ACTUAL OR PERCEIVED ABUNDANCE? INTERPRETING ANNUAL SURVEY DATA IN THE FACE OF CHANGING PHENOLOGIES

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Abstract. Many annual monitoring programs assume that availability—the probability that an animal will be visible, make an audible sound, or leave other evidence of its presence—is not changing systematically from year to year. Until recently, this assumption of unchanging availability seemed reasonable, but recent studies report changes in breeding phenology that are presumed to be linked to climate change. Because the rate of bird song is often correlated with stage of breeding, earlier breeding could shift timing of peak bird availability, changing the number of birds counted during annual surveys on set dates. Such changes could be erroneously interpreted as population trends. To better understand how changes in phenology might affect the probability of detecting birds, we modeled availabilities of 31 species in southern Alabama through the breeding season, documenting strong seasonal variation in availability. Then, using our availability estimates, we investigated whether changes in detection probabilities could underlie observed changes in the abundances of some species. We calculated the expected change in the number of times a species would be recorded during surveys conducted within fixed dates by assuming a 1-week shift in breeding activity. We found that summer residents were more likely to show changes in availability but that such changes in availability did not account for trends in Breeding Bird Survey (BBS) data for Alabama. Our results suggest that while summer residents' availability may be declining during BBS dates, population declines observed in BBS data for Alabama cannot be dismissed as due to shifting phenology.

Key words: detection probability, migratory species, global warming, climate change, phenology, population declines, Breeding Bird Survey.

¿Abundancia Real o Percibida? Interpretando Datos de Monitoreo Anual Frente a los Cambios Fenológicos

Resumen. Muchos programas de monitoreo anuales asumen que la disponibilidad—la probabilidad de que un animal será visible, hará un sonido audible o dejará otra evidencia de su presencia—no está cambiando sistemáticamente de un año al otro. Hasta hace poco, este supuesto de disponibilidad no cambiante parecía razonable, pero estudios recientes muestran cambios en la fenología reproductiva que se presumen están vinculados al cambio climático. Debido a que la tasa de canto de las aves está usualmente correlacionada con el estadio reproductivo, la anidación más temprana podría desplazar la fecha del pico de disponibilidad de las aves, cambiando el número de aves contadas durante los monitoreos anuales en fechas establecidas. Estos cambios podrían ser interpretados erróneamente como tendencias poblacionales. Para entender mejor como los cambios en fenología podrían afectar la probabilidad de detección de las aves, modelamos las disponibilidades de 31 especies en el sur de Alabama a lo largo de la estación reproductiva, documentando una fuerte variación estacional en disponibilidad. Luego, usando nuestros estimados de disponibilidad, investigamos si los cambios en las probabilidades de detección podrían sustentar los cambios observados en las abundancias de algunas especies. Calculamos el cambio esperado en el número de veces que una especie podría ser registrada durante los monitoreos realizados en fechas fijas, asumiendo un desplazamiento de una semana en la actividad reproductiva. Encontramos que los residentes de verano tuvieron una mayor probabilidad de mostrar cambios en la disponibilidad, pero que estos cambios en disponibilidad no explicaron las tendencias en los datos del Monitoreo de Aves Reproductivas (BBS por sus siglas en inglés) de Alabama. Nuestros resultados sugieren que mientras que la disponibilidad de residentes de verano puede estar disminuyendo durante las fechas de BBS, los declives poblacionales observados en los datos de BBS de Alabama no pueden ser desestimados como debidos a cambios en la fenología.

INTRODUCTION

A major focus of conservation biologists is monitoring the abundances of species and taking actions to stop and reverse population declines. Breeding birds are particularly amenable to being counted because they are active and vocal during the day, and birds are perhaps the best-monitored class of animals in North America (Davis 1982). Despite birds' suitability for being counted, the probability of detecting a given individual bird during a designated count period is likely to be less than

one (Johnson 2008, Nichols et al. 2008, Simons et al. 2009). For a bird to be detected it must be visible or make an audible signal such as a song or call, and the observer must perceive and correctly identify the bird. These two components of detection are referred to as the availability and perceptibility of a bird, respectively (Marsh and Sinclair 1989, Johnson 2008, Nichols et al. 2008). Availability is a function of bird behavior, whereas perceptibility is often affected by differences among observers and the conditions under which surveys are conducted (Johnson 2008). The rate at which birds sing (vocalizations per unit of time) has a particularly strong effect on bird availability (Alldredge et al. 2007).

