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ORIGINAL ARTICLE

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Is reduced clutch size a cost of parental care in Eastern Phoebes (*Sayornis phoebe*)?

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Abstract What is the cost of parental care in birds? Previous studies using observational and experimental techniques on nest building and clutch sizes in a small migrant flycatcher, the Eastern Phoebe (*Sayornis phoebe*), led to contradictory results that did not show a consistent cost of current reproductive effort on residual reproductive output. The data presented here indicate that different elements of parental behaviors are indeed costly because they reduce various aspects of phoebes' subsequent reproductive performance. Experimental removal of old nesting structures at previously used breeding sites reduced but did not eliminate the chance of phoebes' settlement in the subsequent year. Comparing sites at which phoebes did and did not build new nests showed that nest builders completed their first clutches later, had lower probabilities of second breeding attempts, and more often lost their nesting attempt due to fallen nest structures than nest reusers. There was, however, no significant effect of nest building on the clutch sizes and rates of cowbird parasitism of first nesting attempts. Overall, sites with newly built nests had lower seasonal reproductive effort than sites with reused nests. I also examined phoebes' relative residual reproductive output in a separate breeding season when nest building was not experimentally manipulated. When controlled for confounding variables this analysis indicated that in those phoebes that did breed for a second time, the relative decrease of the sizes of first to presumed second clutches was greater at sites where first breeding attempts consisted of more total nestlings. These data are consistent with the hypothesis that parental care is costly in Eastern Phoebes and support predictions of trade-offs between the nest building, brood care, and residual egg-investment components of reproduction.

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Introduction

Parental care is any action that increases the chances of offspring survival at a cost to the parent (Clutton-Brock 1991). Yet many observational and experimental studies fail to show a survival cost for the parents or a decrease in their residual reproductive potential due to parental behaviors (e.g., Murphy et al. 2000, but see Veasey et al. 2001). This is somewhat surprising because many of these behaviors, such as brooding or increased foraging and alarm calling, differ qualitatively and/or quantitatively from the adults' typical self-maintenance activities and clearly evolved to improve the survival of dependent young. Theoretically, however, cost-free or even beneficial parental behaviors (from the perspective of the parent's phenotype) are feasible because, for example, clutches, litters, or breeding colonies are often raised in safe or fortified locations, thereby reducing the chances of predation on both the adults providing parental care and their offspring benefiting from this care. Alternatively, parental behaviors may indeed be costly to the parent's fitness but appropriate measures of fitness costs are yet to be used in some observational and experimental studies.

Parental care for dependent young is characteristic of all avian species other than megapodes and obligate brood parasites (Hauber et al. 2001). Because the eggs of all avian species require prolonged periods of safety and warmth before hatching (Martin et al. 2000), this distinctive phase of the reproductive cycle has led to the frequent use of birds as model systems to examine parental behaviors and other life-history traits through manipulating clutch sizes (Lack 1968; Winkler and Wilkinson 1988). Most birds provide safety and warmth for their eggs by constructing temporary structures (i.e., nests; Collias and Collias 1984; Hansell 2000). Avian nest building also lends itself to the examination of the potential costs and/or trade-offs of parental care through manipulation (Weeks 1978; Collias and Collias 1984; Møller 1990; Blem et al. 1999; Cavitt et al. 1999; Hansell 2000; Safran 2002).

Most birds build new nests for each breeding attempt and accrue the costs of nest building for each reproductive cycle (Hansell 2000). Other species that facultatively reuse old nests, such as many cavity dwellers (Martin and Li 1990; Møller and Erritzøe 1996) and mud-nesting species (Winkler and Sheldon 1993), allow for both observations on the natural variation of nest reuse patterns and experimental manipulations of the nest building behavior (Safran 2002) to examine the behavioral, survival, and reproductive consequences of nest construction (Weeks 1978; Barclay 1988; Hill and Gates 1988; Shields et al. 1988; Conrad and Robertson 1993a). Previous research on several nest reusing species suggests that individuals that build completely new nests, on the one hand pay some or all of the following costs compared to reusers of old nests: delayed laying, lower clutch size fewer fledglings, and lower probability of second clutching (Weeks 1978; Barclay 1988; Shields et al. 1988; Conrad and Robertson 1993a; Amat et al. 1999; Cavitt et al. 1999; Gauthier and Thomas 1993; but see Møller 1990; Blem et al. 1999 for cost free nest building). On the other hand, a potential benefit of building new nests is reduced ectoparasitism from infections of overwintering parasites, especially in colonial species (Hoogland and Sherman 1976; Brown and Brown 1986; Shields et al. 1988, but see Møller 1990; Blem et al. 1999). Overall, nest reusers typically have equal or higher seasonal reproductive success than new nest builders (Weeks 1978; Barclay 1988; Hill and Gates 1988; Shields et al. 1988; Conrad and Robertson 1993a).

