survival and nestling mass in altered broods with those in natural broods of the same size. Finally, we wanted to determine if the effort a female expended in her first breeding attempt affected the likelihood of her double-brooding or the success of her second brood.

#### METHODS

The study was conducted from April through August in 1983 and 1984 at two sites approximately 11

km south of Bowling Green, Wood County, Ohio. The study sites were located at Steidtmann Woods, an 80-ha woodlot maintained in part as a nature reserve by Bowling Green State University, and Arlington Woods, a privately owned 35-ha woodlot. The two sites were separated by 1.5 km of cultivated fields. Both sites had adjacent old fields and well-developed undergrowth along the forest edges, which is preferred House Wren habitat in this region (Baldwin and Bowen 1928, Kendeigh 1941). In March 1983, 145 nest boxes were placed in forest-edge habitat around and adjacent to each woodlot. The boxes were placed approximately 50 m apart, the diameter of an average House Wren territory (Kendeigh 1941).

Nest boxes were cleaned before the start of the second breeding season, but old nests were not removed between breeding attempts within a season. If a box was reused within a season, the male wren removed the old nest lining.

Nesting activity was recorded every 4–6 days beginning in late April. Once eggs were found in a nest, it was visited daily until the last egg was laid. House Wrens incubate their eggs ca. 13 days from the day the last egg is laid (Kendeigh 1941), and hatching dates were estimated from laying dates. Nest visits were resumed a day before the estimated hatching date to record the actual hatching date. Data collected for each nest included clutch size, brood size, hatching failure, number of nestlings fledged, and nestling mass at 12 days old. The study ended with the fledging of the last chicks in late August.

Approximately 44% of the females were double-brooded, and the seasonal distribution of clutch completion dates was strongly bimodal (Fig. 1). Second clutches of double-brooded females were significantly smaller than first clutches (paired *t*-test,  $t = 5.53$ ,  $df = 34$ ,  $P < 0.0001$ ). We divided each season into two breeding periods. All nests in which the last egg was laid by 30 June were classed in the first breeding period and were considered first breeding attempts. During this period, 9 of 59 nests started in 1983 and 15 of 40 nests started in 1984 failed before the eggs hatched (usually before the clutches were completed) and before the females were banded. Therefore a few of the successful broods may have been from replacement clutches. Clutches completed on or after 1 July were classed in the second breeding period. The nests found during the second breeding period were not necessarily second broods. Individuals that arrived late in the area or that were unable to find mates during the first period may have nested for the first time during the second period. A female that reared a brood in either the first or the second breeding period, but not in both, was considered a single brooder. A female that successfully reared a brood during each period was considered a double brooder. Although a female may have been able to rear one brood on the study site and another elsewhere (and thus be incorrectly classed as a single brooder), such

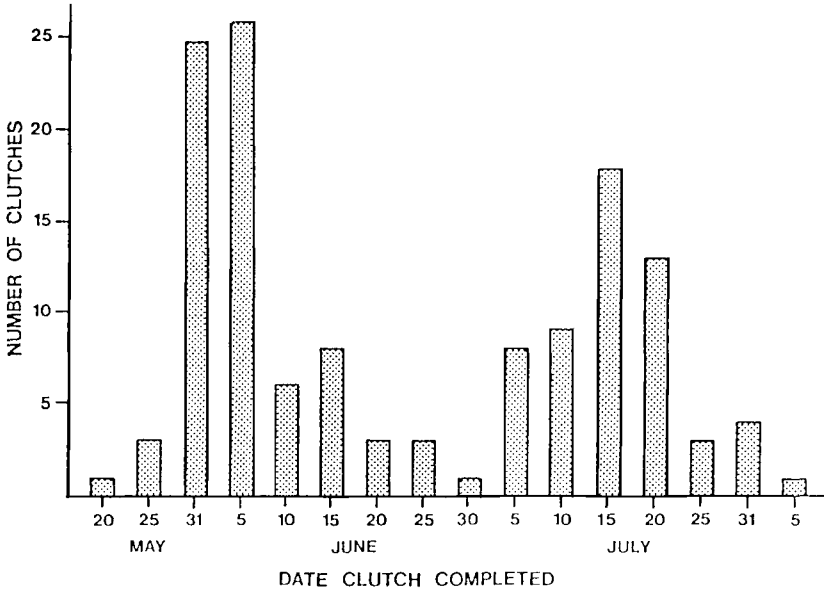


Fig. 1. Distribution of dates on which clutches were completed, 1983-1984.

a situation appears rare (Kendeigh and Baldwin 1937, Kendeigh 1941). Thus, the number of double brooders in this study is only a minimum estimate, but it is probably reasonably accurate.