Primarily within the past decade, conservation and wildlife biologists have developed statistical tools to take into account imperfect detection of birds in models of species' abundance (reviewed in Johnson 2008, Nichols et al. 2008, Simons et al. 2009). The development of this detection theory has provided important new insight into the process of monitoring bird populations, and it has revealed key assumptions in estimates of species' abundance. One key assumption of surveys conducted on fixed dates that are used to track the population trends of species is that the availability of bird species does not change from year to year.

For essentially all bird species, availability changes within a breeding season. A primary reason for changing availability within a breeding season is that song rate of many species varies through the breeding season (Slagsvold 1977, Best 1981, Ralph 1981, Skirvin 1981). This variation in song rate is affected by environmental conditions (Slagsvold 1977, Gordo et al. 2008), whether the bird is paired (Sayre et al. 1980, Hayes et al. 1986, Gibbs and Wenny 1993), and nest stage (Best 1981, Best and Petersen 1982, Wilson and Bart 1985). For example, Lampe and Espmark (1987) showed that song activity of the Redwing (*Turdus iliacus*) peaks 2 weeks before egg laying, and Logan (1983) found an increase in singing during nest building in the Northern Mockingbird (*Mimus polyglottos*). Seasonal variation in song rate may impart variation in the number of individuals available to be detected through the breeding season, potentially biasing the results of studies that fail to correct for seasonal changes in availability (Diefenbach et al. 2007).

Many monitoring programs have attempted to overcome temporal changes in bird availability by standardizing protocols so that birds are surveyed at the same date and time of day each year (e.g., Holmes and Sherry 2001, Linder and Buehler 2005, Sauer et al. 2008). One such program, the North American Breeding Bird Survey (BBS), is the primary tool used to assess the population status of birds in North America (Sauer et al. 2005). The BBS is a database of approximately 3700 routes, each consisting of 50 point counts—fixed-position surveys in which an observer records all birds detected—along a standardized route. Most bird detections during point counts are auditory (Scott et al. 1981, DeJong and Emlen 1985, Sauer

et al. 1994a), so song rate influences detection probability during such surveys greatly (Alldredge et al. 2007). The BBS can provide excellent data for relative abundance within a species, but this sort of count rests on the critical assumption that bird availability does not change systematically over time. Because song rate is tied to state of breeding, an assumption that a species' availability is constant is an assumption that its breeding phenology remains constant across years. Until recently, such an assumption seemed entirely reasonable.

The past century has seen a rise in global temperatures (Houghton et al. 1995) with significant effects on birds (Crick 2004). Bird phenology seems to be particularly influenced by warming temperatures, with many species migrating earlier (e.g., Mason 1995, Jenkins and Watson 2000, Butler 2003, Huppop and Huppop 2003, Marra et al. 2005, Vegvari et al. 2010). Additionally, the dates of many species' nesting have shifted earlier in both Europe (Crick et al. 1997, Winkel and Hudde 1997, McCleery and Perrins 1998, Both et al. 2004) and North America (Bradley et al. 1999, Brown et al. 1999, Dunn and Winkler 1999). The recent, well-documented changes in the phenology of many birds raise questions about the reliability of reported changes in abundance that are based on monitoring programs dependent on an assumption of constant availability (Simons et al. 2007).

The seasonal timing and synchrony of breeding within a population determine the effects that changing phenology will have on perceived abundances. If a species normally breeds near the survey dates and sings at its maximal rate during this period, then annual surveys at this time of year will have maximal ability to detect the species. If, however, the species undergoes a phenological shift and breeds earlier than normal in a given year, such that the peak of singing occurs before the survey date, then fewer individuals will be counted during the survey, even if the same number of birds is present. Conversely, if a species that normally peaks in song activity after the survey date shifts toward earlier breeding, a greater proportion of individuals of that species will be counted as the date of breeding moves closer to the survey period. The synchrony of breeding may also affect trends perceived during surveys. Birds that breed more synchronously show more marked changes in song rate as the breeding season progresses (Slagsvold 1977). Migratory birds tend to breed more synchronously than do residents (Spottiswoode and Møller 2004), so changes in phenology may have a greater effect on the availability of migratory species than on resident species. Several studies have reported declines in neotropical migrants (Holmes et al. 1979, Hall 1984, Leck et al. 1988, Robbins et al. 1989, Holmes and Sherry 2001, Holmes 2007) without due consideration to potential changes in migratory bird phenology.

