

Dynamic selective environments and evolutionary traps in human-dominated landscapes

AMANDA D. RODEWALD,¹ DANIEL P. SHUSTACK,² AND TODD M. JONES

School of Environment and Natural Resources, Ohio State University, 2021 Coffey Road, Columbus, Ohio 43210 USA

Abstract. Human activities can alter selective environments in ways that can reduce the usefulness of certain ornamental traits as honest signals of individual quality and, in some cases, may create evolutionary traps, where rapid changes in selective environments result in maladaptive behavioral decisions. Using the sexually dichromatic, socially monogamous Northern Cardinal (*Cardinalis cardinalis*) as a model, we hypothesized that urbanization would erode the relationship between plumage coloration and reproductive success. Because the exotic Amur honeysuckle (*Lonicera maackii*) provides carotenoids, is a preferred habitat attribute, and increases vulnerability to nest predation, we predicted the presence of an evolutionary trap, whereby the brightest males would achieve the lowest reproductive success. Working at 14 forests in Ohio, USA, 2006–2008, we measured plumage color, monitored reproduction, and quantified habitat within territories. In rural landscapes, the brightest males bred earliest in the season and secured more preferred territories; however, annual reproduction declined with plumage brightness. Coloration of urban males was not associated with territory attributes or reproduction. Female redness across all landscapes was negatively related to reproduction. Poor reproductive performance of otherwise higher-quality males probably resulted from preferences for honeysuckle, which reduces annual reproduction when used as a nesting substrate early in the season. In this way, exotic shrubs prompted an evolutionary trap that was avoided in urban forests where anthropogenic resources disassociated male color and reproductive phenology and success. Our study illustrates how modified selective environments in human-dominated landscapes might shape microevolutionary processes in wild bird populations.

Key words: breeding phenology; *Cardinalis cardinalis*; carotenoids; coloration; evolutionary trap; exotic plant; *Lonicera maackii*; Northern Cardinal; plumage; reproduction; sexual selection; urbanization.

INTRODUCTION

Amid ongoing efforts of biologists to understand how sexually selected traits, such as avian plumage coloration, act as honest signals of quality (Andersson 1982, Hamilton and Zuk 1982, Jennions et al. 2001), the degree to which anthropogenic disturbance may change that relationship is of growing interest. Human activities, especially within cities, can cause rapid changes in a variety of biological, physical, and chemical attributes of the environment. These changes may ultimately influence the usefulness of certain traits as signals or, in some cases, may signal incorrect information, creating ecological or evolutionary traps, where once-adaptive behaviors become maladaptive in the new selective environment. While the term “ecological trap” has been popularly used in the context of inappropriate habitat selection, a range of other behavioral and life-history decisions, including mate selection and timing of

breeding, also may be subject to traps (Schlaepfer et al. 2002).

Carotenoids have long been a focus for studies of honesty of signals because, unlike melanins and structurally derived colors, carotenoids cannot be synthesized and must be obtained from the diet (Gray 1996, Saks et al. 2003). In this way, carotenoid-based plumage can signal condition by way of an individual’s diet and access to food (Hill 1991, Hill and Montgomerie 1994). Recent studies show that carotenoid-based coloration also is mediated by physiological stress and infection (Lozano 1994, Bortolotti et al. 2009, Mougeot et al. 2010). Although carotenoid-based plumage coloration is correlated with reproductive success for a variety of species, including Northern Cardinal (*Cardinalis cardinalis*; Wolfenbarger 1999a, Jawor et al. 2004), House Finch (*Carpodacus mexicanus*; McGraw et al. 2001a), and Barn Swallow (*Hirundo rustica*; Safran et al. 2010), sexual traits evolve under temporally and spatially heterogeneous selective environments (Gosden and Svensson 2008, Cornwallis and Uller 2010) that can produce notable exceptions to associations between traits and fitness (Mand et al. 2005, Kappes et al. 2009).

Environmental changes associated with urban development may have strong influence on birds with

Manuscript received 7 January 2011; revised 21 March 2011; accepted 30 March 2011. Corresponding Editor: W. D. Koenig.

¹ E-mail: rodewald.1@osu.edu

² Present address: Massachusetts College of the Liberal Arts, Biology Department, 375 Church Street, North Adams, Massachusetts 01247 USA.

plumage that is highly dependent upon pigments obtained from their diet, as is the case for carotenoid-based plumages (McGraw et al. 2001b, Hill et al. 2002). Indeed, urbanization has been implicated as a contributor to changes in carotenoid-based plumage pigmentation in Great Tits (*Parus major*; Isaksson and Andersson 2007, Dauwe and Eens 2008, Sillanpaa et al. 2008). There also is the possibility that ecological changes in urban systems can create evolutionary traps. Unfortunately, few studies have directly examined the consequences of urban-associated plumage changes to fitness attributes.

