Reproductive success and developmental stability of eastern bluebirds on golf courses: evidence that golf courses can be productive

by Joshua E. LeClerc, Judy P. K. Che,
John P. Swaddle, and Daniel A. Cristol

Abstract We assessed adult reproductive and nesting success, and developmental instability, survival, and condition of nestling eastern bluebirds (*Sialia sialis*) breeding in nestboxes on and off golf courses. With this information we tested hypotheses predicting that nestboxes on golf-course habitat provided poor nesting and chick-rearing environments due to pesticide pollution or other factors. Contrary to our prediction, nestboxes on golf courses received 28% more bluebird eggs and produced 17% more fledglings than nestboxes on nongolf sites. Individual nests on golf courses appeared to have slightly reduced probabilities of survival during laying and incubation, but we found no depression in the overall Mayfield survival probabilities. Surprisingly, nestling bluebirds raised in golf-course boxes exhibited 39% less fluctuating asymmetry of their tarsus bones, possibly an indicator that nestlings that survived to fledge had been under less stress during development. This may have resulted from stronger selection against asymmetrical nestlings on golf courses, or it may indicate that golf-course nestboxes provide higher-quality habitat for bluebirds. Our results suggest that for this bird species, nestboxes on the golf-course habitat we studied can provide high-quality rearing environments and may serve as population sources. This may not apply to other species, including most birds of conservation concern, which do not nest in protected artificial cavities or forage directly on turfgrass habitat.

Key Words body condition, developmental instability, eastern bluebird, fluctuating asymmetry, golf courses, pesticide, productivity, reproductive success, *Sialia sialis*

Golf courses are opening at rapid rates across North America and around the world (Gange et al. 2003). The full ecological footprint of this change in land use is not well understood, but the most obvious potential impacts are habitat fragmentation, chemical pollution through pesticide application, and loss of native vegetation communities. Golf-course development has important implications for conservation science, but there have been few

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Authors' address: Institute for Integrative Bird Behavior Studies, Department of Biology, College of William and Mary, Williamsburg, VA 23187-8795, USA; e-mail for Swaddle: jpswad@wm.edu.

data to fuel the acrimonious debate over whether golf courses are boon or bane for birds (Gange and Lindsay 2002). The few studies investigating the effects of North American golf courses on bird populations have indicated that some courses can support abundant bird communities, but these may have lower diversity (Terman 1997) and are comprised mostly of widespread, suburban-adaptable species (Blair 1996) and so do not include many species of conservation concern.

> We cannot yet explain why golf-course nestlings were more symmetrical, but we can conclude that 1) pesticides used on these courses did not impose a significant stress on bluebirds..., or 2) bluebirds are avoiding exposure to these pesticides, or 3) golf-course nestboxes are high-quality bluebird habitats for other reasons that outweigh any effects of pesticides....

It is becoming increasingly clear that avian conservation studies must move beyond quantifying species abundance and diversity to also include analyses of life history and fitness metrics (Ruth et al. 2003, Williams 2003). To more fully understand the impact of golf courses on avian conservation, we need to start quantifying individual and population fitness parameters in addition to continuing studies on avian abundance and diversity. Currently, little is known about the relative fitness of any bird species breeding on golf courses versus other human-altered sites. Without such information, managers cannot answer even the most basic questions about the potential role of golf courses in regional conservation planning. For example, it matters greatly whether golf courses are population sources or sinks for species of conservation concern and for their competitors. In this study we focused on breeding performance and life-history traits of eastern bluebirds (*Sialia sialis*) nesting in artificial cavities on golf courses and compared them to bluebirds nesting in artificial cavities on nongolf sites.

The major objective of our study was to compare reproductive success, life-history traits such as clutch size, and developmental instability of eastern bluebird nestlings (see below) being reared in nestboxes on golf-course habitats compared with those developing in nestboxes in other structurally similar habitats (hereafter nongolf sites) that share high levels of human disturbance and development but not the extensive use of pesticides typical of golf courses (Cox 1991).

As a first attempt to explain any differences in nutritional status of nestlings detected between boxes on golf and nongolf sites, we also compared food delivery rates during the nestling period. Our specific hypothesis was that nestling birds growing in nestboxes on golf-course habitats would experience relatively greater developmental stress compared with nongolf nestlings. Therefore, golf nestlings should show greater fluctuating asymmetry (see below) and lower body condition. In addition, we hypothesized that the same factors that caused developmental stress for young birds would cause adult bluebirds associated with nestboxes on golf-course habitats to initiate clutches later, lay smaller clutches, have lower hatching success, and overall experience lower productivity than birds associated with nestboxes on nongolf sites.

Eastern bluebirds are sexually dichromatic, monogamous birds and secondary cavity nesters (i.e., they do not excavate their own cavities). Bluebirds are largely insectivorous during the breeding season, most often gleaning insects directly from the ground (Gowaty and Plissner 1998). Bluebirds often are abundant on golf courses and breed readily, especially when provided with artificial nest cavities (Blair 1996, Terman 1997). The website and educational materials of the North American Bluebird Society, established to ensure the conservation of this once-declining species, recommend golf courses as suitable locations for trails of nestboxes. In many ways golf courses appear to provide habitat ideal for bluebirds: open woodlands, edge habitat, and short grass with plenty of perching sites from which birds can locate prey.

One method of assessing the response of populations to environmental conditions is to assess developmental instability during growth (Møller and Swaddle 1997). Developmental instability is the variation that results from a genotype developing in a particular environment. The greater the instability, the greater the morphological variation for a particular genotype. Developmental instability can provide an indication of how well a genotype is suited to its developmental environment. Therefore, there are some environments in which the genotype produces its intended phenotype with a high degree of probability and other environments in which development is more noisy and the intended phenotype is produced with lower probability (Parsons 1992, Clarke 1993, Graham et al. 1993). The most common method for estimating developmental instability is measurement of fluctuating asymmetry (Ludwig 1932, Zakharov 1981). Fluctuating asymmetry is the small deviation from symmetry that occurs during the development of bilaterally symmetric traits. As both sides (i.e. left and right) are coded by the same genotype and are developing in the same environment, the difference between the sides estimates developmental instability (Møller and Swaddle 1997).