Whether the temporal and energetic costs of nest construction cause variation in a specific component of avian reproductive effort, namely clutch size, has been the subject of extended debates (Lack 1968; Winkler and Wilkinson 1988; Hansell 2000). Two studies, examining old-nest reusing and new-nest building Eastern Phoebes (*Sayornis phoebe*) reported opposing findings on whether clutch size was affected by nest reuse patterns (reusers have larger clutch sizes: Weeks 1978; no difference in clutch size: Conrad and Robertson 1993a). One of these studies (Weeks 1978) has been cited as one of the few examples where clutch size was influenced by nest building in birds (Winkler and Wilkinson 1988; Hansell 2000), although a reanalysis of these data showed no statistical ties between nest building and clutch size (Conrad and Robertson 1993a). Even though Weeks (1978) removed all previously used nests from his study site in his second year of observations, neither his nor Conrad and Robertson's (1993a) results were based on same-year comparisons of phoebe clutch sizes between experimentally manipulated and sham-manipulated control sites (see Erckmann et al. 1990; Møller 1990; Blem et al. 1999; Cavitt et al. 1999; Safran 2002 for other species). Thus, their conclusions were based essentially on correlative data that could only suggest causality and called for further experimentation (see also Hill and Gates 1988).

Observational data on and experimental manipulation of Eastern Phoebes' clutch sizes also led to a similar lack of consistent findings regarding the cost of parental care for enlarged broods in this species. Specifically, clutch sizes of phoebes' second breeding attempts were not reduced, but fledging success of second broods was reduced by an experimental increase of their prior clutch sizes (Conrad and Robertson 1992). No difference in second clutch sizes was observed even though phoebe parents provided more parental care, through delivering more food more frequently, to experimentally enlarged first broods (Conrad and Robertson 1992, 1993b). However, this lack of effect of clutch size treatment on residual reproductive effort may have been masked by other factors that were not experimentally manipulated. For example, genetic, social, and environmental influences associated with the breeding female, its mate, and the breeding site may render the size of second clutches dependent on the size of the first clutches. Therefore, a measure of the relative change between first and subsequent clutch sizes that controls for this non-independence, rather than an absolute measure of the number of eggs laid, should be more appropriate to evaluate the increased cost of care in enlarged broods in double clutching phoebes and perhaps in other iteroparous species within *and* across breeding seasons.

To address some of these unsettled issues and evaluate contrasting correlational data related to the cost of parental care in nesting birds, I used experimental nest removal to examine the relationship between nest building and clutch size in Eastern Phoebes and observed natural variability to calculate a relative measure of residual reproductive effort to evaluate the cost of brood care. Because phoebes are territorial, do not nest colonially, tolerate human disturbance and only females build nests, they provide a feasible experimental system to examine the fitness consequences of nest reuse and brood care in the absence of potentially confounding factors of sociality group size, and nest construction by males (Shields et al. 1988; Safran 2002).

Methods

Study species and sites

Eastern Phoebes (hereafter phoebes) are common migrant passerine birds of North America that often build their mud nests covered with green moss in close association with human-built structures (Weeks 1994 ; Hauber 2001). In 1999, I located phoebe nests near human settlements (for a detailed description of the methods and study sites see Hauber 2001). Once a nest was located, I monitored it during the breeding season (late April–end of July in Ithaca, NY) at intervals of ≤5 days to determine laying date, clutch size, cowbird parasitism, and nesting success. Evidence for nest destruction (i.e., missing of >80% of the nest structure), due to floods, storms, or predation, were also noted. Second and replacement nesting attempts were sought out by searching for additional nests in the vicinity of the original nest. Phoebes were not marked in this study and in some analyses I assumed that repeated nesting attempts within the same year in a previously used nest or in its vicinity (i.e., under the same bridge or under the eaves of the same building) were attributable to the same breeding pair (Klaas 1975; Weeks 1979; Conrad and Robertson 1993c; Hauber unpublished data).