In this study, we examined the relationship between plumage coloration and annual reproductive output for the sexually dichromatic, socially monogamous Northern Cardinal (*Cardinalis cardinalis*). The bright red plumage of cardinals is carotenoid-based and dependent upon diet acquired during molt (Linville and Breitwisch 1997, McGraw et al. 2001b), which occurs in late summer and autumn during periods of high fruit availability. Studies of cardinals indicate that brightness or hue can indicate good condition (Jawor et al. 2004, Jones et al. 2010) and high levels of parental investment (Linville et al. 1998), as well stress (as indicated by immune profile; Maney et al. 2008) and low parental investment (Jawor and Breitwisch 2004). Reproductive success of cardinals also has been positively linked to color (Jawor and Breitwisch 2004, Jawor et al. 2004), as has the ability to secure high-quality territories (Wolfenbarger 1999b). Males establish and actively defend territories and guard females during the breeding season (Halkin and Linville 1999), and the duration of pair bonds varies widely, over 1–6 years in our system (A. D. Rodewald, unpublished data). Rates of extra-pair paternity are low compared to other songbirds, possibly due to the intense mate-guarding of females during their fertile periods (Ritchison et al. 1994). As an urban adaptor, the cardinal reaches its greatest densities in urban environments, probably due to the rich food and nesting resources in cities (Leston and Rodewald 2006, Rodewald and Bakermans 2006).

The invasive and exotic shrub honeysuckle (*Lonicera* spp.) is one example of an urban-associated source of carotenoids during the late summer/early fall when cardinals molt feathers during the post-breeding season (Mulvihill et al. 1992). Fruit is a major dietary component (58%) in fall during molt (Linville and Breitwisch 1997), and two reports indicate that honeysuckle comprised ~10% of their diet in fall (Ingold and Craycraft 1983, Linville and Breitwisch 1997). Although the low protein and lipid content of honeysuckle fruits may make them less preferred when a variety of alternative fruits are available (Ingold and Craycraft 1983), Amur honeysuckle (*L. maackii*) fruits comprise the overwhelming majority of fruits (86%) on our sites in September (Leston 2005). When used as a nesting substrate, honeysuckle increases vulnerability of cardinal nests to predation and can reduce annual

reproductive output (Borgmann and Rodewald 2004, Rodewald et al. 2010), suggesting that the plant may facilitate the creation of an evolutionary trap where brightly colored birds achieve lower reproductive success.

Our previous work demonstrated that male plumage brightness was positively related to body condition (size-adjusted or residual body mass), but that the relationship was significantly stronger in rural than urban landscapes (Jones et al. 2010). Thus, plumage coloration was a less reliable indicator of body condition in urban than rural landscapes, presumably due to anthropogenic resources in urban landscapes. For example, carotenoid-rich exotic fruits may be widely available to birds of all condition states, whereas certain energetically dense birdseed mixtures might improve condition while offering comparatively lower amounts of carotenoids. Even if similar amounts of pigments are ingested, individuals may sequester different amounts of carotenoids into feathers, depending upon other physiological constraints (McGraw and Hill 2001). We hypothesized that if plumage color signaled individual quality, more colorful individuals would secure territories with more highly preferred habitat attributes, breed earlier in the season, and have higher reproductive output than less colorful individuals. However, due to ecological changes associated with urbanization, we predicted that the relationship between plumage coloration and annual reproductive success would relax as landscapes surrounding our forested sites were increasingly urban. Because honeysuckle can depress reproductive success, we further predicted the formation of an evolutionary trap, such that the brightest males would have the lowest levels of reproductive success.

MATERIALS AND METHODS

Study sites.—Cardinals were studied at 14 mature riparian forests (≥ 250 m long and ≥ 100 m wide) located along a rural-to-urban gradient in central Ohio, USA (approximately 40°00' N, 83°00' W). Across the landscape gradient, forests were comparable in both shape and landscape configuration and, thus, differed primarily in the dominant land use type (either agriculture or urban development) within the landscape matrix.

We derived an urban index to represent the amount of urbanization surrounding each forest site. Landscape composition (number of buildings, percentages of agriculture, pavement, lawn, roads) was quantified within a 1 km radius area centered on each study site using recent (2002–2004) digital orthophotos (Table 1). As part of a larger complementary study, we performed a principal components analysis on landscape metrics on sites across the entire study area (Rodewald and Shustack 2008a). The first principal component (hereafter termed the “urban index”) explained 80% of the variation among sites and correlated positively with number of buildings ($r = 0.92$), percent cover by roads ($r = 0.94$), pavement ($r = 0.90$), and lawn ($r = 0.88$), but

TABLE 1. Landscape composition surrounding 14 riparian forest study sites in central Ohio, USA.

Study site	Forest width (m)	No. buildings	Proportion of cover within 1 km				Urban index
			Agriculture	Mowed	Paved	Road	
ngalena	135	34	0.36	0.05	0.01	0.01	-1.27
pubhunt	194	210	0.32	0.08	0.01	0.01	-1.15
prairie	148	58	0.47	0.12	0.03	0.02	-1.12
creeks	133	92	0.10	0.1	0.04	0.02	-0.71
sgalena	163	185	0.14	0.3	0.02	0.01	-0.57
galena	277	360	0.15	0.22	0.04	0.02	-0.48
elkrun	167	812	0.31	0.27	0.06	0.05	-0.16
woodside	104	1227	0.11	0.40	0.07	0.05	0.32
rushrun	150	1611	0	0.41	0.09	0.06	0.75
cherry	165	997	0.02	0.36	0.16	0.07	0.76
kenny	126	1733	0	0.34	0.17	0.06	0.89
casto	202	1776	0	0.42	0.20	0.08	1.25
lou	156	2272	0	0.28	0.23	0.08	1.26
tuttle	160	2285	0	0.34	0.30	0.09	1.61

Notes: The urban index was calculated by performing a principal components analysis on percentages of different land cover classes (agriculture, pavement, lawn, roads) and numbers of buildings within a 1-km radius surrounding each forest site. The first principal component (hereafter termed "urban index") explained 80% of the variation among sites (Eigenvalue = 3.99) and was strongly correlated with number of buildings ($r = 0.92$), percent cover by roads ($r = 0.94$), pavement ($r = 0.90$), and lawn ($r = 0.88$), but negatively correlated with percent cover by agriculture/pasture ($r = -0.83$).

negatively with percent cover by agriculture ($r = -0.83$). Rural landscapes (urban index < 0) were dominated by cropland, pasture, managed grassland, and farms. Urban landscapes (urban index > 0), in contrast, were dominated by residential areas, commercial development, and roads. Building density ranges in our landscapes were 0.1–7.3 buildings/ha (or 10–727 buildings/km²).

