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BREEDING DISPERSAL OF EASTERN BLUEBIRDS DEPENDS ON NESTING SUCCESS BUT NOT ON REMOVAL OF OLD NESTS: AN EXPERIMENTAL STUDY

PATRICIA ADAIR GOWATY
*Institute of Ecology
The University of Georgia
Athens, GA 30602-2602 USA*

JONATHAN H. PLISSNER[1]
*Department of Biological Sciences
Clemson University
Clemson, SC 29634 USA*

Abstract.—One hypothesis to explain both within- and between-season breeding dispersal is that individuals move in response to degradation in the suitability and/or quality of their nesting sites. This hypothesis was experimentally examined by manipulating the suitability and/or quality of nesting boxes used by Eastern Bluebirds (*Sialia sialis*) on one study site in upstate South Carolina. From 12 randomly assigned boxes, old nests, parasites, dead nestlings, old food or feces were not removed, as they were from 12 other randomly assigned boxes. There were 24 nesting attempts in cleaned boxes; 26 in not-cleaned boxes. Third brood nesting attempts occurred in only one of the cleaned boxes but in five of the not-cleaned boxes. Only 59% of individuals stayed to breed again within the season in not-cleaned boxes, whereas 72% stayed in cleaned boxes. Equal numbers of both males and females returned to breed in cleaned and not-cleaned boxes during the next breeding season, however. Both within- and between-season breeding dispersal is significantly more likely after unsuccessful nesting attempts than successful nesting attempts. There was no significant effect of cleaning or not cleaning nesting boxes on the chance of nesting attempts or the numbers of nestlings fledged from nesting boxes.

LA DISPERSIÓN REPRODUCTIVA DE *SIALIA SIALIS* DEPENDE EN EL ÉXITO DEL ANIDAMIENTO PERO NO EN LA REMOCIÓN DE NIDOS VIEJOS: UN ESTUDIO EXPERIMENTAL.

Sinopsis.—Una hipótesis para explicar tanto la dispersión dentro de- como entre- temporadas reproductivas es que los individuos se mueven como respuesta a la degradación en la adecuación y/o calidad de sus lugares de anidaje. Se examinó esta hipótesis experimentalmente al manipular la adecuación y/o la calidad de cajas de anidaje usadas por *Sialia sialis* en un lugar de estudios en el norte de Carolina del Sur. No se removieron nidos viejos, parásitos,

[1] *Current address: USGS/BRD, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, Oregon 97331 USA.*

crías muertas, alimento viejo o heces fecales de 12 cajas aleatoriamente seleccionadas, mientras que estos elementos fueron removidos de otras 12 cajas aleatoriamente seleccionadas. Se dieron 24 intentos de anidar en cajas limpiadas; 26 en cajas no limpiadas. Solo se obtuvo un intento de anidar por tercera vez en una caja limpiada, pero en cajas no limpiadas ocurrió cinco veces. Tan solo un 59% de los individos se quedaron para volver a reproducirse en la temporada en las cajas no limpiadas, mientras que 72% se quedaron en cajas limpiadas. Sin embargo, números iguales de machos y de hembras volvieron a anidar en cajas iimpiadas y no limpiadas en la próxima temporada reproductiva. Tanto la dispersión reproductiva dentro de y entre temporadas es significativamente más probable después de intentos fallidos por anidar que después de intentos exitosos por anidar. No se halló un efecto significativo de limpiar o no las cajas de anidaje en la oportunidad de intentar anidar o en el número de pichones sacados de las cajas de anidaje.

Breeding dispersal is movement from one breeding location to another. It is distinguished from natal dispersal, which is movement from the place of birth or hatch site to the place of first breeding (Greenwood 1980). Two leading hypotheses to explain breeding dispersal are that breeding dispersal may follow nesting failure or predation (Drilling and Thompson 1988; Jackson et al. 1989), and that within-season breeding dispersal may facilitate more rapid renesting after previous nesting attempts or avoidance of areas depleted of essential food resources (Jackson et al. 1989). These hypotheses are not mutually exclusive. A third hypothesis is that breeding dispersal occurs when the quality (variation associated with nesting success) or suitability (likelihood of usage) of nest sites decline. This hypothesis predicts that individuals whose nest sites do not decrease in quality and/or suitability will be less likely to move than individuals nesting at sites that are declining in quality or suitability within a breeding season or between breeding seasons. This hypothesis may be particularly applicable to those species that are secondary cavity nesters. Given variation in the location of nesting cavities, their characteristics, such as depth and previous occupants, their susceptibility to parasites and predators (Møller 1989; but see Koenig et al. 1992; Thompson and Neill 1991), it is easy to imagine that naturally-occurring nesting sites decline in their quality or suitability for nesting with each successive use. We call this the previously-used nest site hypothesis.