To obtain accurate estimates of a species' population trends, it is imperative to understand seasonal changes in availability and determine how changes in phenology may affect availability during surveys. Our study had three goals: (1) to

document changes in the availability of various bird species across the breeding season within our study site in Tuskegee National Forest, Alabama, (2) to determine how a shift in phenology would affect bird availability during annual bird surveys, and (3) to determine whether our estimated changes in bird availability due to shifts in phenology are correlated with population trends as estimated by the BBS within the state of Alabama. We predicted that migratory species should show more seasonal variation in availability than residents, and that this should translate into larger changes in availability due to shifts in phenology during annual surveys. We also predicted that the changes in availability due to changes in phenology should correlate with population trends in BBS data.

METHODS

BIRD SURVEYS

To estimate bird availability we used audio recordings from 13 locations in Tuskegee National Forest (32° N, 85° W, Macon County, Alabama), on the northern edge of the East Gulf Coastal Plain. Each of the 13 locations was along a 2400-m transect oriented northeast–southwest, and each location was separated from other locations by 200 m. The sample area spanned several habitat types including open marsh, hardwood bottomland, upland pine, and mixed hardwood and deciduous forest. We did not record during rain or high winds. We recorded bird vocalizations for 5 min at each station between 07:00 and 08:00 CDT weekly from late April through the end of July, 2008, by using a digital linear recorder (pulse-code modulation; model LS-10, Olympus America, Inc.) held at breast height. McClure and Ligon examined each recording thoroughly, collaborating to determine the presence/absence of each species. Our methods control for weather, time of day, and observer bias in detection probability by using audio recordings made under favorable weather conditions, within the same hour each day, and by having the same two persons review the recordings together. In our analysis, by holding bird perceptibility constant, we were able to base our detection estimates on the availability of birds during the breeding season within our study site. Because point counts in forested habitats rely almost entirely on auditory detection (Faanes and Bystrak 1981, Scott et al. 1981, DeJong and Emlen 1985), our counts produce data like conventional point counts even though we eliminated visual observations and relied entirely on auditory detections.

STATISTICAL ANALYSES

We used generalized linear mixed models with a binomial distribution and a logit link to create availability curves (Cunningham and Rowell 2006). We fit models by using restricted maximum likelihood. For each species analyzed, we built three models representing hypothesized changes in species availability throughout the season: (1) a null model containing only the intercept, (2) a linear model containing a covariate for the week in which each observation was made, and (3) a quadratic model that contained covariates for the week in which each observation was made and that week squared. Models were ranked and compared by Akaike's information criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989). We considered a model competitive for inference if the covariates in the top model were not a subset of covariates in the competing model (Burnham and Anderson 2002, Devries et al. 2008, Arnold 2010). If any competitive model was within two AIC_c units of the top model, we model-averaged across the entire model set (Burnham and Anderson 2002) to develop the final model. We used final models for inference only if the confidence intervals of at least one parameter excluded zero (Chandler et al. 2009). We analyzed species only detected on four or more counts during the study period. Using species detected for at least 4 weeks enabled us to avoid convergence problems inherent with small sample sizes yet still obtain a biologically relevant temporal sampling of bird availability. Because we are less than certain of the presence or absence of a species during our surveys (e.g., a species may have been present but undetected), our availability curves represent indices of availability rather than true availability. Nevertheless, our indices of availability should be useful in examining the availability of a species to a given observer.

We tested observations of each species for spatial autocorrelation with Mantel tests (Legendre and Legendre 1998). We calculated the Mantel test statistic (Mantel 1967) between a geographical distance matrix and a presence–absence matrix for each focal species. We calculated probability values by using 10 000 random permutations.