Feather collection and color measurement.—We collected feathers from 280 Northern Cardinals captured in mist nets during the breeding season from early March to August 2006–2008. Most individuals were captured early in the breeding season (March–May). We collected 6–10 feathers from the breast of each male, and 3–6 feathers from underwing coverts of both wings of females (i.e., 6–12 feathers total per female). Feathers in these areas are known to be important indicators of cardinal plumage and have been used in previous studies (Linville and Breitwisch 1997, Wolfenbarger 1999a, Jawor et al. 2003). Collected feathers were stored in a freezer until measurements were taken.

Prior to measuring color, we superimposed feathers from each individual on 4.5 × 7.5 cm white note cards to imitate the plumage surface (Quesada and Senar 2006). Feathers were then photographed inside an 8 × 8 × 8 inch Digital Concepts Lighting Studio (with two 20-W lights pointed at the feathers) and using a supra-macro feature of a Fujifilm FinePix S8000fd digital camera positioned 2 cm away. We measured hue, saturation, and brightness using Adobe Photoshop CS 2 (Kilner and Davies 1998, Yam and Papadakis 2004, Jones et al. 2010). Feather hue described the point on the color spectrum wheel (0–360°) with 0/360° being the purest red color (i.e., red with few blue or yellow tones). Saturation characterized the density of color, with 0% being least dense and 100% being most dense (with the least amount of gray tones). Brightness was quantified on a percent-

age grayscale with 0% being black and 100% being white.

We randomly measured 10 points within the overlapping area of the superimposed feathers and used the mean as the color metric. Our previous analyses showed high repeatability of these measurements (Jones et al. 2010). Because hue and saturation were highly correlated ($r = -0.71$), we considered only hue and brightness in analyses.

Reproductive output.—To estimate season-long reproduction, we individually marked cardinals with a U.S. Geological Survey stainless steel band and a unique combination of color bands. Field teams monitored all known nesting attempts of banded individuals from late March through September 2006–2008. Nests were generally located early in the nesting stage (often during building or egg-laying) and were then checked at 1–3 day intervals. For nests that successfully fledged young, numbers of young cardinals were determined by either counting the number of nestlings immediately prior to fledging or by observing parents and young for extended periods near the time of fledging. Numbers of young produced were summed across nesting attempts for banded individuals. We considered the apparent number of young fledged over a season to be a reasonable estimate of annual reproduction, given that cardinals have low rates of extra-pair fertilizations relative to most other passerines based on genetic analysis (16% of broods and 13.5% of nestlings were extra-pair) and behavioral traits, such as mate-guarding, when males maintain near-constant contact with fertile mates (Ritchison et al. 1994).

Habitat characteristics.—In a previous study comparing habitat characteristics surrounding nests and randomly selected locations, we showed that cardinals selected territories with a high density of understory vegetation, especially of exotic shrubs (Leston and

Rodewald 2006). Thus, we focused on those preferred habitat attributes for our assessment of territory quality in this study. Understory woody vegetation was measured along two perpendicular 20-m transects centered on each nest. At 20 points located at 2-m intervals along transects, we counted the number of times a standing 3-m pole was contacted by woody vegetation 0.5–3.0 m high, and we specified whether the species was native or exotic. The overwhelming majority of exotic vegetation was Amur honeysuckle, although multiflora rose (*Rosa multiflora*) also occurred at many sites. Measurements were primarily collected in July and August of each year, with a few nests being measured in late June and early September.

Analysis.—Over the three years, we had both estimates of annual output of fledglings and feather samples for 100 females and 75 males. Numbers of young fledged over the season for each individual were log-transformed prior to analysis. Because we were explicitly interested in understanding how the relationship between color and reproductive output changed across the rural-to-urban landscape gradient, we constructed a model with log-transformed number of fledglings as the response variable and the urban index, brightness, and urban \times brightness interaction. Because individuals were the sampling units but the question of interest was at the landscape (site) scale, we used a mixed-effects model with site specified as a random-effect variable. An identical analytic approach was used to examine hue. Although the number of fledglings produced varies annually in our system, relationships with reproductive output were consistent among years (i.e., no significance interaction) for male brightness ($F_{2,56} = 0.99$, $P = 0.38$), male hue ($F_{2,56} = 0.20$, $P = 0.08$), female brightness ($F_{2,82} = 0.33$, $P = 0.72$), and female hue ($F_{2,82} = 1.79$, $P = 0.17$). Consequently, we analyzed data pooled across years.

We tested for an association between coloration (brightness and hue for males and females) and reproductive phenology for 84 females and 59 males for which we had first-egg dates, using the same analytical approach in the previous analyses. For the 54 breeding pairs for which we had color data for both the male and female, we tested for possible assortative mating with a model regressing male brightness, urban index, and urban \times brightness interaction against female hue and another with male hue and female brightness. Although this analysis was not capable of demonstrating mate preferences, our intent was to explore the possibility that the most colorful males and females were paired, which might exacerbate negative consequences of an evolutionary trap.