Enlarged and reduced broods were experimentally established during the first breeding period of both years. We moved two nestlings from clutches of seven to nests with clutches of six (these were the most frequent clutch sizes produced), potentially leaving enlarged broods of eight and reduced broods of five. Foster and donor nests were selected at random from those nests that hatched on the same day so that foster chicks were similar in age to their new siblings. Nestlings were moved within two days of hatching and were never away from a nest for >20 min. No foster chicks were rejected from their new nests, and none died because of handling. Nonmanipulated nests served as controls.

Because some of the nestlings were moved before all the eggs in the donor or foster nest had hatched, some of the experimental brood sizes deviated from those expected because of hatching failure. The proportion of nests affected by hatching failure was not significantly different among enlarged, reduced, and control nests ( $\chi^2 = 1.11$ ,  $df = 2$ ,  $P > 0.05$ ). All enlarged broods were larger than the clutches from which they hatched. Therefore, we did not consider hatching failure a significant problem in the experimental design. Distribution of nonmanipulated and experimental nests in relation to brood size is presented in Table 1.

Nearly all adult females with nests were banded with USFWS aluminum leg bands and color-banded

individually. Females were not caught and banded until several days into the incubation period to prevent desertion (Burt and Tuttle 1983), and no nest failure was attributable to handling the adults.

By age 3 days, nestlings within a nest were marked individually by clipping one claw on each chick. At 9 days, nestlings were banded with USFWS aluminum bands. At 12 days, close to the time of peak mass for wren nestlings (Zach 1982), we weighed nestlings with a Pesola scale to the nearest 0.1 gram. The majority of chicks were measured between 0800 and 1200, and all chicks were measured before 1500.

House Wrens usually fledge between 13 and 15 days after hatching (Kendeigh 1941, Zach 1982). We did not handle chicks after age 12 days to prevent premature fledging. We used the number of nestlings in a nest at day 12 to estimate number of fledglings. All nests were then checked several days later, and

TABLE 1. Distribution of nests among experimental groups in relation to final brood size for first broods (1983, 1984 combined).

Brood size	Reduced broods	Control broods	Enlarged broods
3	3	2	
4	5	3	
5	6	9	
6		19	
7		8	6
8			8

TABLE 2. Reproductive success of nonmanipulated House Wren nests that fledged young. Percentages of eggs that hatched and of hatchlings that fledged are in parentheses.

Breeding period <sup>a</sup>	Clutch size	<i>n</i>	No. of eggs	Hatched ( <i>n</i> [%])	Fledged ( <i>n</i> [%])	No. fledged per nest ( $\bar{x} \pm SE$ )
First	5	4	20	19 (95)	18 (95)	4.5 $\pm$ 0.50
	6	21	126	117 (93)	115 (98)	5.5 $\pm$ 0.21
	7	16	112	102 (91)	98 (96)	6.1 $\pm$ 0.30
Second	4	3	12	12 (100)	12 (100)	4.0 $\pm$ 0.00
	5	18	90	85 (94)	85 (100)	4.7 $\pm$ 0.13
	6	25	150	141 (94)	133 (94)	5.3 $\pm$ 0.20
	7	6	42	38 (90)	35 (92)	5.8 $\pm$ 0.31
	9	1	9	7 (78)	7 (100)	7.0 $\pm$ 0.00

<sup>a</sup>Clutches completed by 30 June are in the first breeding period.

any dead nestlings were subtracted from the estimate. As nestlings could have been preyed on without our detection between nest day 12 and fledging, the estimated number of fledglings is a maximum value.