We used our availability models to assess the effect of a 1-week shift in phenology on the number of individuals perceived in the month of June. We chose a 1-week shift because Butler (2003) found that, in North America, migrants arrived approximately 8 days earlier between 1951 and 1993 than between 1903 and 1950. Also, in Wisconsin, spring events (e.g., trees blossoming, migrants' arrival, nest dates) shifted 7 days earlier over a 61-year period (Bradley et al. 1999). Because bird phenology is assumed to have shifted 1 week earlier, we can estimate previous (historical) bird availability by shifting our observed curve 1 week later. For each species we calculated the difference between the area under the detection curve as observed in 2008 and the area under the curve shifted 1 week later (Fig. 1). The area under the detection curve represents the number of times a species was available for detection (hereafter "detections") per survey station during the study period, given that the species was present. Therefore, the difference between the areas under the 2008 curves and the curves shifted by 1 week represents the change in the number of detections if breeding phenology shifted by 1 week. We calculated detections during June because that is when the majority of BBS surveys are conducted (Sauer et al. 2008).
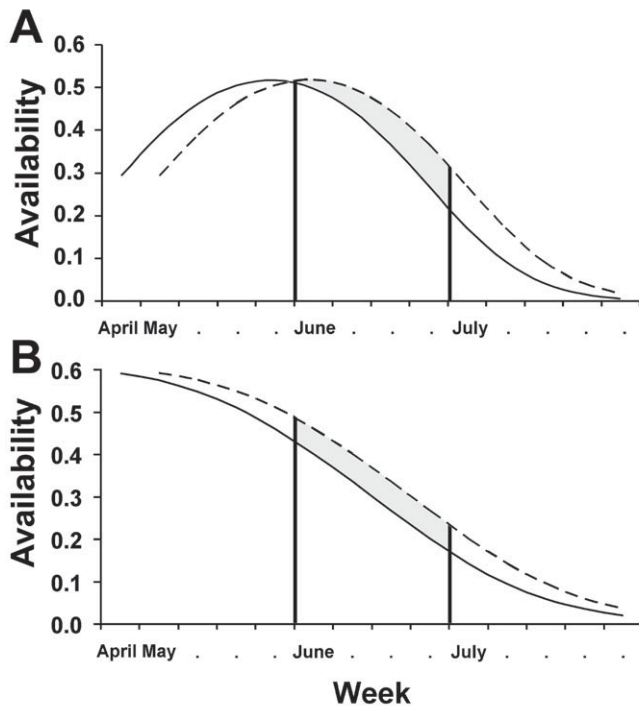
FIGURE 1.   Method for calculating changes in the number of detections per survey of the Acadian Flycatcher (a) and Great Crested Flycatcher (b). The change in the number of detections was calculated as the difference between the areas under the observed curve (solid) and the curve shifted a week later during the month of June.

Because populations of many neotropical migrants began declining in approximately 1978 (Robbins et al. 1989), we calculated changes in observed abundance on the basis of all BBS routes (50 stops at 0.8-km intervals) within the state of Alabama ($n = 102$) for the entire BBS dataset 1966–2007, and from 1978 to 2007 separately (Sauer et al. 2008). We calculated trends in populations from data in Sauer et al. (2008) by using a linear route-regression approach based on estimating equations with the methods described by Geissler and Sauer (1990). This analysis method is commonly used to estimate trends in BBS data (e.g., Robbins et al. 1989, Martin and Finch 1995, Link and Sauer 1998). These estimating equations control for observer differences in detectability (Sauer et al. 1994b, Link and Sauer 1998) but do not incorporate yearly changes in the proportion of birds sampled due to shifts in availability. We considered populations showing nonsignificant trends ($P > 0.05$) in BBS data to be unchanged. We used general linear models to determine if the observed trends in BBS data could be a function of changing bird availability and migratory status. We built models representing four hypotheses to predict the trends in BBS data: (1) a null model containing only the intercept, (2) a model containing a binary factor indicating the migratory status of each species (1 = migrant, 0 = resident), (3) a model containing the calculated change in availability, and (4) a model containing both the binary factor indicating migratory status and the change in availability.

Using AIC_c (Burnham and Anderson 2002), we ranked and compared models separately for BBS trends 1967–2007 and 1978–2007.