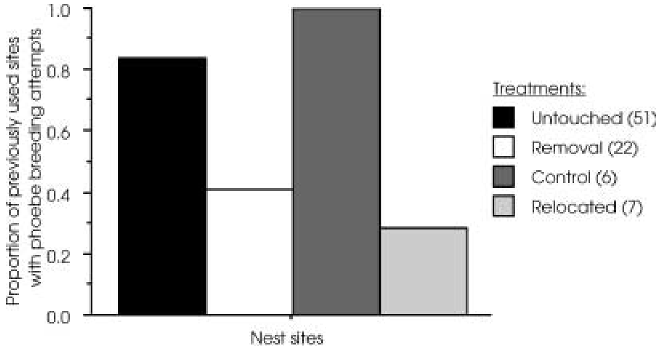

Fig. 1 Proportion of Eastern Phoebe (*Sayornis phoebe*) nesting sites used in 1999 at which breeding was also observed in 2000 following experimental manipulations of old nests

Experimental manipulations of nests

In 2000, prior to the return of phoebes from their wintering grounds in March, I arbitrarily assigned previously used phoebe nests into one of four experimental groups. Nests at "undisturbed" sites were visited, their contents examined, but left intact. Nests at "removal" sites were taken off using a metal spatula. Nests at "control" sites were removed and replaced at their original location with a different phoebe nest, using nails and non-toxic glue. Finally, at "relocated" sites nests were removed and a different nest was placed at a distance of about 2 m from the original location in a seemingly suitable phoebe nesting position (e.g., under eaves or on a bridge I-beam, using personal judgement; Fig. 1). After manipulations I returned to these sites, starting mid-April 2000, to monitor phoebes' breeding activities and reproductive success following the methods from 1999. Only nests with known manipulation histories were included in the subsequent analyses.

Reproductive measures

For each phoebe nest I determined clutch completion dates, using maximum clutch size and assuming one phoebe egg laid per day (Weeks 1994). For nests that were parasitized by Brown-headed Cowbirds (*Molothrus ater*), I further assumed that a single phoebe egg was replaced by each cowbird egg laid in that nest (Klaas 1975; personal observation) and calculated the phoebes' original ("corrected") clutch size by adding the numbers of phoebe and cowbird eggs found in those nests. Because cowbird parasitism reduces phoebe hatching and fledging success (Klaas 1975; Rothstein 1986) and because some of the second nesting attempts were used in a separate study involving clutch manipulations (Hauber, unpublished data), I calculated seasonal reproductive effort and output by summing corrected phoebe clutch sizes laid in nests that successfully fledged at least one nestling (whether phoebe or cowbird) from first and second nesting attempts.

Relationship between brood size and residual reproductive effort

For this portion of the study, I documented the clutch completion date and corrected clutch size of phoebe nesting attempts throughout the breeding season of 2001 when no treatments with nests were performed. To control for some confounds related to duration of parental care, I only used nests that successfully fledged at least one nestling (whether phoebe or cowbird) during the first breeding attempt. For these nests I counted the number of live 5-day-old phoebe and cowbird nestlings to determine the size and composition of broods (total number of chicks and proportion of cowbird chicks, Hauber 2001). I also calculated a relative measure of clutch size change between first and second breeding attempts as (2nd clutch size–1st clutch size)/1st clutch size and then related this measure of residual reproductive effort to clutch completion date, brood size, and brood composition of first breeding attempts. I included both clutch completion date and proportion of cowbirds in these multivariate analyses because of previous studies suggested both a seasonal variability of phoebe clutch sizes (Conrad and Robertson 1993c) and increased provisioning rates of parasitic cowbird nestlings compared to phoebe chicks (Hauber and Montenegro, unpublished data).

Statistical analyses

When measurements were not normally distributed or when comparisons had small sample sizes due to the outcome of the experimental manipulations, I used two-tailed non-parametric tests to analyze these data. Proportional variables were log(x+1) transformed in multiple linear regression analyses.

