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Author(s) : Kerri L. Cornell, Caitlin R. Kight, Ryan B. Burdge, Alex R. Gunderson, Joanna K. Hubbard, Allyson K. Jackson, Joshua E. LeClerc, Marie L. Pitts, John P. Swaddle and Daniel A. Cristol

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REPRODUCTIVE SUCCESS OF EASTERN BLUEBIRDS (*SIALA SIALIS*) ON SUBURBAN GOLF COURSES

KERRI L. CORNELL,¹ CAITLIN R. KIGHT, RYAN B. BURDGE, ALEX R. GUNDERSON,
JOANNA K. HUBBARD, ALLYSON K. JACKSON, JOSHUA E. LECLERC, MARIE L. PITTS,
JOHN P. SWADDLE, AND DANIEL A. CRISTOL

Institute for Integrative Bird Behavior Studies, Department of Biology, College of William and Mary, Williamsburg, Virginia 23187, USA

ABSTRACT.—Understanding the role of green space in urban–suburban landscapes is becoming critical for bird conservation because of rampant habitat loss and conversion. Although not natural habitat, golf courses could play a role in bird conservation if they support breeding populations of some native species, yet scientists remain skeptical. In 2003–2009, we measured reproduction of Eastern Bluebirds (*Siala sialis*) in Virginia on golf courses and surrounding reference habitats, of the type that would have been present had golf courses not been developed on these sites (e.g., recreational parks, cemeteries, agriculture land, and college campus). We monitored >650 nest boxes and 2,255 nest attempts ($n = 1,363$ golf course, $n = 892$ reference site). We used an information-theoretic modeling approach to evaluate whether conditions on golf courses affected timing of breeding, investment, or nest productivity compared with nearby reference sites. We found that Eastern Bluebirds breeding on golf courses reproduced as well as those breeding in other disturbed habitats. Habitat type had no effect on initial reproductive investment, including date of clutch initiation or clutch size ($\bar{x} = 4$ eggs). During incubation and hatching, eggs in nests on golf courses had higher hatching rates (80%) and brood sizes ($\bar{x} = 4.0$ nestlings brood⁻¹) than nests on reference sites (75% hatching rate; $\bar{x} = 3.8$ nestlings brood⁻¹). Mortality of older nestlings was also lower on golf courses and, on average, golf course nests produced 0.3 more fledglings than nests on reference sites. Thus, within a matrix of human-dominated habitats, golf courses may support productive populations of some avian species that can tolerate moderate levels of disturbance, like Eastern Bluebirds. *Received 2 August 2010, accepted 20 April 2011.*

Key words: bird conservation, Eastern Bluebird, golf courses, habitat value, reproductive success, *Sialia sialis*.

Éxito Reproductivo de *Sialia sialis* en Campos de Golf Suburbanos

RESUMEN.—Comprender el papel del espacio verde en paisajes urbanos–suburbanos se está haciendo crítico para la conservación de las aves debido a la marcada pérdida y conversión de hábitats. Aunque no son hábitats naturales, los campos de golf podrían desempeñar un papel en la conservación de las aves si éstos sostienen poblaciones reproductoras de algunas especies nativas, pero los científicos son aún escépticos al respecto. En 2003–2009, medimos la reproducción de *Siala sialis* en campos de golf en Virginia y en ambientes circundantes de referencia correspondientes al tipo de hábitat que habría estado presente si no se hubieran desarrollado los campos de golf en esos sitios (e.g., parques recreacionales, cementerios, áreas agrícolas, campus universitario). Monitoreamos más de 650 cajas de anidación y 2255 intentos de anidación ($n = 1363$ en campos de golf, $n = 892$ en sitios de referencia). Empleamos un enfoque de modelamiento basado en teoría de la información para evaluar si las condiciones de los campos de golf afectaban el momento en que tenía lugar la reproducción, la inversión reproductiva o la productividad de los nidos en comparación con sitios de referencia cercanos. Encontramos que los individuos que se reproducen en los campos de golf lo hacen tan bien como los que crían en otros ambientes perturbados. El tipo de hábitat no tuvo efecto sobre la inversión reproductiva inicial, incluyendo la fecha de iniciación de nidadas y el tamaño de la puesta ($\bar{x} = 4$ huevos). Durante la incubación y la eclosión, los huevos de los campos de golf presentaron mayores tasas de eclosión (80%) y las parvadas fueron de mayor tamaño ($\bar{x} = 4.0$ pichones por parvada) en comparación con los nidos de sitios de referencia (éxito de eclosión 75%; $\bar{x} = 3.8$ pichones por parvada). La mortalidad de los pichones más viejos también fue menor en los campos de golf y, en promedio, los nidos de campos de golf produjeron 0.3 más volantones que los nidos de los sitios de referencia. Por lo tanto, en una matriz de ambientes dominados por humanos, los campos de golf pueden sostener poblaciones productivas de algunas especies de aves que pueden tolerar niveles moderados de disturbio, como *S. sialis*.

¹Present address: Department of Biology, Westminster College, New Wilmington, Pennsylvania 16172, USA. E-mail: duerrck@westminster.edu

IN A RAPIDLY urbanizing world, wildlife conservation will depend increasingly on a sound understanding of the role of green space in human-dominated landscapes (McKinney 2002, Rutz 2008). Wildlife in urban and suburban areas must contend with loss of native vegetation, exposure to environmental pollutants, changes in resource availability, and novel intra- and interspecific interactions (McDonnell and Pickett 1990, Marzluff et al. 2001). Persistence of a population in human-dominated environments depends on adaptation to these changes (Chace and Walsh 2006). Understanding species' distribution patterns and reproductive success in urban habitats is crucial for determining the conservation value of different elements of the developed landscape.

Within the context of degraded anthropogenic landscapes, open green spaces like golf courses may help mitigate negative effects of development on bird populations (Colding and Folke 2009). For example, Hodgkison et al. (2007) compared assemblages of urban-threatened birds, mammals, reptiles, and frogs of suburban eucalypt-based golf courses with nearby suburban residential habitats in Australia. Some golf courses had high conservation value and supported high densities of regionally threatened vertebrates, but others supported only common urban-adapted species. Golf courses are not natural habitats, and their ability to complement existing habitat types in the urban–suburban matrix by supporting viable wildlife populations remains unclear. Scientists and land managers debate whether golf courses offer a suitable environment for birds because of intensive use of chemicals and high levels of human activity (Pearce 1993, Gange et al. 2003, Cristol and Rodewald 2005, Kight and Swaddle 2007).