It is possible that the heights and slopes of availability curves during 2008 are not representative of a species' average availability from year to year. However, species of birds are often stereotyped with respect to the stage of nesting at which they peak in song rate (e.g., Slagsvold 1977, Logan 1983, Lampe and Espmark 1987). In fact, Slagsvold (1977) suggested that song rate could be used to analyze breeding status. Therefore, even if the heights and slopes of curves calculated from 2008 data are not completely accurate representations of a species' availability, the locations of peaks are likely to be representative. We therefore performed a binomial test to determine if the direction of the change in availability (increasing, decreasing, or stable) could correctly predict the direction of observed trends in BBS data. Thus species with trends in detection that matched the trends in BBS data received a "1," and species with trends in detection that differed from BBS trends received a "0." We analyzed BBS trends 1967–2007 and 1978–2007 separately. This binomial test should be robust to uncertainty in the heights and slopes of availability curves as well as to uncertainty in the magnitude of shifts in phenology because it simply analyzes whether the direction of BBS trends matches the direction of changes in availability, regardless of magnitude.

As a means to test the assumption that the population trends in the vicinity of Tuskegee National Forest are representative of changes in bird abundance across the state of Alabama, we examined data from the BBS route that runs through Tuskegee National Forest (Warrior Stand). Using a Pearson's product-moment correlation test, we tested for correlations between trends on the Warrior Stand route relative to trends for birds across all BBS routes in Alabama from 1967 to 2007 and between our calculated changes in availability within Tuskegee National Forest and population trends along the Warrior Stand route. We used R version 2.9.2 (R Development Core Team 2009) for all statistical analyses.

RESULTS

Of 48 bird species detected during the study, 31 were detected on at least four counts, and we analyzed availabilities of those 31 species only. The Prothonotary Warbler, Common Yellowthroat, and Red-winged Blackbird (see Table 1 for scientific names) had competitive models within two AIC_c units of the top model (Table 1), so we model-averaged across their entire model sets to develop their final models. Eleven species showed correlations between availability and the week in which observations were made (Table 1, Fig. 2), indicating changes in availability within the study period. Mantel tests revealed significant ($P < 0.05$) spatial autocorrelation for the Red-eyed Vireo ($r = 0.08$) and Northern Parula ($r = 0.10$). We recognize that this may lead to an increased rate of type I

TABLE 1.   Coefficient values (β) and standard errors (SE) in final models of bird availability, as well as deviance, the difference in AIC$_c$ between a given model and the top-ranked model (ΔAIC$_c$), and model weights (w_i) for generalized linear mixed models examining bird availability in Tuskegee National Forest from late April through July 2008. Models represent hypotheses of unchanging availability (intercept), linear association with the week in which an observation was made (week), and quadratic association with the week in which an observation was made (week^2).