Most field measurements of fluctuating asymmetry (FA) are likely to be largely determined by environmental rather then genetic variation (Fuller and Houle 2002), and FA has been proposed as a sensitive bioassay for monitoring the suitability of environmental conditions (Parsons 1992, Clarke 1993, Graham et al. 1993). Fluctuating asymmetry has been used as a bioassay of the environment with mixed success (Møller and Swaddle 1997, Leung et al. 2000); however, some field sampling of populations has been confounded with the possibility that asymmetric individuals are being removed from the population at early stages by natural selection and researchers are studying a biased sample of the more symmetric individuals (Møller 1997). We have attempted to minimize this important confounding selection mechanism by studying the asymmetry of full-grown left and right tarsus (foot bone) of nestling birds approximately 4 days before they fledge from the nest (i.e., presumably before juvenile mortality affects the demographics of our study populations).

Previous studies indicated that chemical pollution, which might result from pesticide use on golf courses, can affect fluctuating asymmetry of developing characters in many species (Møller and Swaddle 1997, Leung et al. 2000) including birds (Evers et al. 1999, Eeva et al. 2000, Bustnes et al. 2002), but few studies have examined the bluebird genus. One empirical study indicated that lead pollution may not affect fluctuating asymmetry of primary feather length in nestling western bluebirds (*Sialia mexicana*) (Fair and Myers 2002). However, the primary feathers had not finished growing in that study, and asymmetry can change dramatically during the late stages of feather growth (Swaddle and Witter 1997).

Methods

Study area

During the 2003 breeding season (1 April–30 August), we monitored breeding success, morphology, and behavior of eastern bluebirds occupying 199 nestboxes on 9 golf courses and 211 nestboxes at 10 sites with structurally similar habitat at which there was some human traffic, some residential or commercial development, predominant woodland edge, but no known use of pesticides. We verbally confirmed with land managers that pesticides were not used at our off-course sites, and pesticides were observed to be regularly applied at all the golf courses. The nongolf sites were a state park (York River), a Frisbee-disc golf course at a city park (Newport News), the expansive campus of a hospital (Eastern State), 2 portions of a wooded college campus (William and Mary), a public cemetery (Cedar Grove), the undeveloped portions of 2 county recreational facilities (James City–Williamsburg Community Center and District Park), a horse pasture, and a dairy farm. All sites were located on average (± SD) 11.87±6.95 km from a point in York County, Virginia (latitude: $37^{o}17'24''$, longitude: $76^{o}42'25''$). One hundred of the 211 nongolf nestboxes were erected in January 2003 and were classified as new boxes. All other golf and nongolf nestboxes had been in their specific locations for at least a year and were classified as old boxes in our statistical analyses. Hence, new boxes offered nesting sites at new locations, whereas old boxes had offered a nest site in the year prior to our study.

Nestling traits: tarsus asymmetry and body condition

Approximately 4 days before fledging, we weighed each chick (to 0.1 g on an electronic balance) and banded it with a United States Geological Survey metal alloy band. We took a series of uncompressed digital photographs of each nestling's legs and right wing with a Nikon Coolpix 5700 camera (Nikon Corporation, Tokyo, Japan) at a resolution of 2,560 by 1,920 pixels, with the camera mounted on a copy stand so the lens was at right angles to the bird when the bird was held flat against the base of the stand. We fixed graph paper to the base of the copy stand so the paper appeared in every photograph and the digital images could be calibrated. We took 3 photographs of the left tarsus, 3 of the right tarsus, and 1 of the spread right wing. The tarsi were held in a standard position (Figure 1).

From the photographs we measured the distance between the proximal end of the tarsus and the tip of the second scale (counting from proximal to distal) at the distal end of the tarsus (Figure 1). Measurements were taken blind with regard to whether birds originated from a golf course. We performed all measurements in Adobe Photoshop 6.0, and we measured each picture once, resulting in 3 repeat measurements of the left and right tarsus of every bird.

We measured the length of the feather vane that had emerged from the sheath of the still-growing sixth primary feather using the digital image of the right wing. We combined this measure with our measurements of body mass and tarsus length to render an index of body condition. First, we regressed emerged primary length on tarsus length and stored the residuals as a size-standardized index of stage of nestling development. Next,

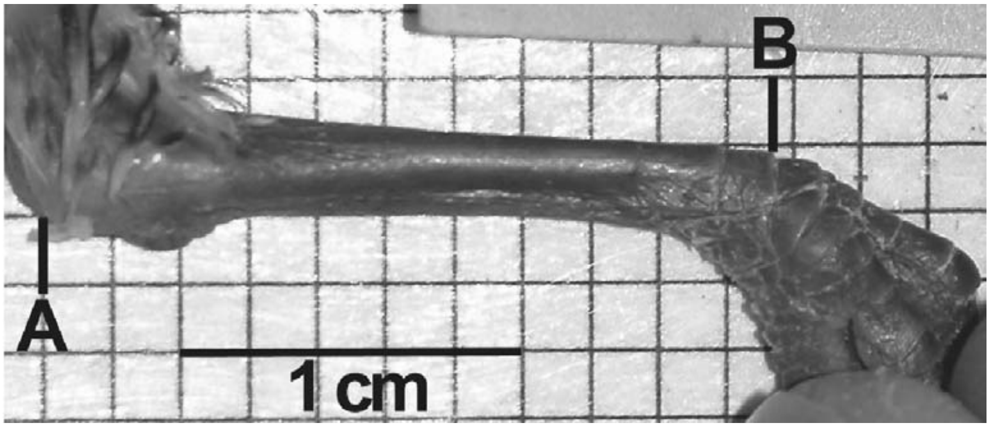

Figure 1. Example digital photograph of nestling eastern bluebird tarsus indicating the 2 points we measured to determine length (between A and B). Photographs were taken during the 2003 breeding season on sites in eastern Virginia.

we took those residuals and regressed them against body mass to store a further residual value that was an indication of excess body mass given the size and stage of development of the bird (i.e., body condition). A greater residual body condition indicates a greater mass for a given size and stage of development.