In this paper we describe an experimental manipulation designed to evaluate the effect of the previous use of nesting cavities on within- and between-season breeding dispersal among cavity nesting Eastern Bluebirds (*Sialia sialis*). The previous-use hypothesis assumes that the quality of nesting cavities declines with each subsequent nesting attempt. It predicts that when nest site quality declines with successive nesting attempts as old nesting material, parasites, nesting detritus, feces, and debris accumulate in nesting boxes, individuals with opportunities to disperse to higher quality or more suitable nesting cavities do so. This hypothesis also assumes that individual birds are themselves unable or unlikely to manage these aspects of nest site suitability and/or quality.

METHODS

Eastern Bluebirds are socially monogamous (Gowaty 1983; Gowaty and Bridges 1991a,b). Females build nests, incubate (14 d), and brood newly hatched young; both males and females guard their nests from conspecific intruders, potential predators, and interspecific nest parasites (Gowaty 1981; Gowaty and Wagner 1988). Both male and female care-givers feed nestlings and fledglings, which fledge when they are 15–22-d old. On our South Carolina study sites the breeding season is often 6-mo long, beginning in early March and ending in late August. Most bluebirds on these study sites attempt at least two broods per season and sometimes as many as four.

Our study sites were the 10,927 ha of Clemson University farms, orchards, and forests in Anderson, Pickens, and Oconee Counties in the piedmont of South Carolina. This experiment took place only on one portion of our "Campus" study site in Pickens County. The terrain is characterized by gently rolling hills. We placed nesting boxes on fence rows surrounding animal farms and orchards, at heights of 1.5–2 m above the ground. All of our nesting boxes were of identical design, dimensions, and colors. Eastern Bluebirds on our study sites breed only in nesting boxes, because contests for the few existing suitable natural cavities are lost to European Starlings (*Sturnus vulgaris*), House Sparrows (*Passer domesticus*), and flying squirrels (*Glaucomys volans*).

In order to evaluate the predictions and assumptions of the previous-use hypothesis, we used 24 territorial sites that had been used successfully by Eastern Bluebirds during previous breeding seasons. We replaced all previously-used nest boxes with new nest boxes for this experiment. We randomly assigned the first of 24 nesting boxes (one per nest site) to one of two treatments; thereafter, in order to control for micro-geographic variation in nesting sites, we assigned each box alternately to a treatment. In one treatment we cleaned 12 boxes after the termination of each nesting attempt (cleaned treatment) when chicks had died, disappeared, or fledged. In the other we did not remove nest box contents after a nesting attempt, so that in the not-cleaned treatment, boxes contained old nesting material, nestling debris, ectoparasites, feces, etc.

There are several assumptions associated with our experimental design. It assumes that alternative, more suitable nesting sites are available to which individuals may disperse. We assumed that nest cavities that we cleaned after each nesting attempt would remain relatively suitable for nesting, whereas cavities not-cleaned would decline in suitability. We also assumed that the birds themselves do not clean out the old nesting debris. We predicted that individuals nesting in cavities declining in suitability would be more likely to disperse than individuals nesting in cavities in which the suitability for nesting was renewed by cleaning after each nesting attempt.

In order to fulfill the assumption that alternative nesting sites were available to which individuals could disperse, we set up a series of additional new boxes to provide suitable places for birds to disperse. Thus, we placed one additional box on fence posts within 200 m of each of the 24 boxes during May of the first experimental season (1988), well after first brood attempts were started. In addition, because we put these new boxes up after initial settling, during at least our first experimental season these boxes increased our ability to detect within-season dispersers. We purposely put these boxes up "late," in places where we had not previously had nesting boxes, so as not to have them interfere with the settling behavior of newly-arriving birds, but so that they would be available for any individuals engaged in within-season breeding dispersal.