Species	Model	β (SE)	Deviance	ΔAIC$_c$[a]	w_i
Great Blue Heron	Week^2	−0.19 (0.119)	25.6	0 (34.68)	0.78
(*Ardea herodias*)	Week	1.62 (1.088)	30.78	2.73	0.20
	Intercept	−3.62 (2.341)	37.14	6.77	0.03
Red-shouldered Hawk	Intercept	−2.08[b] (0.306)	75.35	0 (79.46)	0.56
(*Buteo lineatus*)	Week		74.72	1.49	0.27
	Week^2		73.45	2.37	0.17
Mourning Dove	Intercept	−2.39[b] (0.485)	34.06	0 (38.28)	0.52
(*Zenaida macroura*)	Week^2		30.6	1.08	0.31
	Week		34.06	2.22	0.17
Yellow-billed Cuckoo	Intercept	−1.57[b] (0.24)	112.06	0 (116.16)	0.65
(*Coccyzus americanus*)[c]	Week		112.06	2.1	0.23
	Week^2		111.24	3.43	0.12
Red-bellied Woodpecker	Intercept	−1.6[b] (0.34)	64.1	0 (68.28)	0.65
(*Melanerpes carolinus*)	Week		63.79	1.88	0.26
	Week^2		63.61	3.94	0.09
Downy Woodpecker	Intercept	−2.31[b] (0.316)	25.6	0 (34.68)	0.78
(*Picoides pubescens*)	Week		30.78	2.73	0.20
	Week^2		37.14	6.77	0.03
Pileated Woodpecker	Intercept	−2.247 (0.581)	85.76	0 (89.85)	0.44
(*Dryocopus pileatus*)	Week		83.9	0.23	0.39
	Week^2		83.53	1.99	0.16
Eastern Wood-Pewee	Intercept	−1.45[b] (0.393)	40.9	0 (45.21)	0.58
(*Contopus virens*)[c]	Week		39.73	1.16	0.32
	Week^2		39.7	3.57	0.10
Acadian Flycatcher	Week^2	−0.06[b] (0.021)	129.3	0 (137.60)	0.99
(*Empidonax virescens*)[c]	Week	0.61[b] (0.276)	140.41	8.99	0.01
	Intercept	−1.429 (0.897)	157.27	23.76	0.00
Great Crested Flycatcher	Week	−0.29[b] (0.064)	124.14	0 (130.34)	0.56
(*Myiarchus crinitus*)[c]	Week^2		122.48	0.48	0.44
	Intercept	1.07[b] (0.468)	149.57	23.33	0.00
White-eyed Vireo	Week^2	−0.04[b] (0.015)	159.14	0 (167.45)	0.70
(*Vireo griseus*)[c]	Intercept	−2.76[b] (0.86)	165.91	2.56	0.20
	Week	0.58[b] (0.238)	165.2	3.93	0.10
Yellow-throated Vireo	Intercept	−1.68[b] (0.328)	60.89	0 (65.07)	0.69
(*Vireo flavifrons*)[c]	Week		60.84	2.14	0.23
	Week^2		60.74	4.29	0.08
Red-eyed Vireo	Week	−0.14[b] (0.043)	219.36	0 (225.50)	0.73
(*Vireo olivaceus*)[c]	Week^2		219.34	2.08	0.26
	Intercept	1.13[b] (0.48)	229.88	8.45	0.01
Blue Jay	Week^2	−0.07[b] (0.02)	139.33	0 (147.61)	0.99
(*Cyanocitta cristata*)	Intercept	−3.94[b] (0.206)	154.64	11.11	0.00
	Week	0.95[b] (0.303)	154.26	12.81	0.00
Fish Crow	Intercept	−1.15[b] (0.359)	104.15	0 (108.28)	0.47
(*Corvus ossifragus*)	Week		102.51	0.5	0.36
	Week^2		101.84	2.01	0.17
American Crow	Intercept	−1.4[b] (0.038)	150.08	0 (154.16)	0.55
(*Corvus brachyrhynchos*)	Week		149.07	1.07	0.32