Adult traits: reproductive success and productivity

Approximately once per week we checked every nestbox. We used the following standard scale to describe nestbox contents: 0=empty; 1=incomplete nest; 2=complete nest; 3=eggs present; 4=hatching day; 5=nestlings 2–4 days old (skin bluish); 6=nestlings 5–6 days old (eyes still closed, feathers in sheaths); 7=nestlings 7–10 days old (eyes open, feathers bursting out of sheaths); 8= nestlings 11–13 days old (based on degree of primary feathers eruption); and 9=nestlings 14+ days old; 10= nest no longer active. In addition, on every visit we recorded number of eggs and nestlings present. We defined clutch size as the greatest number of eggs observed in the nest during a nesting attempt, and we defined clutch initiation date as the date when the first egg was laid. In a similar manner, we defined number of nestlings as the greatest number of nestlings observed in the nest at any one time. We defined number of fledglings as the number of nestlings observed in the nest after day 10 minus any dead nestlings found after fledging. To reduce errors in our laying date statistics, we restricted our analyses to nests in which we could estimate the clutch initiation date to within a 5-day period. Unless otherwise noted, we analyzed the influence of laying date for only the first clutch in a box (i.e., those initiated before arbitrary cut-off of 1 June).

Many studies of avian reproductive success report nest success as the simple proportion of successful nests out of all nests detected. Mayfield (1975) pointed out that this "apparent estimator" method overestimates success rates because nests that fail, especially those that fail quickly, are less likely to be included in the sample. Mayfield (1975) proposed correcting for this upward bias by calculating nest survival rates for each day that each nest was exposed to the possibility of failure, but in practice the Mayfield Method has been interpreted in numerous ways. We calculated Mayfield survival estimates for nests on and off golf courses and compared them using a *Z*-statistic as described by Hensler and Nichols (1981). We followed the recommendations of Manolis et al. (2000) for reducing bias by 1) including all nests with uncertain fates, and 2) classifying the last exposure day as a) the last day active for nests with uncertain fates and b) the midpoint of the last day active and the first day inactive for nests with known fates.

To accurately determine whether nestboxes on golf courses contributed to population sources or sinks requires more than 1 year's data, including difficult-to-obtain juvenile survivorship estimates. Despite the shortcomings of our dataset for this task, we deemed it worthwhile to make an attempt. Based on our observations and the literature, we assumed that all females renested after the first attempt, even if it was a success, and that the maximum number of successes or failures for a typical female was 2(Go[illegible]y and Plissner 1998). We obtained an estimate of adult female survivorship from a long-term study on this species in nearby South Carolina (0.382) (Gowaty and Plissner 1998). In the absence of any published estimates for juveniles of any species of bluebird, we opted to make no assumption about this. Instead, we determined how low juvenile survivorship could be for golf courses to still qualify as source habitat. We pooled data from all golf-course nestboxes and classified them as a source if (1–adult survivorship) / (juvenile survivorship)<mean number of female offspring produced by each adult female in 2003(Do[illegible]an et al. 1995).

Some of our nestboxes were occupied by tree swallows (*Tachycineta bicolor*), tufted titmice (*Baeolophus bicolor*), Carolina chickadees (*Poecile carolinensis*), house and Carolina wrens (*Troglodytes aedon* and *Thryothorus ludovicianus*), white-breasted and brown-headed nuthatches (*Sitta carolinensis* and *S. pusilla*), or house sparrows (*Passer domesticus*). However, here we only present eastern bluebird data and have excluded from analyses boxes that were exclusively occupied by other species.

Food delivery by adults

We collected information about adult feeding visits to the nest during the chick-rearing period. We sampled 20 pairs of nests where one member of each pair was on golf course habitat and the other was not. We matched pairs for chick age on observation day (mean±SD difference: 1.1±1.1 day; range 0–3 days), time of day observed (mean±SD difference: 84.5±53.9 min; range 3–178 min), and date observed (mean±SD difference=9.8±7.8 days; range: 0–31 days). To reduce variance, we did not carry out observations during rain or high wind. A lone observer seated approximately 40 m from the nest began recording food deliveries after the first observed delivery and terminated 60 minutes later. Number and age of chicks was confirmed by opening the nestbox after the observation session had terminated.

Statistical analyses

We performed all statistical analyses with SPSS 11.5 for Windows using 2-tailed tests of probability. As siblings within a nest are not independent data points, we averaged morphology and condition data across siblings to give 1 data point per nest. We also Box-Cox transformed signed absolute mean asymmetry to fit a normal distribution (Shapiro-Wilk $S=0.982$, df=85, $P=0.270$) so we could use more powerful parametric analyses in our statistical hypothesis testing (Swaddle et al. 1994). We used parametric analyses throughout and tested to make sure that assumptions of normality and homogeneity of variance were met in all tests. Means are presented± standard deviation, unless otherwise noted. In most analyses we used nestbox as the statistical unit of replication as we were interested in whether nestboxes on our nongolf sites did better in general than nestboxes on golf-course habitat. Our data and interpretations are limited to these particular localities.

Results

Exploratory analysis of asymmetry data

A normal (or leptokurtic) distribution centered on zero asymmetry is typical of a trait showing fluctuating asymmetry. The distribution of signed tarsus asymmetries (L–R) was normal with some degree of leptokurtosis (Shapiro-Wilk test against a null hypothesis of normality, $S=0.992$, df=318, $P=0.069$; leptokurtosis±standard error =0.574±0.137; skewness±standard error=–0.078±0.137) centered around a mean of zero (one-sample *t*-test, $t_{317}=1.363$, $P=0.174$).