Of the 144 nests in which clutches were completed, 23 failed because of predation or desertion. There was no significant difference among clutch sizes in the proportion of nests that failed. We included only nests that fledged at least one chick in analyses of fledging success because we were interested primarily in the ability of the parents to feed their young.

Variation in nestling mass at day 12 could be partitioned among brood sizes, among broods within brood sizes, and among nestlings within broods. To assess properly the effect of brood size on nestling mass (DeSteven 1980), we used a nested analysis of variance (Zar 1984) to test for differences in mass among brood sizes and among experimental groups.

Statistical analyses were performed using Statistical Analysis System software (SAS Institute Inc., 1982). When an analysis of variance was significant, the Student-Newman-Keuls multiple-range test was used to identify significantly different groups. In calculating Chi-squares, categories with expected values of <5 were combined until the expected value was  $\geq 5$ .

## RESULTS

Patterns of variation in the reproductive traits we measured were similar in 1983 and 1984. Therefore, we combined data for the 2 yr to increase sample sizes. Differences between years are reported if they occurred.

### NATURAL NESTS

*Clutch size and fledging success.*—During the first breeding period, hatching and fledging success were similar among clutch sizes (Table 2). Nests with clutches of 7 eggs fledged, on

average, the greatest number of offspring, significantly more than clutches of 5 (one-way ANOVA,  $F = 4.27$ ;  $df = 2, 38$ ;  $P < 0.05$ ). This most productive clutch size was larger than the most common clutch size of 6 in 1983. In 1984, clutches of 7 were most common. There was also a significant difference in number of fledglings among clutch sizes during the second breeding period ( $F = 5.27$ ;  $df = 4, 48$ ;  $P < 0.001$ ). The single clutch of 9 produced the most offspring, whereas clutches of 6 were most common.

*Brood size and fledging mass.*—During the second breeding period, there were significant differences in nestling mass at day 12 among natural broods within brood sizes (nested ANOVA,  $F = 8.15$ ;  $df = 34, 154$ ;  $P < 0.0001$ ). For both breeding periods, additional variation in nestling mass due to brood size was not significant (nested ANOVA, first period,  $F = 2.42$ ;  $df = 3, 24$ ;  $P > 0.05$ ; second period,  $F = 1.90$ ;  $df = 4, 34$ ;  $P > 0.05$ ). The chicks from large and small broods fledged at statistically indistinguishable mass.

### EXPERIMENTAL NESTS

*Experimental group and fledging success.*—Similar analyses were performed for the three experimental groups (control, reduced, and enlarged broods). Enlarged broods fledged significantly more offspring than control or reduced broods, and control broods fledged significantly more offspring than reduced broods (one-way ANOVA,  $F = 38.13$ ;  $df = 2, 64$ ;  $P < 0.0001$ ) (Table 3).

*Experimental group and fledging mass.*—There were significant differences in nestling mass at

TABLE 3. Mean number of fledglings and mean nestling weight on day 12 for experimental groups of House Wren nests during the first breeding period. All means are  $\pm$  SE.

	Reduced broods	Control broods	Enlarged broods
No. fledged	4.14 $\pm$ 0.21 (14) <sup>a</sup>	5.61 $\pm$ 0.18 (41)	7.58 $\pm$ 0.15 (12)
Weight day 12	10.41 $\pm$ 0.08 (59) <sup>b</sup>	10.21 $\pm$ 0.05 (161)	9.80 $\pm$ 0.07 (75)

<sup>a</sup> Number of nests.

<sup>b</sup> Number of nestlings.

day 12 among broods within groups (nested ANOVA,  $F = 3.02$ ;  $df = 47, 245$ ;  $P < 0.0001$ ) (Table 3). In addition, there were significant differences in mass at fledging among experimental groups (nested ANOVA,  $F = 6.61$ ;  $df = 2, 47$ ;  $P < 0.01$ ). Nestlings from enlarged broods were lighter than nestlings from control and reduced broods, and nestlings from reduced broods were heavier than nestlings from control and enlarged broods.