There is a growing international literature on community and species responses to golf courses. The approach taken by most researchers has been to compare biotas on golf courses to those in other nearby land uses that would have been present had the golf courses not been built (i.e., reference sites; reviewed in Colding and Folke 2009). Golf courses have been compared to native desert vegetation (Merola-Zwartjes and DeLong 2005), sand dune–grassland habitat (Terman 1997), agriculture (Sorace and Visentin 2007), and urban centers (Yasuda and Koike 2006). Although the outcome of each comparison is affected by the type of reference habitat selected, there has been no effort at standardization (Jackson and Cristol 2010).

Many studies have examined effects of golf courses on avian species diversity and abundance, providing useful information for assessing the ecological importance of these habitats (e.g., Jones et al. 2005, LeClerc et al. 2005, Merola-Zwartjes and DeLong 2005). However, reproduction and survival, which directly affect whether golf courses serve as population sources in a regional metapopulation, may not respond to habitat alteration in the same way as diversity or abundance (Van Horne 1983). Surprisingly few studies have investigated avian reproductive responses to golf course habitats, and these have provided mixed results. Some researchers have reported that golf courses offer lower-quality breeding habitat because of decreased food resources, high disturbance from mowing and golfers, and pesticide use. For example, in a study of a small sample of Burrowing Owls (*Athene cunicularia*) in Washington, Smith et al. (2005) found that individuals nesting on golf courses had lower annual fecundity than those nesting in other areas with moderately disturbed habitat but little human presence. Stanback and Seifert (2005) reported that Eastern Bluebirds (*Sialia sialis*; hereafter “bluebirds”) breeding on golf courses in North Carolina had marginally later nesting dates,

smaller clutch sizes, and smaller nestlings than bluebirds breeding in hay fields, pastures, and utility rights-of-way.

Others have found that golf courses are no worse for avian breeding than other habitats in the nearby matrix. Rodewald et al. (2005) found that Red-headed Woodpeckers (*Melanerpes erythrocephalus*) frequently nested on golf courses in a suburban landscape in Ohio and may have had similar success compared with those nesting in other suburban habitats. LeClerc et al. (2005) found that bluebirds nesting on golf courses in southeastern Virginia produced a greater number of broods and fledged offspring of higher phenotypic quality (i.e., more symmetric limbs) than those nesting in other disturbed suburban habitats.

Resolving the ecological role of golf courses will require long-term studies that investigate direct measures of productivity for individual species (Hodgkison et al. 2007). In the present study, we assessed the role of golf courses as breeding habitat for bluebirds in southeastern Virginia. We measured multiple reproductive variables of bluebirds breeding in nest boxes on golf courses and in other disturbed habitats in a suburban matrix of the types of habitat that would have been developed had the golf courses not been built on those sites (hereafter “reference sites”). Building on LeClerc et al.'s (2005) results from a single year of data (2003), we add an additional 6 years (2004–2009) and use a contemporary approach to analyze the data set.

Assuming that birds use environmental cues to evaluate habitat quality for nesting, individuals are predicted to preemptively select habitats that offer the best conditions for maximizing fitness returns (Hildén 1965). Superior breeding habitat for birds may include locations with low nest predation, low human disturbance of nesting, and high resource availability (Boutin 1990). Thus, we predicted that clutch initiation would occur earlier and that reproductive investment (e.g., clutch size) would be greater in higher-quality habitats than in other locations. Further, if initial assessment of habitat quality is indeed reflective of breeding conditions, we predicted that hatching success, brood size, and fledging success would also be higher in better breeding sites.

METHODS

Study Species

Bluebirds are secondary cavity-nesters that prefer open habitat intermixed with forest (Gowaty and Plissner 1998). They readily use artificial cavities for nesting along roads, field edges, and other open areas, including golf courses (Gowaty and Plissner 1998). During the breeding season, bluebirds are insectivorous and visually hunt arthropods from perches over sparsely covered ground using a drop-foraging technique. Bluebirds are multibrooded; they can produce up to three successful broods within a season and will renest after nest failure or fledging. Clutch sizes of southeastern U.S. populations range from 3 to 5 eggs, and the incidence of hatching failure is low (Gowaty and Plissner 1998).

Study Area

We studied bluebirds in the City of Williamsburg and in adjacent James City, York, and New Kent counties in southeastern Virginia (central latitude 37°17', longitude 76°42'). We monitored nest boxes for activity at 21 study sites: 8 golf courses and 13 reference sites. In general, golf courses are characterized by open, short-grass

fairways and putting greens with substantial forest-edge habitat. However, there are noteworthy structural habitat differences between the courses we studied. The area and patchiness of forest, unmowed tallgrass areas, wetlands, and residential lots within golf courses varied considerably, as did the amount and proximity of suburban development in the surrounding landscape. Our reference sites included a state park and national park that comprised mixed woodland and heavily used nature trails, and several municipal recreational parks with trails, athletic fields, and a disc-golf playing field. The college, hospital, and church campuses, as well as a public cemetery, supported a mix of buildings, parking lots, forest, and mowed areas. Some sites were also located on agricultural land, including horse pasture, hay fields, and a dairy farm. Our reference sites were selected because they supported vegetation structure that resembled that of golf courses (see below). Although the golf and reference sites were similar in vegetation structure, they were given different chemical insecticide applications. We examined golf course maintenance logs to verify that either organophosphate or pyrethroid insecticides were used during the bluebird breeding season. Also, we consulted with managers of reference sites to confirm that they had been treated with insecticides (Burdge 2008).