Over the 3 repeat measures of the left and right tarsi, the differences in asymmetry among individuals was significantly greater than measurement error within individuals ($F_{317,\,1268}=28.88$, $P<0.0001$). Therefore, we averaged asymmetry measures across the 3 repeats and were confident that tarsus asymmetry measures were not significantly influenced by measurement error. Tarsus asymmetry was not related to tarsus size (Pearson $r=0.099$, $N=318$, $P=0.077$); therefore, we used absolute measures of asymmetry in all analyses.

Measures of fluctuating asymmetry are known to vary with stage of development, and it is important to be sure growth has finished to give accurate asymmetry estimates (Swaddle and Witter 1997, Kellner and Alford 2003). Reassuringly, tarsus length was not related to emerged primary feather length (Pearson $r_{311}=0.080$, $P=0.157$). As emerged primary feather length indicated stage of development, a lack of variation of tarsus length with emerged feather length indicates that tarsi had finished growing by the time we measured birds' legs. In addition, nestling tarsus length was not different from tarsus length of a sample of 12 adult females that we measured during the breeding season (2-sample *t*-test $t_{329}=0.411$, $P=0.682$), strongly suggesting that nestling tarsi had reached full adult length.

Nestling asymmetry and condition

Broods of eastern bluebirds developing in nestboxes on golf-course habitat were significantly less asymmetric than broods developing in boxes at nongolf sites (ANCOVA of mean brood tarsus asymmetry by golf and nongolf sites controlling for age of nestbox, laying date and clutch size, $F_{1,80}=21.41$, $P<0.001$; Figure 2*a*). This pattern does not support our hypothesis that nestboxes on golf-course habitats provided poor chick-rearing habitat and represents a strong relationship between nestbox location and tarsus asymmetry.

To eliminate any possibility of biasing the sample against nestlings that died due to selective events, this analysis can be restricted to the much smaller sample of nests in which all eggs survived to fledging ($N_{\text{golf}}=10$, $N_{\text{nongolf}}=13$), in which case the conclusion weakens but does not change qualitatively (ANCOVA of mean brood tarsus asymmetry by golf and nongolf sites controlling for age of nestbox, laying date, and clutch size, $F_{1,18}=7.56$, $P=0.013$). Another way of looking at whether pre-fledging selective pressure may have favored symmetrical

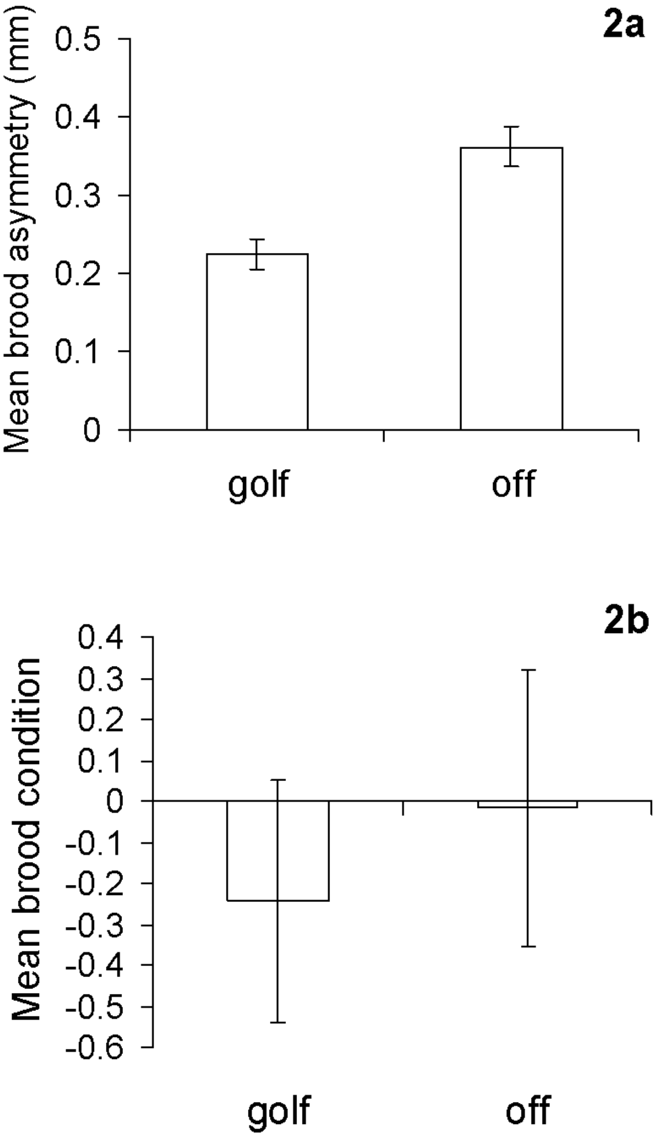

Figure 2. Mean (± standard error) (a) brood fluctuating asymmetry and (b) brood condition for eastern bluebird nests raised on golf courses (golf) and nongolf sites (off) in eastern Virginia during the 2003 breeding season.

individuals is to examine the relationship between proportion of nestlings surviving in a nest and the mean asymmetry of the survivors in that brood. If selection were acting against asymmetrical offspring before we measured the survivors, there would be a positive relationship between proportion of siblings dead and symmetry of survivors. We found such a positive relationship among golf-course nests, but it was absent among nongolf nests (golf: Pearson r_{44}=0.445, P=0.002; nongolf: Pearson r_{39}=–0.129, P=0.42). In contrast to our previous result, this suggests that selection had occurred before we measured tarsi.