Because brood size varied within an experimental group, we also compared number of fledglings and nestling mass of manipulated and control broods of the same size. No natural broods of 8 were available for comparison, so we tested brood sizes of 5 and 7. Broods reduced to 5 nestlings did not fledge a significantly different number of young than natural broods of 5 nestlings (Student's  $t$ -test,  $t = 0.68$ ,  $df = 7$ ,  $P > 0.05$ ), and nestlings from control and reduced broods of 5 nestlings did not fledge at significantly different mass when data for the 2 yr were combined ( $t = 0.31$ ,  $df = 38$ ,  $P > 0.05$ ). In 1983 nestlings from the reduced broods were significantly heavier than those from the control broods ( $t = 2.92$ ,  $df = 33$ ,  $P < 0.01$ ). Broods enlarged to 7 nestlings did not fledge a significantly different number of young than control broods of 7 nestlings ( $t = 0.42$ ,  $df = 12$ ,  $P > 0.05$ ), but nestlings from enlarged broods were significantly lighter ( $t = 3.00$ ,  $df = 52$ ,  $P < 0.01$ ).

#### DOUBLE BROODING

Of the females that nested in the first breeding period, 43% successfully produced a second brood. The distributions of clutch sizes produced by single- and double-brooded females were not significantly different during the first breeding period ( $\chi^2 = 1.18$ ,  $df = 2$ ,  $P > 0.05$ ) or the second breeding period ( $\chi^2 = 0.04$ ,  $df = 1$ ,  $P > 0.05$ ). Similarly, there were no significant differences among experimental groups in the proportion of females that produced a second brood ( $\chi^2 = 0.34$ ,  $df = 1$ ,  $P > 0.05$ ). Therefore, there appeared to be no relationship between the size of the first clutch or brood and the likelihood of double brooding. There was also no correlation between the size of a female's first clutch and that of her second clutch ( $r = 0.05$ ,  $n = 36$ ,  $P > 0.05$ ).

There were no significant differences in mean interbrood interval ( $F = 0.56$ ;  $df = 2, 29$ ;  $P > 0.05$ ), mean clutch size ( $F = 0.66$ ;  $df = 2, 29$ ;  $P > 0.05$ ), or number of nestlings fledged ( $F = 0.11$ ;  $df = 2, 29$ ;  $P > 0.05$ ) during the second breeding period among second broods of females with control first broods, second broods of females with enlarged first broods, and second broods of females with reduced first broods (Table 4). There was a significant difference in nestling mass among broods within categories (nested ANOVA,  $F = 7.53$ ;  $df = 23, 91$ ;  $P <$

TABLE 4. Mean interclutch interval, mean clutch size, mean number of fledglings, and mean weight on day 12 for nests of double-brooded females in the second breeding period. Nests are separated into groups according to the experimental treatment of the females' first brood. All means are  $\pm$  SE.

	Reduced 1st brood	Control 1st brood	Enlarged 1st brood
Interclutch interval	40.67 $\pm$ 2.63 (6)	44.22 $\pm$ 1.81 (18)	43.50 $\pm$ 2.20 (8)
Clutch size	5.83 $\pm$ 0.57 (6) <sup>a</sup>	5.63 $\pm$ 0.58 (18)	5.38 $\pm$ 0.55 (8)
No. fledged	4.50 $\pm$ 0.34 (6) <sup>a</sup>	4.78 $\pm$ 0.34 (18)	4.75 $\pm$ 0.37 (8)
Weight day 12	10.91 $\pm$ 0.10 (26) <sup>b</sup>	10.54 $\pm$ 0.08 (58)	9.86 $\pm$ 0.25 (33)

<sup>a</sup> Number of nests.

<sup>b</sup> Number of nestlings.

0.0001). In addition, there was a significant difference in nestling mass among the categories of nests (nested ANOVA,  $F = 4.69$ ;  $df = 2, 23$ ;  $P < 0.05$ ). Nestlings of females with reduced first broods were significantly heavier, and nestlings of females with enlarged first broods were significantly lighter, than nestlings of double-brooded females with control first broods.