Characterization of Land Use

We quantified land-use patterns of each study site using spatial land-cover data from 2001 and updated to include new areas of development (Commonwealth of Virginia) in ARCGIS (ESRI, Redlands, California). We defined boundaries for each site in terms of areas used for nesting by the bluebirds. We recorded locations of all nest boxes with a global positioning system. Using ARCGIS, we created a minimum convex polygon around all nest boxes within each site and buffered the polygon by 100 m to encompass approximate bluebird foraging territory (Gowaty and Plissner 1998). We calculated site area (in hectares) as the area of the polygon and the 100-m

buffer combined. We classified landcover types into four categories: (1) forest: deciduous, coniferous, and mixed-deciduous forest; (2) open grass: developed open space (including athletic fields and golf-course fairways), hay fields, pastures, shrubs, and cropland; (3) wetland: ponds, creeks, and tidal march; and (4) developed: buildings, roads, gravel, sand traps, and barren dirt. In Table 1, we report area and percent cover of each of these land-use categories for each study site. We excluded 3 of the 13 reference sites from the results shown in Table 1 because exact coordinates of some nest boxes used early in the study were not available. We used a two-tailed *t*-test to compare percent cover of the different land-use categories between golf course and reference sites. We used an arcsine transformation of percentages to adjust for deviations from normality.

Field Methods

During the breeding seasons of 2003–2009, we monitored, on average, 450 nest boxes per season at 21 different study sites (Table 2). The majority of nest boxes at both golf course and reference sites had predator guards (>80%); over time, we added guards to boxes that were previously without them so that >95% had predator guards by 2009. Most predator guards were metal stovepipe or cone baffles mounted on the nest box's pole. We accounted for the presence or absence of a predator guard in our analysis (see below).

We monitored nest boxes for breeding activity weekly from late March through August in each year. We defined a nesting attempt as the appearance of at least one egg. We first observed most nests during laying or incubation and then monitored them until fledging or failure. On each visit, we counted the number of eggs or nestlings present. We defined "clutch size" as the maximum number of eggs recorded for a given nest attempt and "brood size" as the maximum number of nestlings observed in a nest. We also recorded dates of clutch initiation (date first egg laid) and hatching (date first egg hatched). Because of the length of time between nest

TABLE 1. Area, maximum bluebird density (pairs ha⁻¹) and percentage of developed, forested, open-grass, and water land-use types for Eastern Bluebird study sites near Williamsburg, Virginia, 2003–2009.

Habitat	Site	Area (ha)	Maximum density ^a	Percent developed	Percent forest	Percent open grass	Percent water
Reference	A	7.72	0.65	0.00	0.00	91.20	0.00
	B	40.81	0.37	38.81	27.50	29.40	2.50
	C	7.97	0.75	58.54	17.07	21.34	0.61
	D	137.35	0.36	26.21	19.07	52.49	1.10
	E	10.64	0.66	0.00	8.22	88.13	0.91
	F	36.58	0.68	7.17	58.43	30.81	3.45
	G	56.11	0.39	0.00	71.34	25.89	2.16
	H	13.31	0.90	13.50	28.83	44.16	0.00
	I	7.14	1.54	1.36	20.41	76.87	0.00
	J	149.20	0.23	0.68	84.08	11.07	3.19
Golf course	K	298.06	0.31	5.04	55.18	30.15	9.13
	L	148.62	0.17	12.91	34.10	47.14	4.32
	M	193.37	0.36	2.06	43.07	47.66	5.83
	N	45.86	0.78	0.00	34.00	60.91	4.24
	O	84.05	1.15	2.89	30.92	63.47	1.33
	P	165.67	0.18	6.86	49.97	39.35	2.73
	Q	46.16	0.58	1.37	15.05	80.11	2.32
	R	196.91	0.22	16.56	41.01	38.56	3.55

^aMaximum density is the maximum number of breeding pairs at each site in a given year during our study.

TABLE 2. Numbers of monitored nest boxes and boxes used for nesting, number and proportion (in parentheses) of boxes used for breeding that had baffles, and number of nest attempts in reference habitats and golf courses near Williamsburg, Virginia, 2003–2009.

Year	Reference				Golf			
	Boxes monitored	Boxes used	Boxes used with baffles	Nest attempts	Boxes monitored	Boxes used	Boxes used with baffles	Nest attempts
2003	210	97	85 (0.88)	128	371	123	67 (0.54)	168
2004	296	85	83 (0.98)	111	445	92	53 (0.58)	147
2005	289	84	83 (0.99)	109	413	68	54 (0.79)	109
2006	246	81	80 (0.99)	104	334	70	55 (0.79)	122
2007	251	95	93 (0.98)	128	425	97	55 (0.57)	156
2008	248	115	114 (0.99)	163	524	187	181 (0.97)	282
2009	253	100	99 (0.99)	149	622	217	173 (0.8)	379
Total				892				1,363

checks, it was sometimes necessary to estimate these dates by back-calculation based on hatching dates or nestling age on later visits.

Nestlings usually fledge between 17 and 18 days after hatching (Gowaty and Plissner 1998), and therefore we made a final count of nestlings 14 days after hatching to reduce the risk of premature fledging. The final fate of a nest during the last week of the nestling period was determined by observing adults and listening for nestlings. We classified a nest as “depredated” if it was empty when nestlings were less than 16 days old and as “fledged” if it was empty, soiled, and flattened after day 16. For fledged nests, we used the number of nestlings recorded in the nest at day 14 as a primary measure of nest productivity. For failed nests, we recorded cause of failure if it could be determined. Main known reasons for failure included predation, abandonment during incubation, nestling starvation or adult mortality, and nest takeover by another cavity-nesting species. We used a chi-square contingency-table analysis on the frequency of each of the causes to determine whether the failure was associated with habitat type (golf course or reference site). Results are presented \pm SE.

Density of breeding pairs on each study site was estimated as the maximum number of unique boxes used for breeding in any year during our study, adjusted by site area. We compared average maximum densities between golf and reference sites using a two-tailed *t*-test for unequal variance. We compared the mean percentage of boxes used for nesting by bluebirds that had predator guards in each year between reference sites and golf courses with a two-tailed *t*-test, adjusted for violations of normality with an arcsine transformation. We also evaluated the percentage of nests that successfully produced at least one fledgling in boxes with and without predator guards among habitat types with a chi-square contingency-table analysis. Results are presented \pm SE.