We examined relationships between plumage coloration and territory characteristics using canonical correlation analysis (PROC cancorr, SAS). In cases where we had measured vegetation surrounding multiple nests for an individual during a single year, we averaged habitat metrics across nests. Across the years, we measured

habitat surrounding nests for 27 males and 29 females breeding in rural forests (urban index < 0), and 51 males and 67 females in urban forests (urban index > 0). Separately for each landscape, we tested for associations between coloration and numbers of native and exotic woody understory stems, which are the habitat attributes known to be strongly selected by cardinals in our study area (Leston and Rodewald 2006).

RESULTS

Annual reproduction.—Contrary to our original expectations, the annual number of young produced by males (log-transformed) declined with plumage brightness, but only in the rural landscapes, as indicated by the significant plumage brightness \times urban interaction (Table 2, Fig. 1A). Annual reproductive output was unrelated to male hue (Table 2).

For females, redder hues (closer to 0° in the hue metric) were associated with fewer numbers of young produced over the season (Table 2, Fig. 1B), but reproduction was not a function of urbanization directly nor via an urban by hue interaction. Annual reproductive output was unrelated to female brightness (Table 2).

Timing of breeding.—Reproductive phenology of males was related to a strong brightness \times urbanization interaction (Table 2, Fig. 2), and was unrelated to hue. The most brightly colored males bred earliest in the season in rural landscapes, with the opposite trend for urban males. For females, neither hue nor brightness was unrelated to first egg date (Table 2).

Territory quality.—The relationship between male brightness and nest location differed between rural and urban landscapes. Understory vegetation surrounding nests was related to male brightness in rural (Wilks' lambda $F_{2,24} = 3.46$, $P = 0.05$), but not urban landscapes (Wilks' lambda $F_{2,48} = 0.74$, $P = 0.48$). In rural forests, increasingly bright males located nests in patches with a greater number of exotic woody stems, which was largely comprised of Amur honeysuckle (Pearson's $r = 0.47$; $F_{1,25} = 6.96$, $P = 0.01$; Fig. 3), but no difference in native woody stems (Pearson's $r = 0.001$; $F_{1,25} = 0$, $P = 0.98$).

Understory vegetation was not significantly related to male hue (Wilks' lambda: rural, $F_{2,24} = 0.37$, $P = 0.69$; urban, $F_{2,48} = 0.56$, $P = 0.57$), female hue (Wilks' lambda: rural, $F_{2,26} = 0.11$, $P = 0.90$; urban, $F_{2,64} = 0.38$, $P = 0.68$), or female brightness (Wilks' lambda: rural, $F_{2,26} = 0.01$, $P = 0.99$; urban, $F_{2,64} = 2.87$, $P = 0.06$).

Pairing.—Although female hue and male brightness were weakly correlated (Pearson's $r = 0.26$, $P = 0.05$, $n = 54$), we found no evidence of statistically significant associations between male and female coloration when accounting for site as a random effect variable and considering possible interactive effects (Table 2).

DISCUSSION

Our study illustrates how anthropogenic disturbance and human activity within metropolitan areas can alter

TABLE 2. Parameter estimates (β and SE) and F statistics for analyses examining relationships between reproductive output and phenology and coloration of Northern Cardinals (*Cardinalis cardinalis*).

Factor(s)	Reproductive output			Timing of breeding			Assortative pairing					
							Female hue			Female brightness		
	β (SE)	F	P	β (SE)	F	P	β (SE)	F	P	β (SE)	F	P
Males												
Brightness	-0.05 (0.02)	5.98	0.02	-0.12 (0.39)	0.09	0.76	0.18 (0.11)	2.70	0.11	0.09 (0.17)	0.31	0.58
Urban	-3.40 (1.58)	4.62	0.04	-80.65 (28.31)	8.12	<0.01	2.63 (8.22)	0.10	0.75	-2.52 (12.57)	0.04	0.84
Brightness × urban	0.04 (0.02)	4.92	0.03	0.87 (0.39)	7.16	0.01	-0.03 (0.09)	0.09	0.77	0.01 (0.14)	0.00	0.95
Hue	0.004(0.03)	0.02	0.90	-0.09 (0.6)	0.02	0.88	0.23 (0.15)	2.33	0.14	0.18 (0.22)	0.64	0.43
Urban	-0.23 (0.34)	0.46	0.50	-0.77 (6.52)	0.01	0.91	0.96 (1.76)	0.30	0.59	-0.95 (2.68)	0.12	0.73
Hue × urban	0.03 (0.03)	1.02	0.32	-0.35 (0.54)	0.40	0.53	-0.06 (0.15)	0.17	0.68	-0.05 (0.21)	0.06	0.81
Females												
Brightness	0.01 (0.02)	0.24	0.62	-0.17 (0.35)	0.24	0.63						
Urban	1.06 (0.62)	0.72	0.40	9.51 (26.35)	0.13	0.72						
Brightness × urban	-0.01 (0.01)	0.56	0.46	-0.13 (0.30)	0.19	0.66						
Hue	0.06 (0.03)	5.43	0.02	-0.12 (0.58)	0.04	0.84						
Urban	0.82 (0.53)	2.37	0.13	-5.05 (11.63)	0.19	0.67						
Hue × urban	-0.04 (0.03)	1.85	0.18	0.15 (0.56)	0.07	0.80						