There was no difference in mean brood condition when comparing nestboxes on golf-course habitats with nestboxes on nongolf sites (ANCOVA of mean brood condition by golf and nongolf sites controlling for age of nestbox, laying date and clutch size, $F_{1,80}$=0.044, P= 0.835; Figure 2*b*). Mean brood tarsus asymmetry was not significantly related to mean brood condition $F_{1,83}$= 1.82, P=0.182; r^2=0.021).

Although we conservatively controlled for effects of age of nestbox in our analyses, we were concerned that the 100 new nestboxes (all situated on nongolf sites) might have attracted more inexperienced parents (e.g., younger birds) than boxes that had been present in previous years. Therefore, we explored whether nestling tarsus asymmetry and mean brood condition differed between new nestboxes and old boxes. Reassuringly, there were no differences in mean brood condition between boxes of different age (ANCOVA of mean brood condition by age of nestbox controlling for presence on golf and nongolf sites, $F_{1,82}$=0.338, P=0.563; N_{new}=30, N_{old}=55). There also was no difference in mean brood tarsus asymmetry between boxes of different age (ANCOVA of mean brood tarsus asymmetry by age of nestbox controlling for presence on golf and nongolf sites, $F_{1,82}$=1.200, P=0.276; N_{new}=30, N_{old}=55).

Reproductive success and life-history characteristics

As some nestboxes were occupied by other species, a smaller sample of our nestboxes actually was available to breeding bluebirds (N_{golf}=183, N_{nongolf}=162; Table 1). Of the boxes available on golf courses, 26.2% were never occupied, 43.7% contained 1 bluebird nest during the season, 29.5% contained 2 nests, and 0.5% contained 3 nests. Of the nongolf nestboxes, 38.3% were never occupied, 45.7% contained 1 nest, only 14.2% contained 2 nests, and 1.8% contained 3 bluebird nests during the season. Chi-square analysis indicated that golf boxes

Table 1. Summary of Chi-square analysis of number of nestboxes[a] with 0, 1, 2, and 3 eastern bluebird nests during the 2003 breeding season comparing golf-course (golf) and nongolf (off) sites in eastern Virginia.

Site		0 nests	1 nest	2 nests	3 nests	Total
Golf	Observed	48	80	54	1	183
	Expected[b]	58.35	81.69	40.84	2.12	183
Off	Observed	62	74	23	3	162
	Expected[b]	51.65	72.31	36.16	1.88	162
	χ^2	3.91	0.074	9.03	1.26	14.27
	P	0.048	0.786	0.0027	0.262	0.0026

[a] We excluded nestboxes occupied by other species and therefore not available to bluebirds.

[b] Expected values were calculated assuming that golf-course and nongolf nestboxes are equally likely to be inhabited by bluebirds.

were less likely to be unoccupied and more likely to contain 2 bluebird nests than nongolf boxes (see Table 1). In addition, golf boxes were more likely to contain active bluebird nests than nongolf nestboxes, but this comparison does not take into account any differences in nestbox density or other structural differences between habitats. Initial analysis of nestbox densities (calculated from GPS coordinates as sum of squared linear distances among nestboxes averaged for each site) indicated there was not a systematic difference in nestbox density between golf and nongolf sites (pooling data from adjacent sites, t_6= 0.81, P=0.451).

The Mayfield survival probability, the chance of a nest surviving the entire period from laying through fledging with at least one chick still alive, did not differ between golf and nongolf nestboxes (Table 2). Nests on golf courses had a significantly lower probability of surviving the brief laying period (approximately 6% lower), but there was no difference during incubation or the nestling period (Table 2). Because our study population nested in easily located artificial cavities and was checked regularly, the apparent estimator method provided a close approximation to the Mayfield Method (golf: 112 successes/191 nests=0.586; nongolf: 80 successes/123 nests =0.650). Across the entire season, 67.4% of the 752 eggs laid in nests on golf-course habitat hatched, as opposed to 70.2% of the 508 nongolf eggs. Of these, 74.6% of 507 nestlings from boxes on golf-course habitat fledged, whereas 80.4% of 287 nestlings from nongolf boxes fledged. These comparisons suggest that over the entire breeding season there was no difference of biological significance in the overall reproductive success of bluebird nests in boxes on golf and nongolf sites.

We wished to control for 2 confounding nestbox variables that differed between the nestboxes on golf and nongolf sites. First, age of nestbox varied among sites (as noted above). Second, fewer boxes on golf courses had anti-predator guards (golf course: 40.5% guarded; nongolf: 79.6% guarded). Both of these factors are likely

Table 2. Mayfield survival probabilities (± standard deviation) and Z-statistics and probabilities for eastern bluebird nests on golf courses (golf) and nongolf (off) sites in eastern Virginia during the 2003 breeding season.

	Period (length)			
Sites	A: laying (4 days)	B: incubation (12 days)	C: nestling (15 days)	D: overall[a] (31 days)
Golf	0.918 ± 0.005	0.767 ± 0.003	0.839 ± 0.003	0.591 ± 0.002
Off	0.977 ± 0.003	0.805 ± 0.004	0.831 ± 0.003	0.653 ± 0.002
Z	2.45	0.82	0.19	1.38
P	0.014	NS	NS	NS

[a] D =A*B*C.