Results

Settlement patterns

In 2000, experimental manipulation of nest structures used in the prior year caused variation in settlement patterns of breeding Eastern phoebes (overall χ^2=22, df=3, P<0.0001, Fig. 1). Specifically, breeding activity was more likely to be observed at sites where nests were left undisturbed (43 of 51) than at sites where nests were removed [9 of 22, P=0.0004; Fisher's Exact test (hereafter FEt)]. At control sites, where the old nest was removed and replaced with a different nest as its previous location, phoebes were also more likely to breed (6 of 6) than at relocated sites where old nests were removed and a different nest was placed at a nearby new location (2 of 7; P=0.021, FEt). When considering undisturbed sites with intact nests only (n=33), phoebes were more likely to reuse the existing old nest (30, 91%) than build a new nest (3, 9.1%; P<0.0001, binomial test with random expectation 50%).

Effects of nest use/reuse patterns

Based on the availability and use of old nests at undisturbed, removal, and control sites, I classified phoebes into one of three categories: breeding in new nests where no undisturbed nests were available (Experimental New: EN, n=11), breeding in new nests where undisturbed nests were available (Natural New: NN, n=3), and breeding in undisturbed nests (Old Nests: ON, n=37). To detect effects of experimental manipulation, I carried out statistical comparisons on data from phoebes at EN and ON sites. I also report data for NN sites for comparisons with previous, correlational studies. In some cases, the specific response variables were unknown or could not be estimated due to human interference with research efforts (Hauber 2001); therefore sample sizes are noted for each analysis and figure separately.

Nesting sites, predation and Brown-headed Cowbird parasitism

Preliminary analyses indicated that nest location (eaves, bridges, or barns) was related to the probabilities of both cowbird parasitism and fallen nests but not to clutch sizes and second clutching (Hauber 2001). However, there was no bias in the location of ON and EN nests in my sample ($\chi^2=0.019$, $df=2$, $P=0.99$). I recorded evidence of nest predation (e.g., broken egg-shells, missing nestlings prior to fledging, etc.) in only a handful of instances of first nesting attempts (0 of 11 EN sites and 4 of 30 of ON sites where nests did not otherwise fall due to weather; $P=0.56$, FEt, $\beta>0.76$) for an overall predation rate on first clutches of 9.8%. Whether phoebe nests were parasitized by cowbirds also did not depend on use patterns of old or new nests: 3 of 11 EN nests and 11 of 35 ON were parasitized on the first nesting attempts ($P>0.99$, FEt, $\beta>0.54$) for an overall parasitism rate in first clutches of 30%.

First clutches

Known laying dates of phoebes at the different sites varied with nest manipulation: EN phoebes completed their first clutches on average 4.2 days later than ON pairs ($U=84$, $P=0.027$; Mann-Whitney test; Fig. 2). There was no difference in the total number of phoebe eggs per clutch (corrected for cowbird eggs, see Methods) in the different experimental groups ($U=174$, $P>0.68$, Fig. 2, $\beta>0.50$). When comparing the proportions of phoebe nests that had less than the modal clutch size (5 eggs) at EN (2 of 11, 18%) and ON (5 of 34, 15%) sites, there was also no significant difference ($P>0.99$, FEt). Using a Fisher's Exact test it would take approximately 117 of consistantly similar sizes clutches in each treatment group to detect a statistical difference, with $\alpha=0.05$ and $\beta=0.5$, between proportions of these approximate magnitudes (20% vs. 10%).

Second clutches

Second nesting attempts were detected at phoebe nests with successfully fledged first clutches at different rates depending on nest reuse patterns: phoebes in EN sites had second clutches less frequently (54%) than ON sites (87%, $P=0.042$; FEt, Fig. 3). When these phoebes did have a second clutch, EN and ON sites had similar dates of clutch completion (EN: day 50±2.6, $n=4$; ON: day 47±1.7, $n=17$, May 1, 2000=day 1; $U=25$, $P>0.39$) and total number of eggs/clutch (EN: 4.4±0.25 eggs, $n=4$; ON: 4.6±0.11, $n=21$; $U=29$, $P>0.25$).

Fallen nests during the breeding season

The probability that phoebe breeding attempts failed at least once due to falling nest structures in 2000 was related to nest reuse patterns: EN sites had higher probability of fallen nests (46%) than ON sites (6.9%, $P=0.011$; FEt, Fig. 4), despite the more frequent occurrence of second clutches and, thus, longer duration of use at undisturbed nests. (Fig. 3).