We used unique combinations of plastic colored leg bands to mark all unmarked adults at each nest box during the first and subsequent nesting attempts of 1988. We monitored all subsequent nesting attempts to observe movements or disappearances of breeders and the outcome of each nesting attempt. We classed a nesting attempt successful if at least one nestling fledged. It is easier to observe whether individuals stay or are gone from nesting sites than it is to observe where dispersing individuals may have gone. So, here we use philopatric to refer to those individuals that did not disappear from their original breeding site.

Because most of the variables we tested are categorical, we used categorical models analysis to examine most of our questions. We set significance levels at $P \leq 0.05$. We conducted power analyses (Cohen 1988) after completion of our tests, and thus, use our a posterori knowledge as a guide to the likelihood of Type II errors.

RESULTS

Between-year philopatry was associated with whether a nesting site was successful the previous year. If nests were successful, 56% of individuals stayed; if nests were unsuccessful, only 15.4% stayed ($G = 6.27$, $P = 0.02$).

Seventy-two percent of individuals stayed at their original breeding sites when we cleaned nesting boxes, compared to 57% of individuals at boxes we did not clean ($G = 1.32$, $P = 0.25$; Power for small effect [$\alpha = 0.05$] = 0.11–0.29). Pooled over cleaned or not-cleaned boxes, 68% of males and 60% of females stayed at their original nesting boxes ($G = 0.348$, $P = 0.56$; Power for small effect [$\alpha = 0.05$] < 0.11). If nesting attempts were successful (i.e., fledged at least one nestling), significantly more individuals stayed (65.6%) for subsequent breeding attempts than did individuals that stayed when nesting attempts were not successful (26.7%) ($G = 6.38$, $P = 0.01$).

To test the assumption that nest-site quality declined, we tested for differences between treatments in nesting success. We found no significant difference between treatments in the likelihood that at least one nestling fledged. At cleaned boxes, 43.8% of nesting attempts were successful, and at not-cleaned boxes 50% of nesting attempts were successful ($G = 0.10$, $P = 0.76$; Power for small effect [$\alpha = 0.05$] = 0.11–0.29). We then investigated if there were some other, perhaps more subtle factors, associated with our inability to reject the null hypothesis. So we re-examined our data for differences in degree of nesting success. In these analyses, we looked for differences in the mean number of nestlings fledged from cleaned and not-cleaned nesting boxes, rather than whether these nests were successful or not. For the first broods of 1988, the nesting attempts that occurred immediately prior to our manipulations, there were no statistical differences in the numbers of nestlings fledged from boxes in the two treatments. At 12 cleaned nests 3.25 ± 0.70 (mean + SE) nestlings fledged, while at 12 not-cleaned nests 2.33 ± 0.64 nestlings fledged (t = 0.97, df = 22, P = 0.17; Power = 0.04), indicating that our random assignments were probably indeed random with respect to these reproductive success variables. Furthermore, there were no statistical differences in the number of nestlings fledged from cleaned and not-cleaned nesting boxes after our manipulations. At 11 cleaned boxes 1.7 ± 0.54 nestlings fledged during second brood attempts and at the 10 not-cleaned boxes that were used during second brood attempts 2.1 ± 0.62 nestlings fledged (t = 0.454, df = 19, P = 0.33; Power = 0.15), suggesting that there was no significant decrease in the quality of nesting cavities that contained old nesting material and associated debris for the duration of one breeding season, at least.

Only one (8%) cleaned box was unused during 1989, the breeding season following our experimental manipulations. Three (25%) of the not-cleaned boxes were unused. This difference was not significant (G = 1.25, P = 0.27, Power = 0.11), so cleaned and uncleaned boxes were chosen equally often for breeding by nest site limited bluebirds.

The likelihood that individuals remained philopatric was also not associated with our experimental manipulations (G = 0.39, P = 0.53, Power = 0.08). Fifty percent and 53% of individuals from the previous breeding season remained at their original boxes whether boxes were cleaned or uncleaned, respectively. Individuals were equally philopatric at cleaned and not-cleaned boxes. Fifty-six percent of females and 43% of males stayed at cleaned boxes between years, however, but 33% of females and 50% of males stayed at not-cleaned boxes. This difference is not significant (G = 1.17, $P > 0.05$, Power < 0.10), but suggests that females may be more likely than males to leave uncleaned boxes between years.