Reproductive Variables

We investigated seven measures of reproductive potential: (1) date of clutch initiation, (2) clutch size, (3) brood size, (4) proportion of eggs in a complete clutch that survived to hatching (hatching success), (5) proportion of nestlings in a brood that survived to fledging (brood success), (6) proportion of eggs in a clutch that survived to fledging (fledging success), and (7) number of young fledged per nest attempt (nest productivity). By evaluating multiple parameters at different stages of nesting, we aimed to identify the stage(s) of nesting responsible for any difference in reproductive

performance between habitats. These seven metrics were the dependent response variables in our modeling analyses (see below). For all statistical evaluations, the unit of analysis was the individual nest attempt ($n = 2,255$).

Laying statistics.—Two different laying statistics, date of clutch initiation and clutch size, represented reproductive investment in the early stages of nesting. Initiation of first nesting attempts in the spring can vary from year to year, depending on environmental conditions (Martin 1987). To control for this variation, we standardized date of clutch initiation based on the first egg of the first nest in each year. For our evaluation of date of clutch initiation, we limited our sample to include only first nesting attempts, or clutches initiated within 30 days of the first egg of a year. This 30-day interval encompassed most of the initial breeding effort on golf courses and in reference habitats but was conservative because it eliminated most re-nesting attempts following failure early in the season. In order to increase sample sizes, other reproductive variables were not limited to first nesting attempts, and we accounted for the fact that clutch and brood sizes may decline as the breeding season progresses in our analysis (see below).

Hatching success and brood size.—We evaluated reproductive potential during intermediate stages of the nesting cycle by considering hatching success (proportion of eggs that hatched per nest attempt) and brood size. For hatching success, we considered only complete clutches; thus, this metric captures the amount of egg loss during the incubation phase. For brood size, we included any nest in which at least one egg hatched. This metric reflects the amount of nestling mortality.

Brood and fledging success.—The number of fledglings produced by each nesting attempt is a key indicator of breeding-habitat quality. To capture reproductive success in the later stages of nesting, we evaluated nest productivity and brood success (the number and proportion of nestlings that survived to fledge, respectively). We included all nests that hatched at least one egg; hence, these metrics capture differential mortality of nestlings. We also evaluated fledging success, or the proportion of eggs that survived to fledge from all complete clutches initiated throughout the nesting season; this metric describes survival over the entire nesting cycle.

Sample sizes varied among analyses of reproductive variables because complete data were not available for all nests (e.g., if a nest failed prior to hatching). Also, monitoring for some nests with

complete clutches was inadvertently discontinued prior to determination of nest fate.

Statistical Analysis

We used an information-theoretic model-selection approach (Burnham and Anderson 2002) to (1) evaluate and compare linear combinations of variables that we hypothesized could explain variation in reproduction and (2) determine whether reproduction differed between golf courses and reference sites, on the basis of our knowledge of the breeding ecology of bluebirds. We created a single model set containing four models and performed separate evaluations of this set for all reproductive response variables (Table 3). We included three main effects known to influence bluebird productivity in all models: (1) annual variation in productivity (year), (2) presence-absence of a predator guard on a nest box, and (3) date of clutch initiation. Date was included as a predictor variable in all

models (except for those models in which it was evaluated as a response term) because, on average, spring nest attempts have larger clutch sizes and fledge more young than summer broods (Gowaty and Plissner 1998). The first model of the set included only year, predator guard, and date of clutch initiation. We included this model so that we could compare the degree to which adding information about the breeding habitat (golf course vs. reference site) improved our ability to explain variation in reproduction. Model 2 included the additive effect of habitat. Model 3 included a habitat*year interaction term to represent our hypothesis that the effect of breeding habitat varies depending on the year, such that in some years, breeding on a golf course rather than a reference site might result in higher nest productivity, whereas in other years the reverse might occur. Finally, model 4 included a habitat*predator guard interaction to represent our hypothesis that rates of nest failure due to predation may vary depending on habitat type.

TABLE 3. Models of laying statistics, brood size, hatching success, nest productivity, brood success, and fledging success for Eastern Bluebirds nesting on golf courses and reference habitats near Williamsburg, Virginia, 2003–2009.

Reproductive variable	Model ^a	K ^b	QIC _μ ^c	ΔQIC ^d	w _i ^e
Date of clutch initiation	PG	8	855.00	0.00	0.50
	PG + habitat	9	856.00	1.00	0.30
	PG + habitat + year*habitat	15	862.00	7.00	0.02
	PG + habitat + PG*habitat	10	857.00	2.00	0.18
Clutch size	CID + PG	9	-87,430.32	43.78	0.00
	CID + PG + habitat	10	-87,384.90	89.20	0.00
	CID + PG + habitat + year*habitat	16	-87,474.10	0.00	1.00
	CID + PG + habitat + PG*habitat	11	-87370.77	103.33	0.00
Hatching success	CID + PG	9	742.80	0.00	0.65
	CID + PG + habitat	10	744.72	1.92	0.25
	CID + PG + habitat + year*habitat	16	752.33	9.53	0.01
	CID + PG + habitat + PG*habitat	11	746.62	3.82	0.10
Brood size	CID + PG	9	-21,274.88	71.08	0.00
	CID + PG + habitat	10	-21,310.36	35.60	0.00
	CID + PG + habitat + year*habitat	16	-21,345.96	0.00	1.00
	CID + PG + habitat + PG*habitat	11	-21,300.84	45.12	0.00
Brood success	CID + PG	9	411.26	0.00	0.44
	CID + PG + habitat	10	411.90	0.64	0.32
	CID + PG + habitat + year*habitat	16	422.26	10.99	0.00
	CID + PG + habitat + PG*habitat	11	412.52	1.26	0.24
Fledging success	CID + PG	9	683.28	0.00	0.62
	CID + PG + habitat	10	685.10	1.83	0.25
	CID + PG + habitat + year*habitat	16	691.76	8.49	0.01
	CID + PG + habitat + PG*habitat	11	686.56	3.28	0.12
Nest productivity	CID + PG	9	-1,734.14	12.79	0.00
	CID + PG + habitat	10	-1,746.93	0.00	0.79
	CID + PG + habitat + year*habitat	16	-1,741.98	4.94	0.07
	CID + PG + habitat + PG*habitat	11	-1,743.49	3.44	0.14

^aModel structure: all models include year as factor (not shown); PG = predator guard; CID = clutch initiation date; "habitat" refers to golf course or reference site.