	Week^2		148.84	2.95	0.13
Carolina Chickadee	Intercept	−1.91[b] (0.224)	137.02	0 (141.09)	0.59
(*Poecile carolinensis*)	Week		136.32	1.37	0.30
	Week^2		136.2	3.34	0.11

TABLE 1.   Continued.

Species	Model	β (SE)	Deviance	ΔAIC$_c$[a]	w_i
Tufted Titmouse	Week	−0.1[b] (0.04)	224.1	0 (230.27)	0.57
(*Baeolophus bicolor*)	Week^2		223.1	1.04	0.34
	Intercept	0.16 (0.4)	229.8	3.61	0.09
Carolina Wren	Intercept	−0.23 (0.182)	243.64	0 (247.71)	0.65
(*Thryothorus ludovicianus*)	Week		243.46	1.88	0.26
	Week^2		243.44	3.96	0.09
Blue-gray Gnatcatcher	Intercept	−1.54[b] (1.053)	153.03	0 (157.10)	0.66
(*Polioptila caerulea*)	Week		153.03	2.08	0.23
	Week^2		152.53	3.68	0.11
Northern Parula	Week^2	−0.07[b] (0.026)	102.01	0 (110.35)	0.96
(*Parula americana*)[c]	Week	0.66[b] (0.333)	110.32	6.17	0.04
	Intercept	−2.26[b] (1.003)	120.05	13.8	0.00
Prothonotary Warbler	Week^2	−0.05 (0.048)	56.35	0 (65.01)	0.66
(*Protonotaria citrea*)[c]	Week	0.12 (0.551)	59.91	1.28	0.34
	Intercept	0.75 (1.39)	82.49	21.67	0.00
Pine Warbler	Week	−0.5[b] (0.168)	40.4	0 (46.77)	0.58
(*Dendroica pinus*)	Week^2		38.78	0.62	0.42
	Intercept	0.77 (0.761)	57.42	14.83	0.00
Louisiana Waterthrush	Week	−0.27[b] (0.129)	41.62	0 (47.93)	0.64
(*Parkesia motacilla*)[c]	Week^2		41.2	1.8	0.26
	Intercept	−0.71 (0.718)	47.47	3.7	0.10
Common Yellowthroat	Week^2	−0.01 (0.0188)	82.77	0 (91.42)	0.39
(*Geothlypis trichas*)	Week	0.27 (0.32)	85.52	0.49	0.31
	Intercept	−1.34 (1.26)	87.78	0.54	0.30
Hooded Warbler	Intercept	−1.53[b] (0.285)	78.83	0 (82.98)	0.42
(*Wilsonia citrina*)[c]	Week^2		75.16	0.69	0.30
	Week		77.46	0.78	0.28
Eastern Towhee	Intercept	−1.5[b] (0.464)	40.75	0 (45.06)	0.66
(*Pipilo erythrophthalmus*)	Week		40.74	2.31	0.21
	Week^2		39.18	3.21	0.13
Summer Tanager	Week^2	−0.11[b] (0.042)	71.12	0 (79.49)	0.99
(*Piranga rubra*)[c]	Intercept	−7.3[b] (2.335)	84.87	9.49	0.01
	Week	1.68[b] (0.637)	84.87	11.6	0.00
Northern Cardinal	Intercept	−0.16 (0.213)	242.54	0 (246.61)	0.64
(*Cardinalis cardinalis*)	Week		242.54	2.07	0.23
	Week^2		241.44	3.06	0.14
Indigo Bunting	Week	0.11[b] (0.05)	160.01	0 (166.19)	0.61
(*Passerina cyanea*)[c]	Week^2		159.97	2.08	0.21
	Intercept	−1.74[b] (0.508)	164.54	2.44	0.18
Red-winged Blackbird	Week^2	−0.03 (0.037)	41.05	0 (49.84)	0.45
(*Agelaius phoeniceus*)	Week	0.18 (0.474)	43.75	0.38	0.37
	Intercept	−1.79 (1.64)	47.48	1.88	0.18