## DISCUSSION

### NATURAL NESTS

In natural, nonmanipulated House Wren nests fledgling production was related directly to clutch size. There was little variation in hatching or fledging success that was related to clutch size, and larger clutches tended to produce more offspring. Furthermore, increasing number of fledglings did not appear to be achieved at the expense of offspring "quality" as indicated by mass at day 12. Therefore, larger clutches probably contributed more offspring to future breeding populations than smaller clutches.

These observations are inconsistent with Lack's original prediction that the most common and most productive clutch size should be the same. In the first breeding period of 1983, clutches of seven fledged significantly more young than clutches of five or six, although clutches of six were more common. Similarly, the most productive clutch size was larger than the most common clutch size in the second breeding period of both years.

### MANIPULATED BROODS

In several bird species a positive correlation exists between mass at fledging and survival after fledging (e.g. Perrins 1965, 1980; Lack 1966; van Haartman 1971; Loham 1977; Murphy 1978; Garnett 1981). In our study only 2 chicks of 356 banded in 1983 returned to the study site in 1984, too small a sample to test this correlation. But if nestling mass at fledging predicts post-fledging survival in House Wrens, then our brood manipulations suggest that parents may not have been able to rear successfully more offspring than they attempted. Broods that were enlarged fledged more offspring than the control and reduced broods did, but the nestlings were significantly lighter at fledging. More importantly, nestlings in broods enlarged to seven

were significantly lighter than nestlings in control broods of seven. We believe that parents of enlarged broods were unable to supply their nestlings with as much food as parents of control nests. Enlarging broods in the first breeding period may also have affected negatively the success of those parents' second broods. Second-brood nestlings of females with enlarged first broods were significantly lighter than second-brood nestlings of females with control or reduced first broods. We suggest that parents attending enlarged first broods were stressed by the additional effort and that the effects persisted.

The brood reductions produced nestlings that were significantly heavier. In particular, nestlings from broods reduced to five were significantly heavier than nestlings in natural broods of five (1983). Removal of nestlings from first broods apparently reduced reproductive stress and enabled females to produce nestlings in their second broods that were heavier than second-brood nestlings of females with control and enlarged first broods.

Our data were consistent with the hypothesis that clutch size is related to territory quality or parental ability. However, we did not measure these attributes directly, and the return rate of females between years (10%) was not high enough for critical tests. For several species there is evidence that clutch sizes are larger in years or habitats with greater food abundance (Martin 1987). In the majority of studies of passerines in which females were provisioned with food before or during egg laying, no increase in clutch size was observed (Davies and Lundberg 1985, Murphy and Haukioja 1986, Martin 1987). However, it is possible that females in our study used other cues to adjust their clutch size to the number of young they could expect to feed at a later date. We also lack data on parental condition or foraging ability. However, the significant variation in nestling mass among broods within brood sizes implies a great deal of variation in territory quality, parental ability, or both.

In a similar study of House Wrens in Illinois, Finke et al. (1987) observed that females were able to rear more offspring from experimentally enlarged broods. However, they noted that chicks from enlarged broods were not significantly lighter at fledging, and that enlarging a female's brood had no negative effect on her subsequent reproductive attempts. They concluded that House Wrens do not seem to max-

imize reproductive output in each attempt. Several factors could have contributed to the differences between our studies. There are habitat differences between the Illinois and Ohio study sites. Our wrens preferred nest boxes on woodlot edges and seldom used boxes placed in the interior, whereas the majority of Finke et al.'s boxes and birds were interior (C. F. Thompson pers. comm.). If territory quality is important, it could be that the habitat at our study site was less suitable or had a poorer food supply than the Illinois site. Similarly, annual fluctuations in environmental conditions and food availability may have made it possible for extra chicks to be reared in some years but not in others (Gillespie 1977, Murphy 1983, Boyce and Perrins 1987). The presence of differences between studies points to the need for long-term, multi-site studies to characterize accurately the biology of this, or any, wide-ranging species.

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 ERRATUM

In the article, "Older males have bigger knobs: correlates of ornamentation in two species of curassow," by Richard Buchholz (1991, *Auk* 108: 153-160), the second paragraph of Results (p. 156) should begin "I detected no blood parasites . . ." We regret any misunderstanding that may have resulted.