^bK is the number of parameters.

^cPenalized quasi-likelihood information criteria generated with generalized estimating equations; best model has lowest value.

^dScaled QIC_μ; best model has ΔQIC_μ = 0.

^eModel weight; interpreted as a probability.

We used generalized estimating equations (Liang and Zeger 1986, Zeger and Liang 1986) in SAS PROC GENMOD (SAS Institute, Cary, North Carolina) to account for potential correlations among nest observations from the same study site over multiple years. We assessed the linearity of relationships between dependent and independent variables for each analysis by examining plots of observed versus predicted values; in all cases, models appropriately fit the data. The degree of support for each model in the set was evaluated using the penalized quasi-likelihood information criterion (QIC_{μ}) and normalized model weights (w_i). The model in each set with the lowest QIC_{μ} value was considered to be the best fit to the observed data among the models evaluated. We interpreted models with $\Delta QIC_{\mu} < 2$ to be well supported by the data and models with ΔQIC_{μ} values of 3–5 to be moderately supported (Burnham and Anderson 2002). We also report evidence ratios for some pairs of models, or the ratio of Akaike weights between two models (w_i/w_j), to describe which is a better fit to the data (Burnham and Anderson 2002).

RESULTS

Characterization of land use.—The proportions of different land types present on study sites varied considerably (Table 1). On average, golf courses did not differ from reference habitats in percent developed land ($t = 1.49$, $df = 11$, $P = 0.16$), forested land ($t = 1.74$, $df = 16$, $P = 0.10$), open grassland ($t = 0.57$, $df = 14$, $P = 0.58$), and wetland ($t = 1.18$, $df = 11$, $P = 0.26$). Thus, golf courses and reference sites were similar in the proportions of different land types present. The total extent of area was greater for golf courses than for reference sites ($t = -2.88$, $df = 11$, $P = 0.01$).

Breeding density and nest-box occupancy.—The maximum density of bluebird breeding pairs ranged from 0.17–1.15 pairs ha^{-1} ($\bar{x} = 0.49 \pm 0.14$) on golf courses to 0.23–1.54 pairs ha^{-1} ($\bar{x} = 0.65 \pm$

0.12) on reference sites (Table 1). Mean density of bluebirds did not differ between habitat types ($t = 1.06$, $df = 16$, $P = 0.30$). The average proportion of nest attempts per nest box used was higher on golf courses ($\bar{x} = 1.59 \pm 0.01$) than on reference sites ($\bar{x} = 1.35 \pm 0.01$; $t = 4.24$, $df = 12$, $P = 0.001$), but only by 0.24 attempts per box (Table 2).

Laying statistics.—The type of habitat occupied had little influence on the timing of breeding. There was high annual variation in date of clutch initiation over the course of the study, and there were no apparent systematic differences between golf courses and reference habitats (Fig. 1). Three models, which included additive effects of year, predator guard, and habitat, as well as the interaction of predator guard and habitat, were supported by the data ($\Delta QIC_{\mu} \leq 2$; Table 3). The best model included year and predator guard only ($w_i = 0.50$); it had 1.6 \times more support in the data than the model that also included habitat, and more than 2.5 \times the support of the model that included the predator guard*habitat interaction (Table 3). The effect of habitat on date of clutch initiation was small; on average, bluebirds on golf courses initiated clutches <0.4 days later than those on reference sites (Fig. 1 and online Appendix 1; see Acknowledgments for link to online supplementary materials). These patterns were based on 847 nest attempts ($n = 505$ on golf courses, $n = 342$ on reference) initiated within the first 30 days of the first egg laid in each year.

Investment in clutch size by bluebirds did not appear to differ systematically between golf course and reference habitats over the study period (Fig. 2). The model with habitat*year interaction, representing our hypothesis that the effect of habitat on clutch size depended on the year, had complete support by the data (Table 3; $w_i = 1.00$). The direction of the effect of habitat was inconsistent among years: clutches on golf courses were larger in some years, and smaller in others, than those on reference sites (Fig. 2). The effect of habitat on clutch size was small: clutches on golf courses ($n = 1,217$) had only 0.02 more eggs than reference clutches ($n = 806$; Fig. 2 and online Appendix 2).

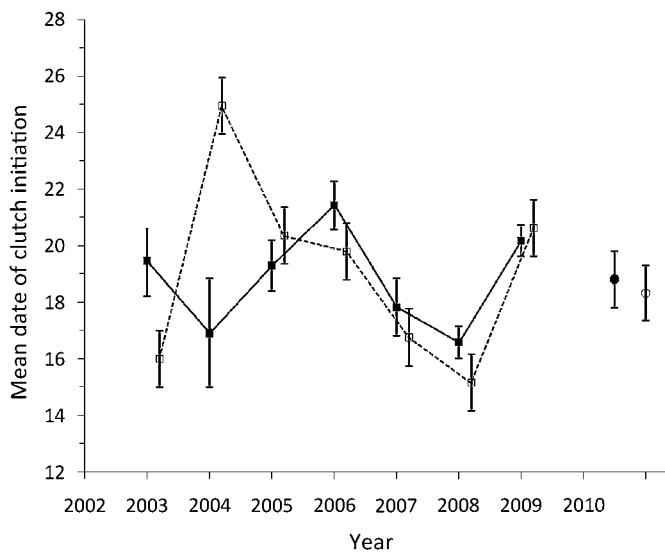


FIG. 1. Mean date of clutch initiation with error bars (\pm SE) for Eastern Bluebird nests on golf courses (filled squares) and reference habitats (unfilled squares) in Virginia, 2003–2009. Grand means for all years (\pm SE) are shown to the right for golf courses (filled circle) and reference habitats (unfilled circle).