DISCUSSION

The likelihood of within- and between-season breeding philopatry is associated with nesting success. Bluebirds were more likely to remain at nest sites when nests were successful than when nesting failed. This observation is consistent with other observations about Eastern Bluebirds. In Michigan, the likelihood of breeding philopatry, both within and between-seasons, is associated with successful nesting attempts (Pinkowski 1977). In an earlier observational study on this and nearby study sites, Eastern Bluebird females were significantly more likely to move after their first nesting attempts if these were unsuccessful rather than successful (P. A. Gowaty, published in Rohwer 1986, table 3). It is also consistent with reports of within-season breeding dispersal for several other species (reviewed in Jackson et al. 1989).

There were no significant differences in within and between-season dispersal from cleaned versus uncleaned boxes. We are unable confidently to accept the null hypothesis however, because of the low power of our tests. It seems likely that our experimental period (one and one-half seasons) may have been too short relative to our sample sizes for the detection of significant differences. Thus, we must consider it a viable hypothesis that Eastern Bluebirds prefer cleaned nesting boxes, and that this is a result we might have observed had we run the experiment longer or included more nesting boxes in our experiment. However, it is unlikely that we or other experimentalists will tackle this problem further. Our "effect sizes" (Cohen 1988) were only around 0.10, sizes considered very small (Cohen 1988). Using these effect sizes and tables in Cohen (1988), we determined that, in order to increase power to 0.52–0.90, our sample sizes would need to be approximately 400–1000 nests, sample sizes that we consider prohibitive. Thus, a conservative conclusion from our present study is that if there is a difference in breeding dispersal away from cleaned versus uncleaned boxes, it is quite small, perhaps smaller than our potential limits of resolution.

However, given the interesting result of Davis et al. (1994), our result of no difference in breeding dispersal from cleaned and uncleaned nest boxes appears quite reasonable. These researchers experimentally evaluated dispersal *to* nesting boxes containing old nests versus empty nesting boxes. They observed that Eastern Bluebirds in Kentucky strongly prefer nest boxes containing old nests, and suggest an alternative argument that because boxes with old nests harbor *Nasoia vitripennis* larvae that themselves parasitize blowflies (*Protocalliphora sialis*) that suck bluebirds' blood, that old nests enhance blowfly control and thus may enhance nest box quality for Eastern Bluebirds. Their observations suggest that one assumption of our previous-use hypothesis, namely that the quality of nesting cavities declines with each subsequent nesting attempt, may not always be met. If this is the case, our observation of no difference in breeding dispersal from cleaned versus not cleaned cavities would be the expected result in areas where blowfly parasitism of Eastern Bluebirds is not severe, which seems to be the case on our South Carolina study sites (J. Loye and P. A. Gowaty, unpubl. data).

In contrast our results concerning statistical association between successful nesting and whether we clean nesting boxes or not are more conclusive. Equal numbers of nesting attempts were successful and the mean number of fledglings from uncleaned boxes was slightly (and non significantly) higher than at cleaned boxes. Thus, we have no evidence that not cleaning boxes increased predation or decreased health of nestlings. This result is consistent with other observations. For example, ectoparasite loads in Eastern Bluebird nests in South Carolina are low compared to more northern populations (J. Loye and P. A. Gowaty, unpubl. data). During 17 yr of observing breeding Eastern Bluebirds in South Carolina, we attributed no nestling deaths to ecto parasite infections (pers. obs.). Furthermore, Eastern Bluebirds remove ectoparasites from nests even when parasites are isolated deep within the nesting material (D. Droge and P. A. Gowaty, unpubl. obs.). In addition, Eastern Bluebirds typically maintain nests free of waste and debris. Adult provisioners never defecate inside of nest boxes and almost always remove nestling fecal material from nesting boxes (pers. obs.). If nestlings die before they are 7-d-old, adults readily remove their bodies (Gowaty, unpubl. obs.). Bluebirds sometimes remove nesting material from nesting boxes, before nesting females build over the remains of old nests. Hartshorne (1962) reported that Eastern Bluebirds removed infertile eggs, foreign objects such as pieces of crayon, and dead nestlings experimentally placed in nests in nesting boxes. Thus, another reason for our results may be failure of yet another of our initial assumptions, in that sometimes Eastern Bluebirds do seem capable of manipulating the suitability and/or quality of their nest cavities. Therefore, in sum we conclude that on South Carolina study sites at least, leaving old nests and nesting debris in nesting boxes has little or no effect on nest site suitability or quality for Eastern Bluebirds.

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