Notes: All analyses used mixed models with site as a random effect variable. A model was run separately for each color metric (either brightness or hue) and included the following terms: color + urban + color × urban. Degrees of freedom for type 3 tests of fixed effects are indicated for each response variable: for reproductive output, $df = 1, 59$ for males and $1, 85$ for females; for timing of breeding, $df = 1, 45$ for males and $1, 69$ for females; for assortative pairing, $df = 1, 39$. In assortative pairing, female hue and brightness are tested against male hue and brightness.

the selective environment in ways that might ultimately shape microevolutionary processes in wild bird populations. Along the rural-to-urban landscape gradient, we found spatial heterogeneity in the extent to which plumage coloration of male Northern Cardinals was associated with reproduction. In the more urban landscapes, brightness of male plumage was disassociated with timing of breeding, territory attributes, and annual reproduction, which might ultimately lead to relaxed selection for color in urban environments. In rural landscapes, patterns were consistent with an evolutionary trap. Despite being in better condition (Jones et al. 2010), initiating breeding earlier in the season, and nesting within territories containing more preferred habitat attributes, brightly colored males in rural landscapes produced fewer young over the season than duller males. The poor reproductive performance of the presumably higher quality males likely resulted from their preference to secure territories with dense patches of the early-leafing Amur honeysuckle (Leston and Rodewald 2006) that is known to reduce reproductive success when used early in the breeding season (Borgmann and Rodewald 2004, Rodewald et al. 2010). These patterns suggest that exotic shrubs prompt a potential evolutionary trap in rural landscapes, where bright color provides a competitive advantage that allows individual to breed early in the most highly preferred territories (Wolfenbarger 1999b) that ultimately depress reproductive success. In urban forests, however, this potential trap was averted because male plumage color was disassociated with attributes related to reproduction, including timing of breeding, territory quality, and reproductive success.

Although sexual ornamentation may impose costs that reduce fitness (Promislow et al. 1992), the lower reproductive output of bright rural cardinals also could arise from behavioral or life-history choices based on previously reliable cues that are maladaptive in human-modified environments, termed evolutionary traps by Schlaepfer et al. (2002). In our study system, cardinals strongly select breeding sites and territories with dense patches of the exotic shrubs, especially Amur honeysuckle (Leston and Rodewald 2006). Not only are nests placed in honeysuckle more likely to be depredated (Borgmann and Rodewald 2004), but also the penalty for selecting honeysuckle as a nesting substrate is most severe early in the breeding season. In fact, cardinals that initiated their first nest attempt in honeysuckle fledged 20% fewer young over the entire season (i.e., summing across all nest attempts) than did birds choosing other substrates (Rodewald et al. 2010). This same study found that early-season predation risk for nests in honeysuckle is probably a consequence of lower nest-site diversity early in the season, when >70% of all nests are located in early-leafing exotic shrubs, which should facilitate searching by predators. If we put our current study in the context of this previous work, then more brightly colored males in rural forests are expected to experience the penalty most severely because they secure territories with greater amounts of honeysuckle and initiate breeding earlier than duller males. In this way, our study provides an interesting contrast with Wolfenbarger (1999b), who showed that the primary advantage to redder cardinal males was the acquisition of higher quality territories and earlier initiation of breeding, which were the key determinants of higher

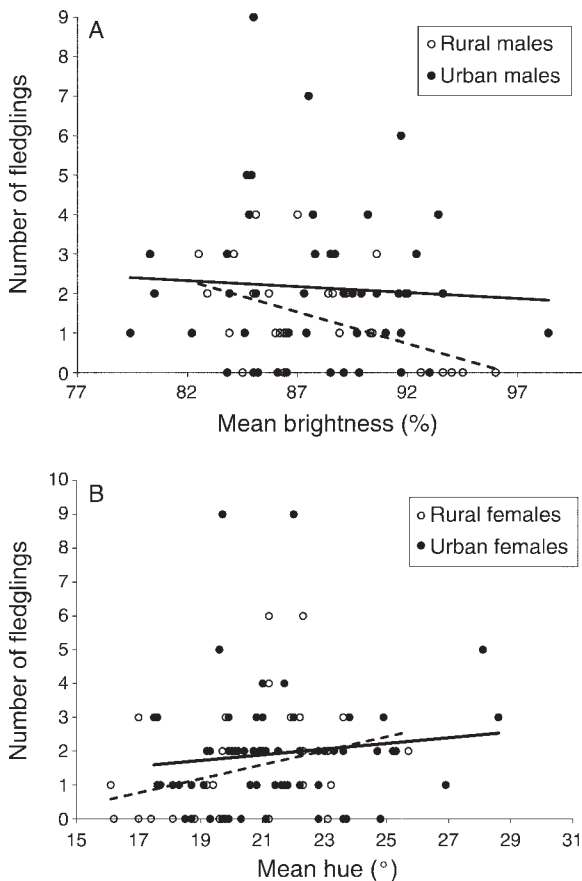


FIG. 1. Relationship between number of fledglings produced over the breeding season and (A) mean plumage brightness for male Northern Cardinals (*Cardinalis cardinalis*) and (B) mean plumage hue (lower values indicate redder plumage) for females in Ohio, USA, 2006–2008. Feather hue described the point on the color spectrum wheel (0–360°) with 0/360° being the purest red color (i.e., red with few blue or yellow tones). Brightness was quantified on a percentage grayscale with 0% being black and 100% being white. Although analyses were conducted using the continuous urban index, we graphically display trend lines for categories of rural (urban index < 0; dashed line) and urban (urban index > 0; solid line) landscapes.

reproductive success. We suggest that exotic shrubs led to lower reproductive output of more brightly colored males in our rural landscapes in ways that are consistent with an evolutionary trap. This potential trap apparently operates most strongly at the individual, not site, level given that (1) the relationship between reproduction and urbanization was not statistically significant when tested alone for each sex, and (2) our previous work showed similar levels of annual reproduction for cardinals in rural and urban forests (Rodewald and Shustack 2008b).