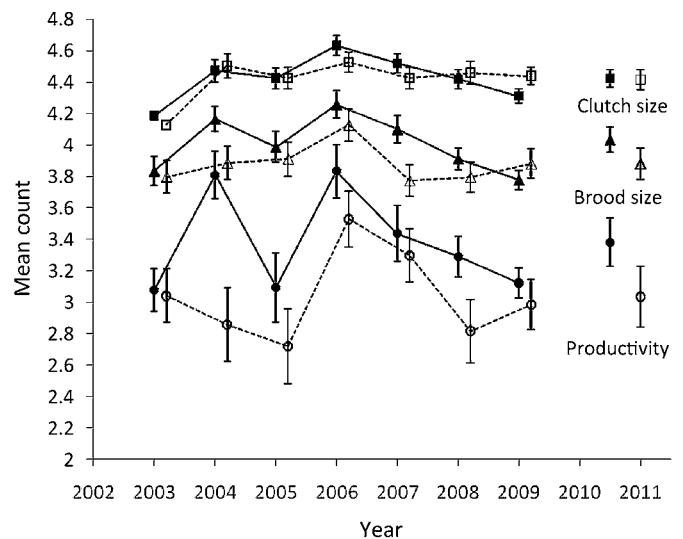


FIG. 2. Mean clutch size (squares), brood size (triangles), and nest productivity (circles) with error bars (\pm SE) for Eastern Bluebird nests on golf courses (solid line) and reference habitats (dashed line) in Virginia, 2003–2009. Grand means for all years (\pm SE) are shown to the right for golf courses (filled shapes) and reference habitats (unfilled shapes).

Hatching success and brood size.—Our data supported the hypothesis that habitat affected the proportion of eggs hatched per nesting attempt: nest boxes on golf courses had higher hatching success (Fig. 3A). Both the model without the habitat term and the model with habitat as an additive variable were supported by the data, having $\Delta QIC_{\mu} < 2$ ($w_i = 0.65$ and $w_i = 0.25$; Table 3). The model without the habitat term had 2.5× more support in the data than the model with habitat. The proportion of eggs that hatched over all years was, on average, 3% greater for golf course clutches than for reference clutches (Fig. 3A and online Appendix 3). Our analysis included 1,190 nest attempts on golf courses and 792 nest attempts on reference sites.

Individuals breeding on golf courses reared larger broods than individuals at reference sites. Annual variation in brood size was greater than annual variation in clutch size, but brood size in the two habitats varied in parallel (Fig. 2). As was true for clutch size, there was overwhelming support in the data for our hypothesis that the effect of habitat on brood size depended on the year (habitat*year model, $w_i = 1.0$; Table 3). However, in contrast to clutch size, for which the direction of the habitat effect was inconsistent across years, average broods on golf courses were larger than those on reference sites by 0.13 nestlings, which would be the equivalent of 15 more nestlings per 100 nests (Fig. 2 and online Appendix 2).

Brood success, fledging success, and nest productivity.—We found support for the hypothesis that choice of breeding habitat also affected levels of nestling mortality in bluebirds. On average, nestlings reared in nests on golf courses survived better than nestlings on reference habitats (Fig. 3B). For brood success, three models were supported by the data ($\Delta QIC_{\mu} < 2$), including the model without habitat ($w_i = 0.44$), the model with habitat ($w_i = 0.32$), and the model with the predator guard*habitat interaction ($w_i = 0.24$; Table 3). The model without habitat had only 1.4× more support than the model with habitat included and only 1.8× more support than the model with the predator guard*habitat interaction term. The proportion of nestlings that survived to fledging was highest among nests in boxes with predator guards on golf courses ($\bar{x}_{\text{brood success}} = 0.64 \pm 0.01$) and lowest among nests in boxes without predator guards on reference sites ($\bar{x}_{\text{brood success}} = 0.50 \pm 0.09$). For fledging success, the models with and without habitat as an additive factor were supported by the data (Table 3). The model with the predator guard*habitat interaction was moderately supported ($\Delta QIC_{\mu} = 3.28$, $w_i = 0.12$). The difference between habitat types for the proportion of nestlings in a brood that survived to fledge was larger than the difference in hatching rates (brood success = 4.5% difference vs. hatching success = 3.1% difference; Fig. 3A, B and online Appendix 4). The difference between habitats in the proportion of eggs per nest that survived to fledge (fledging success) was even larger (5.6%; Fig. 3C and online Appendix 5). Our sample for fledging success included 1,643 nest attempts ($n = 969$ golf courses, $n = 674$ reference site).

Type of nesting habitat played an important role in bluebird nest productivity (number of fledglings produced per nest attempt). Nests on golf courses in every year fledged more offspring than nests in reference habitats (Fig. 2). The best model was the habitat model, which had a 79% chance of being the best fit to the data compared with the other models that we considered (Table 3). Nest attempts on golf courses produced, on average, 3.3 fledglings compared with 3.0 fledglings per nest attempt in reference sites