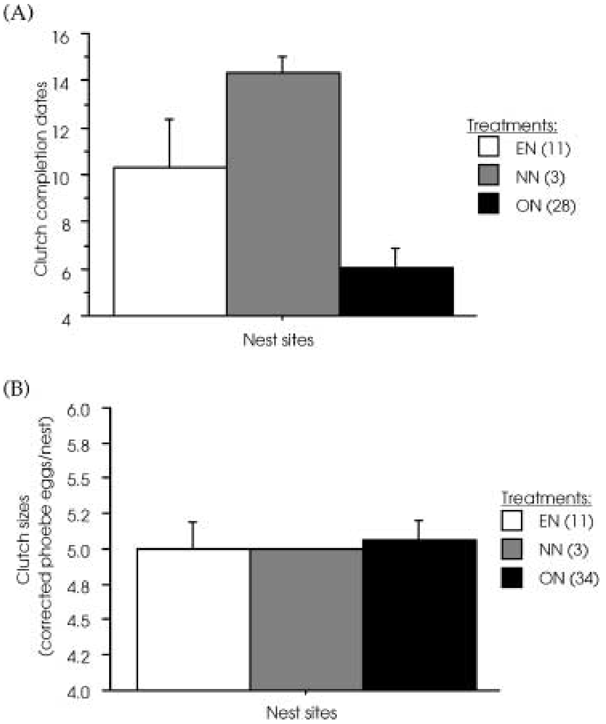

Fig. 2 Clutch completion dates (**A**) and clutch sizes (**B**) of Eastern Phoebe first nesting attempts at previously used breeding sites (treatments are: *ON* old nests reused, *NN* natural new nests, *EN* experimental new nests, *numbers in brackets* indicate sample sizes. 1 May 2000=day 1, mean+SE are indicated)

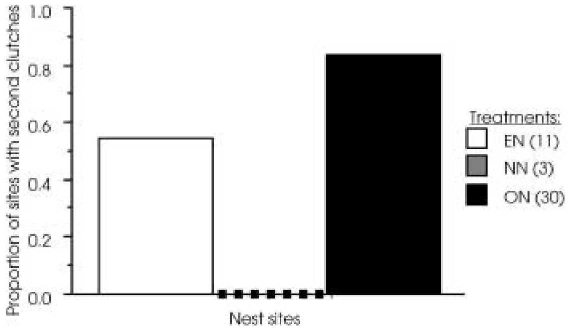

Fig. 3 Probability of second clutching by Eastern Phoebes after successfully fledged first nesting attempts in 2000

Seasonal reproductive effort and output

Data from nest sites without predation indicated that phoebes that built new nests laid overall fewer eggs than phoebes that nested in old nests (EN: 7.0±0.78 eggs/season, $n_{EN}=8$; ON: 9.1±0.38 eggs/season, $n_{ON}=24$; $U=41$, $P<0.014$; NN: 5.0±0 eggs/season, $n_{NN}=3$). The

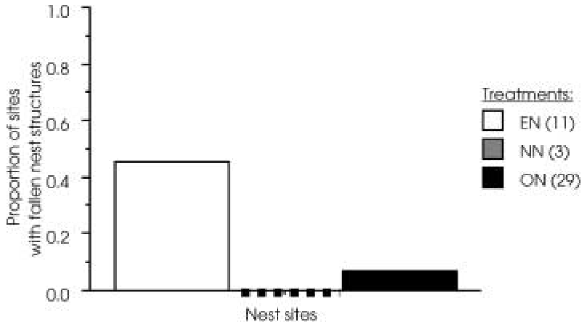

Fig. 4 Proportion of previously used phoebe nesting sites where breeding attempts failed due to fallen nest structures in 2000

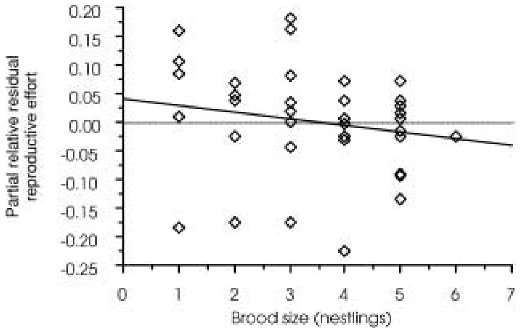

Fig. 5 Partial linear regression relationship between relative residual reproductive effort and brood size of Eastern Phoebes' first breeding bouts in 2001 when controlled for clutch completion date and the proportion of parasitic Brown-headed Cowbird (*Molothrus ater*) nestlings of first broods