We propose that two conditions allowed males breeding in urban forests to escape this particular evolutionary trap. First, anthropogenic resource subsidies in urban forests relaxed the relationship between

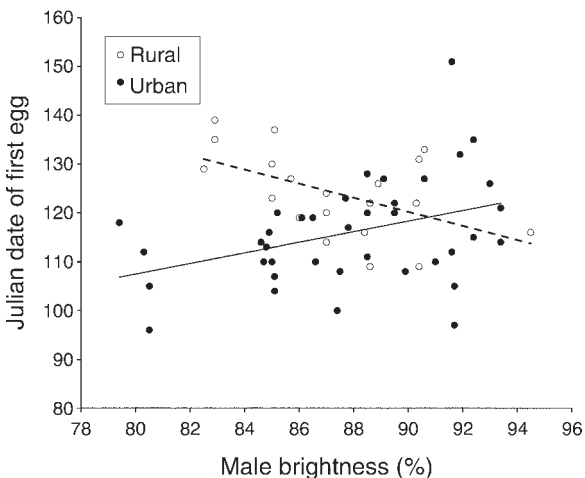


FIG. 2. Brightly colored males bred earlier in the season than duller males in rural, but not urban, landscapes (Julian day 1 is 1 January). Although analyses were conducted using the continuous urban index, we graphically display categories of rural (urban index < 0; dashed line) and urban (urban index > 0; solid line) landscapes.

plumage coloration and individual condition (Jones et al. 2010). Urban birds had access to plentiful carotenoid-rich (exotic fruits) and/or energetically dense (birdseed) foods (Leston and Rodewald 2006). Cardinals rely heavily upon fruits during molt (Linville and Breitwisch 1997), and honeysuckle is one example of an urban-associated source of carotenoid-rich food for birds (Mulvihill et al. 1992). Hence, pigments important for plumage coloration were likely to be accessible to males

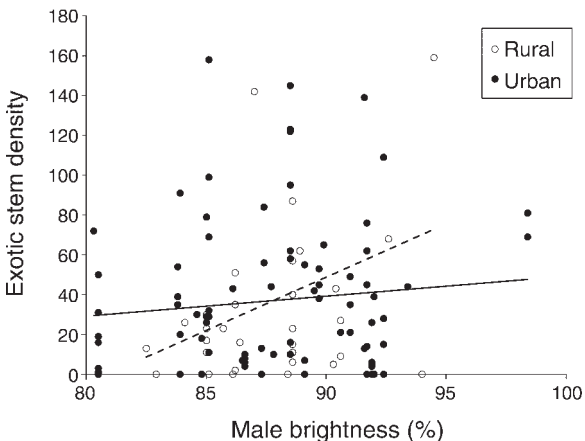


FIG. 3. In rural landscapes (urban index < 0; dashed line), more brightly colored males nested in territories with greater density of exotic woody stems, 2006–2008. Even without the points where exotic stems >100, the relationship between the two variables in rural landscapes remains significant at $P=0.05$. In urban landscapes (urban index > 0; solid line), density of exotic stems was not significantly related to male brightness. Note that stem density is an index: the number of hits of exotic vegetation at sampling points within territories, rather than a count of stems per unit area.

over a wider range of conditions than in rural landscapes (Jones et al. 2010), making color a less useful signal of quality. At the same time, birds relying upon birdseed may have achieved good condition through comparatively carotenoid-poor foods. Second, because invasion by honeysuckle is promoted by urbanization and honeysuckle dominates the understory strata of urban forests (Borgmann and Rodewald 2005), territories containing patches of exotic shrubs are more widely available for urban cardinals (A. D. Rodewald, *unpublished data*). In rural landscapes, the preferred shrub is patchily distributed and present at lower density than in urban forests, which may evoke competition from breeding cardinals. There also remains the possibility that urban birds faced higher levels of physiological stress and infection that affected their body's use of carotenoids (Lozano 1994, Bortolotti et al. 2009, Mougeot et al. 2010). Higher cardinal densities in urban sites are consistent with the idea that urban birds face more intense intraspecific interactions, although we have no data to support or refute this idea.

Although our data failed to show assortative mating based on coloration, we raise a number of important caveats. First, our analysis was limited by a relatively small sample size of pairs for which we had color metrics on both individuals. This may have constrained our ability to detect patterns using our full statistical models. Indeed, a simple correlation analysis indicated a weak positive association between female hue and male brightness. Second, birds may use a combination of cues, of which color is one (Candolin 2003). Third, tacit in our test of assortative mating is the assumption that coloration indicated female quality. However, this assumption was not supported by Jones et al. (2010), who found no relationship between female hue and condition, nor by our present examination of reproduction. Fourth, sexual selection may already be relaxed in our study system, given the documented disassociations with condition for urban birds and the apparent evolutionary trap for rural birds. Thus, we caution that the absence of a significant relationship between male brightness and female hue does not eliminate the possibility that birds used color as a signal of quality.