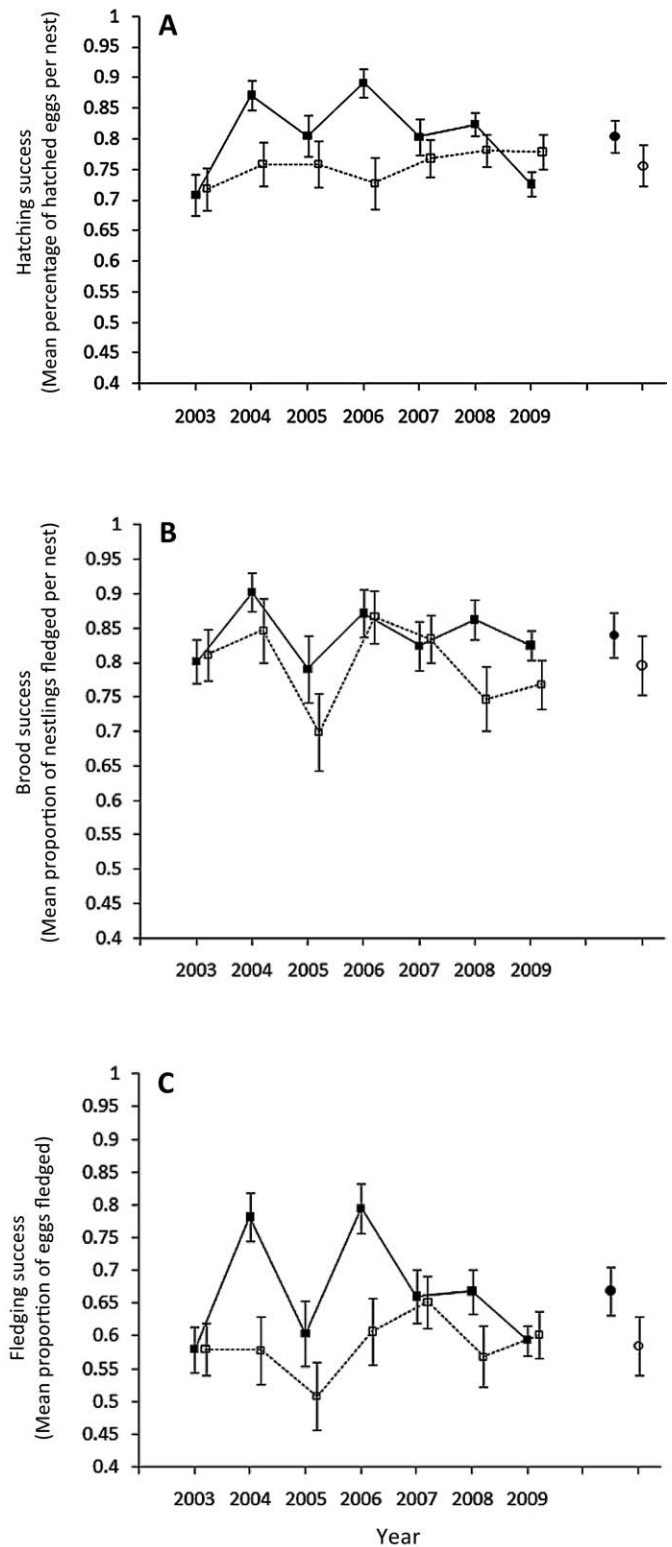


FIG. 3. Mean (A) hatching success, (B) brood success, and (C) fledging success with error bars (\pm SE) for Eastern Bluebird nests on golf courses (filled squares) and reference habitats (unfilled squares) in Virginia, 2003–2009. Grand means for all years combined (\pm SE) are shown to the right for golf courses (filled circle) and reference habitats (unfilled circle).

(Fig. 2 and online Appendix 6). Thus, reproductive investment by breeders on golf courses yielded 30 more offspring for every 100 breeding attempts than an equal unit of investment by breeders in reference habitats. We used 1,418 nests with known numbers of fledglings in our analysis ($n = 836$ golf course, $n = 582$ reference site). Nest productivity patterns combined with brood and fledging success results suggest that nestling mortality in later stages of the nesting cycle is likely a key factor determining differences between habitats.

Nest failure and predator guards.—The proportion of nests that fledged offspring was high. Out of 1,777 known-fate nests from both habitats, only 31.3% ($n = 556$) failed to fledge at least one offspring. The percentage of nests that failed was higher on reference sites (35.2% = 259 of 735) than on golf courses (28.5% = 297 of 1,042; $\chi^2 = 9.09$, $df = 1$, $P = 0.003$). The main causes of failure included predation (60.4%), abandonment during incubation (22.8%), nestling starvation or adult mortality (7.6%), nest takeover by other secondary cavity-nesting species such as House Wrens (*Troglodytes aedon*; 2.9%), and unknown causes (6.2%). Cause of failure was not associated with habitat type ($\chi^2 = 5.79$, $df = 4$, $P = 0.21$).

Among the boxes that were used for nesting by bluebirds, the mean percentage that had predator guards in each year did not differ between reference sites and golf courses (Table 2; $t = 1.98$, $df = 12$, $P = 0.07$). On reference sites, the percentage of nests that were successful (produced at least one offspring) did not depend on whether or not a box had a predator guard (62.5% success without guard vs. 64.8% success with guard; $\chi^2 = 0.05$, $df = 1$, $P = 0.81$). On golf courses, nests in boxes with predator guards were more likely to fledge offspring (59.8% success without guard vs. 74.7% success with guard; $\chi^2 = 19.08$, $df = 1$, $P < 0.0001$).

DISCUSSION

Golf courses support productive breeding populations of Eastern Bluebirds in our region. Although density of breeding pairs was similar between golf and reference sites, breeding output on golf courses was higher. The difference between golf courses and reference habitats was most apparent later in the nesting cycle, in that bluebirds breeding on golf courses produced more offspring than those in reference habitats because of higher success of nestlings rather than events during laying. As expected, there were high levels of annual variation among the 7 years for all reproductive variables that we evaluated. Despite this variation, brood success, fledging success, and nest productivity were, on average, higher on golf courses. Golf course broods produced, on average, 0.3 more fledglings per nesting attempt than reference broods. Thus, assuming that a typical female produces 2 broods season⁻¹ and breeds for 2 years, with equal investment in eggs, a bluebird breeding on a golf course would contribute 1 more offspring to the population than it would have on a reference site.

Our results confirm LeClerc et al.'s (2005) initial report from the same study area that bluebirds on golf courses in southeast Virginia were highly productive. LeClerc et al. (2005) found that nest boxes on golf courses produced 17% more fledglings than nest boxes on reference sites and that nestlings reared on golf courses were of higher phenotypic quality (i.e., lower fluctuating asymmetry of tarsus). Although we did not evaluate nestling tarsus asymmetry in our study, the observations from 2003 appear to represent a consistent difference for this species on these sites.

Reproductive responses to developed suburban habitats can vary by species and region and, in some cases, within the same species and region. Our results are not consistent with Stanback and Seifert's (2005) report from neighboring North Carolina of poorer breeding performance by bluebirds on golf courses than in nearby agricultural habitats. Specifically, they found that golf course breeders initiated clutches 1 day later, on average, and laid marginally smaller clutches compared with reference nests. They detected lower arthropod abundance on golf courses, and nestlings reared on golf courses were also in poorer condition, which suggests that reduced food availability was the primary reason for the observed differences between habitats. By contrast, two separate studies have measured feeding rates by bluebirds in Virginia, but neither detected differences between golf course and reference sites (LeClerc et al. 2005, Burdge 2008).