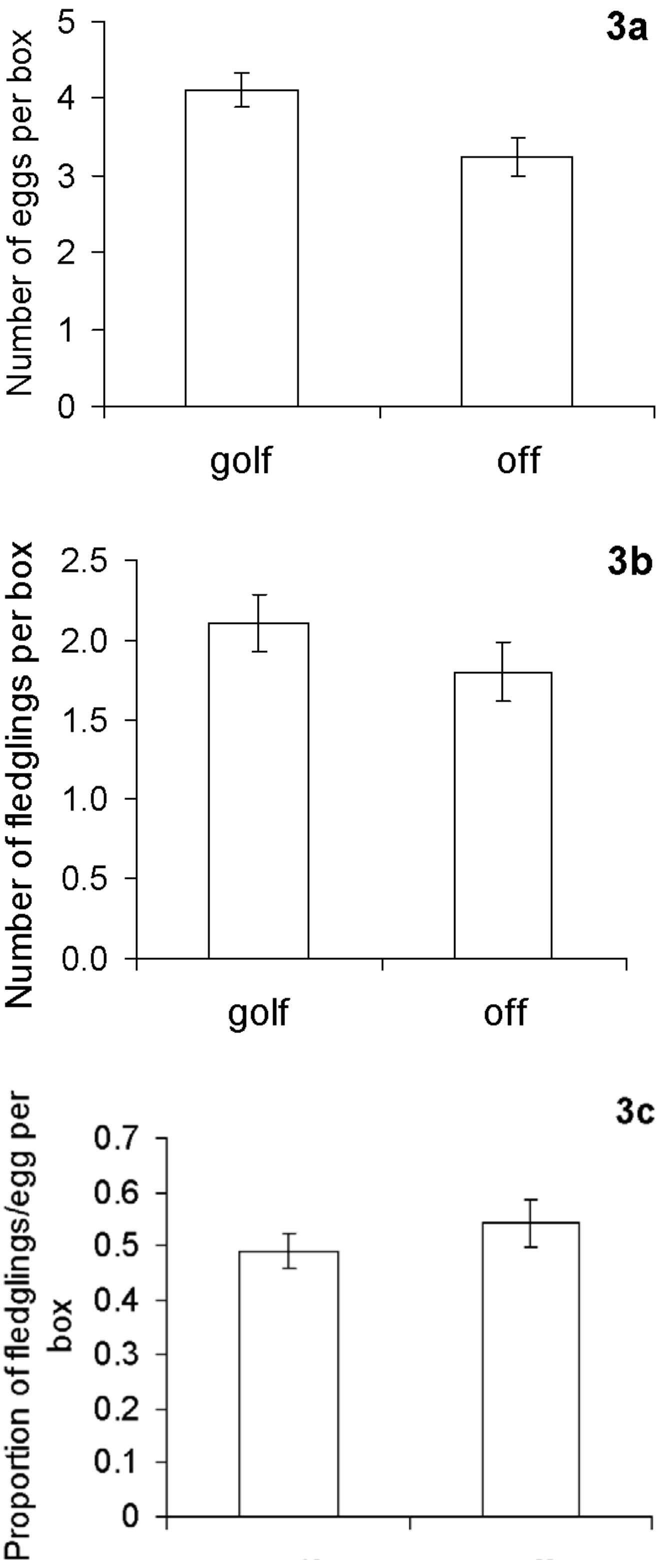

Figure 3. Mean (± standard error) nestbox productivity data of eastern bluebirds comparing golf courses (golf) and nongolf sites (off) in eastern Virginia during the 2003 breeding season. (a) Number of eastern bluebird eggs per nestbox; (b) number of eastern bluebird fledglings per nestbox; and (c) proportion eastern bluebird fledging/egg per nestbox.

to affect nestbox productivity; therefore, we controlled for these effects in analyses of covariance in all the productivity analyses below.

Number of bluebird eggs laid per box (which included multiple clutches for some nestboxes) was greater for nestboxes in golf-course habitat than on nongolf sites (ANCOVA, $F_{1,332}=12.78$, $P<0.001$; Figure 3*a*). Likewise, number of young birds successfully fledged per box was greater for nestboxes on golf sites than nongolf sites (ANCOVA, $F_{1,332}=7.64$, $P=0.006$; Figure 3*b*). However, the proportion of successful fledglings per egg laid in a nestbox did not differ between nestboxes on golf and nongolf sites (ANCOVA, $F_{1,223}=1.24$, $P=0.725$; Figure 3*c*).

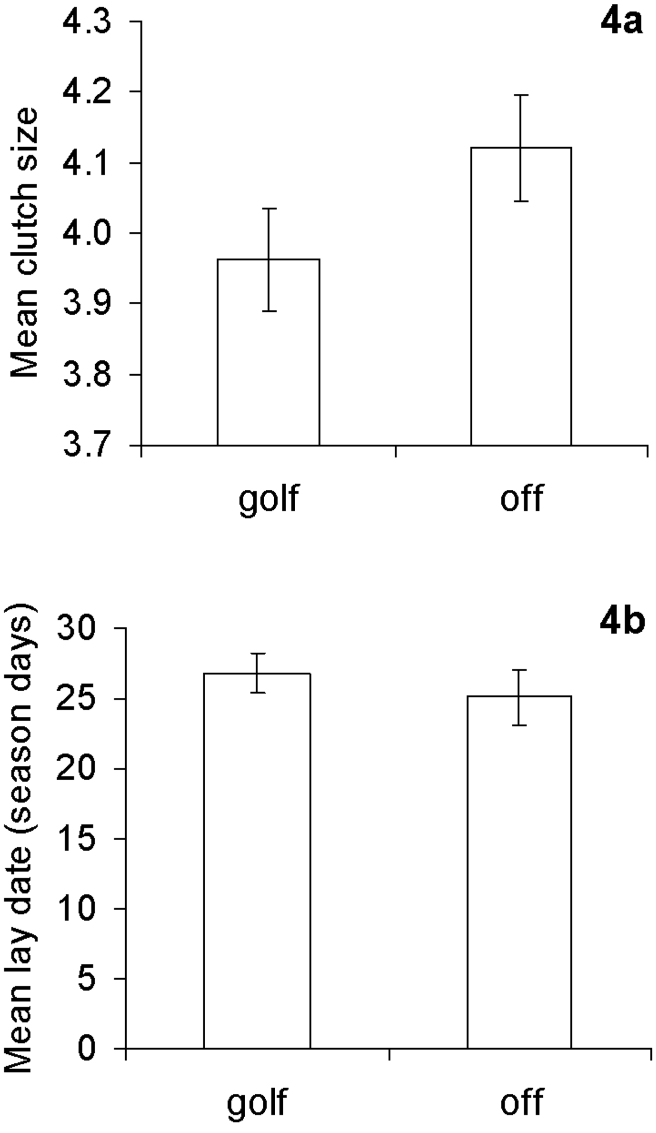

Figure 4. Mean (± standard error) (a) clutch size and (b) laying date (days since first egg was laid on 6 April 2003) of eastern bluebird first clutches on golf courses (golf) and nongolf sites (off) in eastern Virginia during the 2003 breeding season.