Our work makes two contributions to our understanding of evolutionary and ecological processes operating in human-dominated systems. First, our study provides evidence that human-induced changes to ecosystems can both create evolutionary traps that alter relationships between sexual and natural selection (via exotic shrubs in rural landscapes) and facilitate escape from evolutionary traps (via anthropogenic resources in urban landscapes). Second, because coloration was not a useful signal of male quality in urban landscapes, urbanization has the potential to affect the evolution of sexual ornamentation and potentially lead to relaxed selection for color in the urban environments. The long-term consequences of human-modified selective environments ultimately depend upon a variety of factors,

including movement, gene flow, and temporal heterogeneity of selective forces.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation (DEB-0340879, DEB-0639429, and REU Supplements to A. D. Rodewald), the Ohio Division of Wildlife and U.S. Fish and Wildlife Service through the State Wildlife Grants Program, and a Schwab Associate Scholarship grant to T. Jones from The Ohio State University. This work would not have been possible without dedicated efforts of L. J. Kearns, I. J. Ausprey, and J. R. Smith-Castro. We appreciate helpful comments from P. G. Rodewald, P. P. Marra, T. B. Ryder, and W. M. Masters, which improved this manuscript. We thank the following for their work in the field: B. T. Adams, Elizabeth Ames, Christine Austin, S. C. Buescher, L. M. Koerner, S. E. Lehnen, W. W. Li, L. L. MacArthur, A. Petersen, J. E. Price, E. C. Rogers, K. Uppstrom, B. Van Allen, and R. M. Zajac. We are grateful to Franklin County Metro Parks, Columbus Parks and Recreation, Ohio Division of Wildlife, The Nature Conservancy, City of Bexley, Gahanna Parks and Recreation, and private landowners for their cooperation and access to sites.

LITERATURE CITED

- Andersson, M. 1982. Sexual selection, natural-selection and quality advertisement. *Biological Journal of the Linnean Society* 17:375–393.
- Borgmann, K. L., and A. D. Rodewald. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. *Ecological Applications* 14:1757–1765.
- Borgmann, K. L., and A. D. Rodewald. 2005. Forest restoration in urbanizing landscapes: Interactions between land uses and exotic shrubs. *Restoration Ecology* 13:334–340.
- Bortolotti, G. R., F. Mougeot, J. Martinez-Padilla, L. M. I. Webster, and S. B. Piertney. 2009. Physiological stress mediates the honesty of social signals. *PLoS ONE* 4:e4983.
- Candolin, U. 2003. The use of multiple cues in mate choice. *Biological Reviews* 78:575–595.
- Cornwallis, C. K., and T. Uller. 2010. Towards an evolutionary ecology of sexual traits. *Trends in Ecology and Evolution* 25:145–152.
- Dauwe, T., and M. Eens. 2008. Melanin- and carotenoid-dependent signals of great tits (*Parus major*) relate differently to metal pollution. *Naturwissenschaften* 95:969–973.
- Gosden, T. P., and E. I. Svensson. 2008. Spatial and temporal dynamics in a sexual selection mosaic. *Evolution* 62:845–856.
- Gray, D. A. 1996. Carotenoids and sexual dichromatism in North American passerine birds. *American Naturalist* 148:453–480.
- Halkin, S. L., and S. U. Linville. 1999. Northern Cardinal (*Cardinalis cardinalis*). No. 440 in A. Poole and F. Gill, editors. *The Birds of North America*. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites. *Science* 218:384–387.
- Hill, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature* 350:337–339.
- Hill, G. E., C. Y. Inouye, and R. Montgomerie. 2002. Dietary carotenoids predict plumage coloration in wild house finches. *Proceedings of the Royal Society of London B* 269:1119–1124.
- Hill, G. E., and R. Montgomerie. 1994. Plumage color signals nutritional condition in the House Finch. *Proceedings of the Royal Society of London B* 258:47–52.
- Ingold, J. L., and M. J. Craycraft. 1983. Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio in Fall. *Ohio Journal of Science* 83:256–258.