total predicted number of successfully hatched and fledged phoebe eggs (observed values corrected for cowbird parasitism and summed between first and second nesting attempts, see Methods), varied between experimental groups: overall EN sites had fewer total eggs across breeding attempts in 2000 than ON sites (EN: 5.0±0.89 eggs/season, n_{EN}=10; ON: 7.7±0.60, n_{ON}=30; U=72, P<0.013; NN: 5.0±0 eggs/season, n_{NN}=3). The direction of this difference remained consistent, but marginally non-significant, when limiting the comparison to the seasonal outputs of phoebes that did not raise parasitic cowbird nestlings (EN: 5.4±0.1.1 eggs/season, n_{EN}=8; ON: 7.4±0.75 egg/season, n_{ON}=19; U=43, P<0.074). For all nests combined, seasonal reproductive success was related to both the probability of second clutching ($F_{1,47}$=66, P<0.0001) and fallen nests ($F_{1,47}$=119, P<0.0001, interaction: $F_{1,47}$=1.0, P>0.32, ANOVA), both of which factors were related to experimental manipulation of nest reuse patterns (EN vs ON, Figs. 3, 4).

Relationship between brood size and residual reproductive effort

In 2001, those phoebes that bred successfully multiple times (at n=40 nest sites) had clutch sizes that were significantly smaller during their second than for first breeding attempts (difference: –0.5±0.17, Z=–2.7, P<0.0071, Wilcoxon signed test). There was evidence for a weak statistical non-independence between subsequent clutch sizes: larger first clutches tended to be followed by even smaller second clutches (ρ=–0.23, P<0.15, Spearman rank correlation). The relative measure of residual reproductive effort (see Methods) was negatively related to clutch completion date (P<0.0013), brood size (P<0.024), and proportion of cowbirds per brood (P<0.033) of first clutches: Transformed $\text{Difference}_{\text{clutch size}} = 0.24 - 0.010 \times \text{Date}_{\text{clutch completion}} - 0.050 \times \text{Number}_{\text{nestlings}} - 0.60 \times \text{Transformed Proportion}_{\text{cowbirds}}$ (overall r^2=0.31, P<0.013, Fig. 5).

Discussion

Some previous studies on Eastern Phoebes detected a difference in the clutch size and/or laying date of phoebes that naturally built new nests versus those that reused old nests (Weeks 1978; Conrad and Robertson 1993a; but see Hill and Gates 1988). My sample only included n=3 phoebes that naturally built new nests (NN), and the clutch size in all of these nests was 5 eggs, which was also the modal phoebe clutch size in my study in both newly built and reused nests. Despite the small sample size, in agreement with previous studies on phoebes and other nest reusers, such as Brown Thrashers (*Toxostoma rufum*, Cavitt et al. 1999) and Barn Swallows (*Hirundo rustica*, Barclay 1988; Shields et al. 1988), the sites in my study with the NN nests both had later clutch completion dates (U=1.0 P<0.006, Fig. 2) and were less likely to have second clutches (P=0.0068, FEt, Fig. 3) than sites with reused old nests. The results of the experimental nest manipulation employed in this study were consistent with these and prior (Weeks 1978 ; Conrad and Robertson 1993a) correlational trends and thus allow the establishment of causality between specific reproductive traits and nest reuse behavior in Eastern Phoebes.

When available, phoebes preferentially (>90%) refurbished old nests rather than build new structures. This suggests that the benefits of nest reuse, such as earlier laying, more likely double clutching, and smaller chance of fallen nests (containing eggs or nestlings) mostly outweigh the potential costs associated with nesting in old structures. In addition, presumed costs of nest reuse, such as ectoparasitic infestations or increased rates of depredation, may not in fact be disproportionally associated with old nests in phoebes and other species (Møller 1990; Blem et al. 1990 but see Brown and Brown 1986). Accordingly, I found no difference in the proportion of depredated or cowbird-parasitized clutches between nest reusers and builders. Also, I rarely noticed ectoparasitic infestations on nestlings during the phoebes' first breeding attempts. Perhaps the solitary nature of most phoebe nests and the green moss covering the mud-based nest structure protect phoebes from haematophagous arthropods (Wimberger 1984; Clark and Mason 1985) and thus from a main cost of nest reuse (Hansell 2000).