There was no difference in size of first clutch for nestboxes in golf-course habitats versus those at nongolf sites (ANCOVA controlling for age of nestbox and presence of predator guard, $F_{1,306}=0.457$, $P=0.500$; Figure 4*a*). In addition, clutch size (pooling across all sites) was not related to mean brood condition ($F_{1,83}=1.02$, $P=0.317$) or mean brood tarsus asymmetry ($F_{1,83}=0.225$, $P=0.636$).

There was no difference in laying date of first clutches in nestboxes on golf versus nongolf sites (ANCOVA controlling for age of nestbox and presence of predator guard, $F_{1,\ 133}=0.011$, $P=0.915$; Figure 4*b*). Laying date (of first clutches) was negatively related to mean brood condition ($F_{1,83}=3.806$, $P=0.054$; $r^2=0.044$; laying date $=23.45–1.203*$mean brood condition), indicating that later broods were in poorer body condition. Also, laying date (of first clutches) was negatively related to (Box-Cox transformed) mean brood tarsus asymmetry ($F_{1,83}=5.538$, $P=0.021$; $r^2=0.063$; laying date$=40.38–24.74*$ mean brood asymmetry), indicating that later broods were more symmetric. Laying date (of all clutches) was not related to clutch size ($F_{1,\ 136}=2.347$, $P=0.128$).

Adult feeding rate

We compared number of food deliveries per chick between nestboxes on golf and nongolf sites using a paired *t*-test where nests were matched for chick age, date, and time of day. There was no difference in the mean rate of food delivery per chick for birds nesting on or off golf courses (golf: 3.74±1.68 deliveries per hour; nongolf: 3.56±2.03 deliveries per hour; paired $t_{19}=0.36$, $P=0.72$).

Are golf courses population sources or sinks?

We asked whether 100 hypothetical adult females on golf-course habitat would produce enough surviving female offspring to replace themselves during their lifetimes. If so, golf-course habitat in this region can be considered a source of bluebirds into the larger metapopulation. Golf-course bluebirds produced on average 1.69 fledglings per successful nest, and their nests had a success rate of 0.586. Using the method of Donovan et al. (1995) and the assumptions outlined above, we calculated that these hypothetical females would have fledged 222 female offspring. Given this level of productivity, as long as juvenile survivorship was above 0.28 (i.e., 28% of fledged females survive to breed), golf-course habitat would serve as a population source. Thus, given the previous assumptions, golf courses may be exporting birds to other types of habitat or the regional bluebird population is growing.

Discussion

Contrary to our predictions, breeding demographic, productivity, and developmental instability metrics indicated that both adult and nestling eastern bluebirds do no worse occupying nestboxes on golf courses than occupying nestboxes at nongolf sites with structurally similar habitat (parks, campuses, livestock pastures, and recreational facilities). However, we analyzed data from only a single breeding season. Surprisingly, nestboxes on golf-course habitats received 28% more eggs and fledged 17% more young than those off golf-course habitat. Our data come from a single season in which there was an abundance of unseasonably cool weather and above-average rainfall. Accordingly, our hatching rates (67–70%), fledging rates (75–80%), and overall nest success (59-–65%) were at the low end of or below published estimates for this species (hatching: 83%, fledging: 75–90%, overall: 55–84%)(Gowaty and Plissner 1998).

Although bluebirds laid 28% more eggs and fledged 17% more young per nestbox on golf-course habitats, survivorship of individual nests was not significantly different between nestboxes on golf and nongolf sites. In fact, rates of failure of nests during laying and incubation tended to be higher for nestboxes on golf-course habitat. Because nestboxes were partially or wholly protected from predators, our study could have missed a difference in predation pressure between golf-course and nongolf sites and thus may not be generalizable to species that nest in vulnerable microhabitat, such as ground-nesting Neotropical migrants. Also, we collected data from only one breeding season, which may not be representative of other years.

Our fluctuating asymmetry analyses indicated that fledglings developing in nestboxes on golf courses were more symmetric. If nestling mortality was higher on golf courses, our asymmetry differences could have been due in part to developmental selection (i.e., selection against asymmetric individuals [Møller 1997]) where the most stressed nestlings die, leaving only the most symmetric individuals to be measured at fledging. In nestboxes on the nongolf sites developmental selection may be weaker and mean nest asymmetry therefore greater at the fledgling stage. This has been shown to occur in response to pesticide effects in fish (Allenbach et al. 1999; i.e., in situations of high pesticide concentrations only the most symmetric individuals survive). We attempted to minimize developmental selection effects in our study design by assessing asymmetry of nestlings as opposed to juveniles or adults. However, the Mayfield survival estimate for the laying and incubation stages suggested that there could have been subtle differences in mortality rates of unhatched young. Our finding that golf-course nestlings were more symmetric even when including only those nests in which all eggs survived to fledge suggested that the higher symmetry of golf-course nestlings was not the result of selection against asymmetrical siblings. In contrast, the significant correlation between proportion of dead siblings and symmetry suggested the opposite. The fact that this relationship did not occur among nongolf nests further strengthens the argument that the difference in fluctuating asymmetry between golf-course and nongolf bluebirds was the result of stronger selection against asymmetric young on golf courses. Whether such selection occurred and what factors might mediate it remains to be determined. In summary, nestboxes on golf-course habitat may have provided better-quality rearing environments than nongolf sites, resulting in better developmental conditions, or they may have provided a worse environment that eliminated less symmetrical offspring at an early stage. In either case the end result was not detrimental to bluebird reproductive success, as nestboxes on golf-course habitats produced a greater number of, and more symmetrical, fledglings. Other metrics, such as fledgling condition, adult food delivery rates, and nest survivorship, gave us no reason to conclude that nestboxes on golf-course habitat were a less suitable environment than nestboxes on other disturbed habitats that lack intensive pesticide use.