Within-region differences in reproduction for the same species can result from multiple factors, including variation in arthropod diversity and abundance (Rosenberg et al. 1987, Bolger et al. 2000), differences in predator communities (Kristan et al. 2003), and variation in land-management practices. Also, the relative reproductive performance of bluebirds on golf courses depends on the exact reference sites selected for comparison as well as on the specific turf-management practices on each course. Our Virginia reference sites spanned a greater diversity of developed habitats, including some that may have been less productive than the North Carolina reference sites studied by Stanback and Seifert (2005).

Ecological Mechanisms

Food.—Food availability, nutritional quality of prey, prey capture efficiency, and nestling provisioning rates may affect productivity of bird populations (Martin 1987). LeClerc et al. (2005) found that nestling provisioning rates were the same on golf course and reference sites. Burdge (2008) analyzed prey samples collected from nestlings via ligatures and did not find differences in overall number, biomass, or types of arthropods between habitats. Finally, element content (carbon:nitrogen:phosphorus ratios) of arthropods did not differ between golf course and reference sites, which suggests that the overall nutritional quality of food was equal between habitats (J. Swaddle unpubl. data). Thus, it seems unlikely that differences in food availability or nutritional value are primary mechanisms driving differences in reproduction in this system. However, adults may be able to forage more efficiently and expend less energy on golf courses because fairways and greens are consistently mowed to produce more open areas with short grass (Rosenberg et al. 1987). The consistency of conditions on golf courses may affect incubation and brooding behaviors, which could explain the higher hatching rates, brood sizes, and nest productivity on golf courses.

Pesticides.—Insecticides used on golf courses can have substantial physiological and behavioral effects on birds (e.g., Rainwater et al. 1995, Stansley et al. 2001) and may result in reduced survival or reproduction. For example, Bishop et al. (2000) found that six species of passerines, including bluebirds, responded to pesticide spraying in orchards with severely reduced reproductive success. On golf courses, bluebirds collect arthropod prey from fairways and greens, which makes them particularly susceptible to pesticide exposure through direct contact or ingestion of contaminated prey. However, Burdge (2008), working on some of the golf courses that we did, found no evidence of pesticide effects on

nestlings or residues in dead arthropods collected on fairways. Thus, although we cannot rule it out, we have no reason to suspect a deleterious effect of pesticides on nestling bluebirds on the golf courses that we studied.

Predation.—Predators of birds sometimes increase in abundance in developed areas (Kristan et al. 2003). Common nest predators at our study sites included snakes (*Elaphe obsoleta* and *Coluber constrictor*) and Southern Flying Squirrels (*Glaucomys volans*) (Gowaty and Plissner 1998, K. Cornell et al. pers. obs.). Although most of our nest boxes were fitted with predator guards, and relatively few nests failed, predation was the dominant cause of nest failure on all of our sites. We did not detect a difference in predation rates between golf course and reference habitats, but further study is necessary, because our design excluded most predators. Differences in predation pressure may exist between golf courses and reference sites because one habitat type supports more predators, makes it easier for them to find nests, or concentrates predators from surrounding developed areas. For example, our reference sites comprised a smaller area than the golf courses, which may mean that predation pressures from the surrounding matrix are greater than on golf courses. One of the biggest remaining questions for wildlife research on golf courses concerns the response of predator populations, and this will require the study of artificial nests or nests that are not protected from predation.

Effects of Golf Courses on Other Life-history Variables

In addition to the reproductive variables reported here, other life-history characteristics of individuals can affect population-level responses to habitat quality. For example, both postfledging survival and frequency of multiple brooding by females influence recruitment into the breeding population. Jackson et al. (2011) estimated survival of fledgling bluebirds using radiotelemetry on some of the same golf courses and reference sites studied here. They found no evidence that inhabiting a golf course increased mortality during the fledgling period, although golf course fledglings often quickly dispersed into habitat that was significantly more forested and less grassy. These results are consistent with our finding that bluebirds reproducing on golf courses appear to perform as well as those in other disturbed habitats.

Bluebirds in our region will follow successful nesting attempts with second, and sometimes third, broods (Gowaty and Plissner 1998). It is not known whether the frequency of multiple brooding differed between habitats in our study area. However, initiation of first nest attempts was synchronous among golf course and reference sites, and hatching and fledging success rates were high in both habitats across the breeding season; thus, we would expect females to have equivalent time available to initiate multiple broods at golf courses and reference sites.

Conservation Implications

A recent review of studies investigating the role of golf courses in global biodiversity conservation proposed that they can be valuable because of their ability to support wildlife, particularly in anthropogenically dominated agricultural and urban landscapes (Colding and Folke 2009). However, it is clear that individual species respond to development in different ways and, thus, population-level information from specific habitats is critical for determining the potential conservation value of urban–suburban green space. Specifically, data on reproduction and survival, linked

as they are to population viability, must be obtained to provide direct information about the value of a particular habitat. The present study is the most comprehensive investigation to date of avian reproduction on golf courses. Our results show that reproductive success of bluebirds on golf courses was comparable to reproduction in nearby disturbed habitats. Accordingly, golf courses could be valuable for conservation of avian species that can tolerate moderate to high levels of disturbance, like the bluebird, because they may complement the other patches of wildlife habitat within the urban–suburban matrix.

It is important to note, however, that the building of golf courses results in loss of natural habitats, which may be critical for some species, particularly for those of high conservation concern. Although golf courses may resemble natural habitats more than some other green space, many support only common urban-adapted species. As such, it may not necessarily be the specific attributes of golf courses that have value for bluebirds. Rather, their conservation value may be in the preservation of uninterrupted open green areas within the matrix of more intensively developed habitats. If we can better understand what it is about golf course habitats that make them suitable for bluebirds and determine which other species can thrive there (e.g., Burrowing Owls, various woodpeckers, and flycatchers), we may be able to optimize the role of golf courses in bird conservation by designing and managing them appropriately.

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