Despite the manipulative nature of this investigation regarding old nests, more data on the breeding birds' identity are needed to tease apart its the potential effects on phoebes' settlement patterns due to individual variation in life history traits (e.g., sex, age, experience, and dominance), and its reproductive consequences. For example, settlement at territories may be governed by decision rules of territorial male phoebes that return first from wintering grounds (Weeks 1979). In turn, nest building tactics may be related to female decision rules because it is female phoebes that construct nests (Conrad and Robertson 1993c) and age or condition dependent settlement patterns could influence differentially the various components of the reproductive output of phoebes across nest treatment sites, especially because second clutching is related to age class in female phoebes (Conrad and Robertson 1993c). In my study I found that at removal sites relatively fewer breeding attempts were initiated (Fig. 1). Therefore, in this aspect the present study is similar to the experimental works of Erckmann et al. (1990) and Rutnagur (cited in Hansell 2000) who also found that at sites where old nests or nesting materials of Red-winged Blackbirds (*Agelains phoeniceus*) and Rooks (*Corvus frugileus*) were respectively removed prior to breeding season, fewer breeders set up nests. Similarly, Weeks (1978) himself reported just such a result following his manipulations: after having removed all phoebe nests within his study site, in the subsequent year he was able to locate fewer breeding pairs of phoebes compared to the prior, non-removal year. Whether fewer breeding events in the presence of fewer or no old nests are due to either the decreased proportion of phoebes opting to breed or increased dispersal by phoebes returning from wintering grounds remains uncertain.

Even though phoebe nests are placed at locations that are typically protected from harsh weather (Hill and Gates 1988), they are not necessarily safe from all environmental factors. For instance, nests placed under bridges are sometimes destroyed by flooding streams (Weeks 1994; personal observation). Therefore, the presence of an intact old phoebe nest could be used by returning phoebes as an indicator of structural stability and safety of a previously used nesting site. This nesting site quality indicator hypothesis (Shields et al. 1988) may explain preferential settlement patterns at surviving nests by phoebes (Weeks 1977) and other species (Erckmann et al. 1990; Cavitt et al. 1999; but see Blem et al. 1999).

Although individuals were not marked in this study, other studies demonstrated that phoebes typically returned to nest at their previously used territory and used the same nesting site where they had nested in the prior year (Klaas 1975; Audubon 1804 quoted in Weeks 1994). Returning phoebes perhaps remember the exact location of their previously used nest and settle in it preferentially if the previously used nest has remained intact between breeding seasons. To support this "memory for nest site" hypothesis I found that phoebes nested at the same spot (<10 cm) from which the previous year's nests were removed at 6 of 9 removal sites and at 2 of 2 relocated sites (72%; Fig. 1). Alternatively, previously used nest locations may be the best available positions ("microsites" *sensu* Shields et al. 1988) where nests can be built successfully within phoebe territories. This second mechanism would create 'traditional' nest locations that could potentially last across several breeding seasons even beyond the lifespan of phoebes. There is indeed evidence for the use of phoebe nesting sites well beyond the average lifespan of individual phoebes (Weeks 1994) and, again, in my study in 8 of 11 removal and relocated sites the newly built nests were positioned at the exact location of the old, removed nests. Future studies are much needed to examine the neurobiological and sensory mechanisms of nest selection and site fidelity in birds (Sherry et al. 1993 ; Hauber and Sherman 2001), especially in long-distance migrants such as the Eastern Phoebe (Weeks 1994). Irrespective of the mechanism, whether based on memory or suitable location (or, probably, a combination of both since nesting site characteristics may change from year to year), the presence of surviving old nests could be used by adult phoebes as an indicator of nesting site quality to male phoebes settling at a territory and/or female phoebes choosing among mates with territories that do or do not contain old nests.

Is reduced clutch size then a cost of parental care in Eastern phoebes? Comparing sites at which phoebes did and did not build new nests showed that nest builders completed their first clutches later, had lower probabilities of second breeding attempts, and more often lost their nesting attempt due to fallen nest structures than nest reusers. However, there was no significant effect of nest building on the clutch sizes of first nesting attempts. Overall, sites with newly built nests had lower seasonal reproductive effort and output than sites with reused nests. Similarly, an analysis of phoebes' relative residual reproductive output in a separate breeding season, when nest building was not experimentally manipulated, indicated that in those phoebes that did breed for a second time the relative decrease of the sizes of first to presumed second clutches was greater at sites where the first breeding attempts consisted of more nestlings. These data are consistent with the concept of costly parental behaviors in Eastern Phoebes, but also indicate that various aspects of the reproductive output may be differentially affected by separate components of parental care provided for avian young.

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