We originally predicted that birds developing in nestboxes on golf-course habitats would experience greater developmental stress and that reproductive success would be reduced by the pesticides associated with course maintenance. Such a pattern would be consistent with most other studies of chemical stress in birds (e.g., Evers et al. 1999, Eeva et al. 2000, Bustnes et al. 2002). In addition, there were other possible reasons to predict that nestling birds would have greater asymmetries when developing in nestboxes on golf courses. For example, increased habitat fragmentation has been associated with increased fluctuating asymmetry in several passerines (Anciaes and Marini 2000), and poor nutrient condition of nestling diets increases asymmetry (Ohlsson and Smith 2001, Grieco 2003). If golf courses provide contaminated nesting sites with poor availability of insects and high habitat fragmentation, we would have expected nestlings on golf courses to show greater asymmetry than nestlings developing on our nongolf sites and reproductive success to be lower. We cannot yet explain why golf-course nestlings were more symmetrical, but we can conclude that 1) pesticides used on these courses did not impose a significant stress on bluebirds (Rainwater et al. 1995), or 2) bluebirds are avoiding exposure to these pesticides, or 3) golf-course nestboxes are high-quality bluebird habitats for other reasons that outweigh any effects of pesticides (e.g., greater food availability, less competition with other cavity-nesting species).

We did not find any evidence that adult bluebirds breeding in nestboxes on golf courses either initiated their nests significantly later in the season or laid smaller clutches. As with many of our other results, these data are consistent with the view that our golf-course nestboxes are not providing significantly lower-quality breeding habitats than the nongolf boxes. In addition, it has been suggested previously that golf courses provide habitat for floating individuals that are unable to secure territories on preferred nongolf sites (Terman 1997). If this were true, we would have expected territory establishment and breeding to be delayed on golf courses. We did not find evidence of delayed breeding; therefore, our data do not support the "floater" scenario.

Our observation that bluebirds on golf-course habitats were highly productive suggests that golf courses with nestboxes could be population sources for this species. Populations on golf-course habitat are capable of exporting excess individuals to other sites of lower quality and playing an important role in bluebird metapopulation dynamics. This is good news for the once-declining eastern bluebird but does not necessarily translate to a positive assessment of the importance of golf courses to bird species of conservation concern. Eastern bluebirds on golf courses nest almost exclusively in human-provided nestboxes and favor the most human-impacted parts of courses (the fairways as opposed to relict native vegetation communities). Therefore, our findings are important in demonstrating that high reproductive success is possible for at least one bird species on golf-course habitat, but it remains to be seen whether this generalizes to species less adaptable to human disturbance. Data from other species that use our nestboxes but forage exclusively in the wooded portions of golf courses will be instructive, but future studies also should focus on species nesting outside of predator-protected nestboxes.

There are additional limitations of our study that need to be emphasized. It is possible that the unusually wet year in which we conducted this study disrupted normal patterns of pesticide application and bioaccumulation. Heavy rainfall may have led to increased run-off and dilution of topically applied pesticides. We intend to continue our field study in future years to investigate whether the findings of this 1-year study are repeatable. Also, we were not able to collect direct information on pesticide concentrations, for financial reasons. Therefore, we recommend that future investigations of the effects of golf courses on avian ecology include quantification of pesticide levels. We know that pesticides are used at every golf course in this study and pesticides were not used at the nongolf sites, but we cannot make a direct link between our data and any particular quantity of pesticide use or accumulation.

It generally is assumed that golf courses do not provide suitable habitat for many bird species (discussion in Terman 1997). This assessment does not apply equally to all species. Our data indicated that eastern bluebirds were productive in nestboxes on golf-course habitats and may actually fledge offspring of higher phenotypic quality (i.e., they are more symmetric), although our data were limited to a 1-year study. The increased productivity appears to be driven by a relative increase in number of active nests per nestbox on golf courses. Specifically, golf-course boxes were less likely to be unoccupied and more likely to contain 2 active clutches per season than nongolf nestboxes. Although nestboxes on golf-course habitat attracted high numbers of breeding bluebirds and these adults produced a relatively larger number of high-phenotypic-quality birds (compared with boxes on nongolf sites), egg mortality was marginally higher in those nestboxes but not significantly so. Our data indicated that nestboxes on golf-course habitats in our region can provide suitable habitat for bluebirds, at least for the year in which we conducted this study. Further study will be necessary to determine whether this is true for any other species and whether this pattern for eastern bluebirds is repeatable in future years.

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Joshua E. LeClerc (third from left) recently completed an M.A. degree in the Department of Biology at the College of William and Mary, where he also completed his undergraduate studies. His primary graduate research was on whether golf courses provide habitat for bird species of conservation concern. ***Judy P. K. Che*** (far left) recently graduated with an undergraduate degree in biology at the College of William and Mary, where she also has done research on sexual selection in European starlings. She recently started her doctoral studies in a Ph.D. program at the University of Maryland. ***John P. Swaddle*** (far right) is an associate professor in the Biology Department at the College of William and Mary. He earned his B.Sc. in a double major of psychology and zoology and his Ph.D. in zoology from the University of Bristol, U.K. His research interests include developmental stability, sexual selection, avian molt, flight mechanics, and the behavioral ecology of birds. ***Daniel A. Cristol*** (second from left) is an associate professor in the Biology Department at the College of William and Mary. He earned his B.S. in natural resources at Cornell University and his Ph.D. in biology from Indiana University. His research interests include the role of memory in migration, evolution of foraging techniques, and conservation of birds on human-impacted habitats.

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