- Isaksson, C., and S. Andersson. 2007. Carotenoid diet and nestling provisioning in urban and rural great tits *Parus major*. *Journal of Avian Biology* 38:564–572.
- Jawor, J. M., and R. Breitwisch. 2004. Multiple ornaments in male northern cardinals, *Cardinalis cardinalis*, as indicators of condition. *Ethology* 110:113–126.
- Jawor, J. M., N. Gray, S. M. Beall, and R. Breitwisch. 2004. Multiple ornaments correlate with aspects of condition and behaviour in female northern cardinals, *Cardinalis cardinalis*. *Animal Behaviour* 67:875–882.
- Jawor, J. M., S. U. Linville, S. M. Beall, and R. Breitwisch. 2003. Assortative mating by multiple ornaments in northern cardinals (*Cardinalis cardinalis*). *Behavioral Ecology* 14:515–520.
- Jennions, M. D., A. P. Møller, and M. Petrie. 2001. Sexually selected traits and adult survival: a meta-analysis. *Quarterly Review of Biology* 76:3–36.
- Jones, T. M., A. D. Rodewald, and D. P. Shustack. 2010. Variation in plumage coloration of Northern Cardinals in urbanizing landscapes. *Wilson Journal of Ornithology* 122:326–333.
- Kappes, P. J., B. J. M. Stutchbury, and B. E. Woolfenden. 2009. The relationship between carotenoid-based coloration and pairing, within- and extra-pair mating success in the American Redstart. *Condor* 111:684–693.
- Kilner, R., and N. B. Davies. 1998. Nestling mouth colour: ecological correlates of a begging signal. *Animal Behaviour* 56:705–712.
- Leston, L. F. V. 2005. Are urban riparian forests ecological traps for understory birds? Habitat selection by Northern Cardinals (*Cardinalis cardinalis*) in urbanizing landscapes. Thesis. Ohio State University, Columbus, Ohio, USA.
- Leston, L. F. V., and A. D. Rodewald. 2006. Are urban forests ecological traps for understory birds? An examination using Northern Cardinals. *Biological Conservation* 131:566–574.
- Linville, S. U., and R. Breitwisch. 1997. Carotenoid availability and plumage coloration in a wild population of Northern Cardinals. *Auk* 114:796–800.
- Linville, S. U., R. Breitwisch, and A. J. Schilling. 1998. Plumage brightness as an indicator of parental care in northern cardinals. *Animal Behaviour* 55:119–127.
- Lozano, G. A. 1994. Carotenoids, parasites, and sexual selection. *Oikos* 70:309–311.
- Mand, R., V. Tilgar, and A. P. Møller. 2005. Negative relationship between plumage colour and breeding output in female great tits, *Parus major*. *Evolutionary Ecology Research* 7:1013–1023.
- Maney, D. L., A. K. Davis, C. T. Goode, A. Reid, and C. Showalter. 2008. Carotenoid-based plumage coloration predicts leukocyte parameters during the breeding season in northern cardinals (*Cardinalis cardinalis*). *Ethology* 114:369–380.
- McGraw, K. J., and G. E. Hill. 2001. Carotenoid access and intraspecific variation in plumage pigmentation in male American Goldfinches (*Carduelis tristis*) and Northern Cardinals (*Cardinalis cardinalis*). *Functional Ecology* 15:732–739.
- McGraw, K. J., G. E. Hill, R. Stradi, and R. S. Parker. 2001a. The influence of carotenoid acquisition and utilization on the maintenance of species-typical plumage pigmentation in male American goldfinches (*Carduelis tristis*) and northern cardinals (*Cardinalis cardinalis*). *Physiological and Biochemical Zoology* 74:843–852.
- McGraw, K. J., A. M. Stoehr, P. M. Nolan, and G. E. Hill. 2001b. Plumage redness predicts breeding onset and reproductive success in the House Finch: a validation of Darwin's theory. *Journal of Avian Biology* 32:90–94.
- Mougeot, F., J. Martinez-Padilla, G. R. Bortolotti, L. M. I. Webster, and S. B. Pieltney. 2010. Physiological stress links parasites to carotenoid-based colour signals. *Journal of Evolutionary Biology* 23:643–650.
- Mulvihill, R. S., K. C. Parkes, R. C. Leberman, and D. S. Wood. 1992. Evidence supporting a dietary basis for orange-tipped relictrees in the Cedar Waxwing. *Journal of Field Ornithology* 63:212–216.
- Promislow, D. E. L., R. Montgomerie, and T. E. Martin. 1992. Mortality costs of sexual dimorphism in birds. *Proceedings of the Royal Society of London B* 250:143–150.
- Quesada, J., and J. C. Senar. 2006. Comparing plumage colour measurements obtained directly from live birds and from collected feathers: the case of the Great Tit *Parus major*. *Journal of Avian Biology* 37:609–616.
- Ritchison, G., P. H. Klatt, and D. F. Westneat. 1994. Mate guarding and extra-pair paternity in Northern Cardinals. *Condor* 96:1055–1063.
- Rodewald, A. D., M. H. Bakermans. 2006. What is the appropriate paradigm for riparian forest conservation? *Biological Conservation* 128:193–200.
- Rodewald, A. D., and D. P. Shustack. 2008a. Urban flight: understanding individual and population-level responses of Nearctic–Neotropical migratory birds to urbanization. *Journal of Animal Ecology* 77:83–91.
- Rodewald, A. D., and D. P. Shustack. 2008b. Consumer resource matching in urbanizing landscapes: Are synanthropic species over-matching? *Ecology* 89:515–521.
- Rodewald, A. D., D. P. Shustack, and L. E. Hitchcock. 2010. Exotic shrubs as ephemeral ecological traps for nesting birds. *Biological Invasions* 12:33–39.
- Safran, R. J., K. J. McGraw, M. R. Wilkins, J. K. Hubbard, and J. Marling. 2010. Positive carotenoid balance correlates with greater reproductive performance in a wild bird. *PLoS ONE* 5:e9420.
- Saks, L., K. McGraw, and P. Horak. 2003. How feather colour reflects its carotenoid content. *Functional Ecology* 17:555–561.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17:474–480.
- Sillanpaa, S., J. Salminen, E. Lehikoinen, E. Toivonen, and T. Eeva. 2008. Carotenoids in a food chain along a pollution gradient. *Science of the Total Environment* 406:247–255.
- Wolfenbarger, L. L. 1999a. Is red coloration of male Northern Cardinals beneficial during the nonbreeding season? A test of status signaling. *Condor* 101:655–663.
- Wolfenbarger, L. L. 1999b. Red coloration of male northern cardinals correlates with mate quality and territory quality. *Behavioral Ecology* 10:80–90.
- Yam, K. L., and S. E. Papadakis. 2004. A simple digital imaging method for measuring and analyzing color of food surfaces. *Journal of Food Engineering* 61:137–142.