[a] Minimum AIC$_c$ value in parentheses.

[b] Confidence interval does not include zero.

[c] Migrant.

error for these two species (Dormann et al. 2007) but believe that it does not affect the inference drawn from our study because visual inspection of the data shows obvious changes in availability throughout the study period (Fig. 2). It should also be noted that our data are far more likely to suffer from spatial autocorrelation than are BBS data because the distance between our survey stations is 200 m, while the distance between BBS stops is 800 m.

The availabilities of migrant species were more likely than those of residents to change through the sampling period: that of eight of 13 migrants but only three of 18 residents changed (Fisher's exact test, $P = 0.02$). The intercept-only model was the best predictor of BBS trends 1967–2007 and 1978–2007 (Table 2). The model containing the calculated change in availability showed a nonsignificantly negative correlation between the BBS trends and change in availability
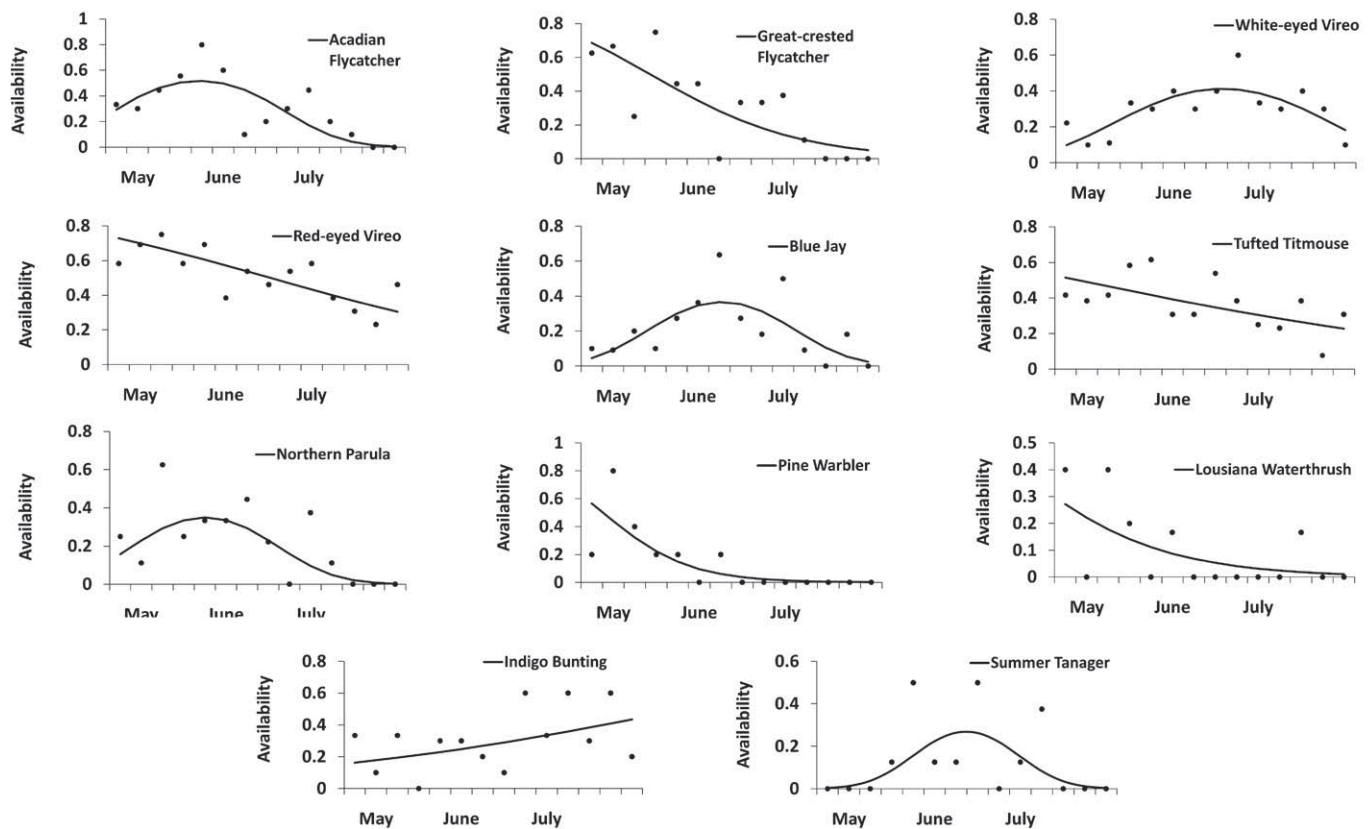
FIGURE 2. Results of generalized linear mixed models for birds showing changes in availability from late April through July 2008 in Tuskegee National Forest Alabama. Points represent the weekly average availability of a given species.

TABLE 2. Deviance, the difference in AICc between a given model and the top-ranked model (ΔAIC_c), and model weight (w_i) for general linear models describing the relationship between population trends according to the Breeding Bird Survey (BBS) and change in availability (Δ availability), migratory status, and both change in availability and migratory status (Δ availability + migratory status). Models were built from BBS data from 1967–2007 and 1978–2007 separately.

Interval	Model	Deviance	ΔAIC_c [a]	w_i
1967–2007	Intercept only	100.31	0.00	0.52
	Δ Availability	97.14	1.47	0.25
	Migratory status	99.99	2.36	0.16
	Δ Availability + migratory status	97.14	4.12	0.07
1978–2007	Intercept only	111.30	0.00	0.49
	Δ Availability	106.53	1.10	0.28
	Migratory status	111.14	2.41	0.15
	Δ Availability + migratory status	106.46	3.73	0.08

[a] Minimum AIC_c values are 128.80 for 1967–2007 and 132.03 for 1978–2007.

(1967–2007: $\beta = -4.027$, SE = 4.141, $t = -0.972$, $P = 0.339$; 1978–2007: $\beta = -4.943$, SE = 4.337, $t = -1.140$, $P = 0.264$; Fig. 3). The direction of the change in detections matched the direction of BBS trends of 13 species for the entire BBS dataset (Table 3, binomial test: $P = 0.10$) and 12 species from 1978 to 2007 (Table 3, binomial test: $P = 0.07$). Therefore, we could not reject the hypothesis that the direction of the change in availability was random with respect to the direction of trends in the BBS. Population trends along the Warrior Stand route were significantly correlated with BBS trends across Alabama ($r = 0.39$, $t = 2.27$, df = 28, $P = 0.03$) and were not correlated with calculated changes in availability within Tuskegee National Forest ($r = -0.22$, $t = -1.22$, df = 28, $P = 0.23$).

DISCUSSION

A critical assumption of animal surveys that are conducted at the same time each year, like the BBS, is that the availability of target species does not change systematically over the years. To begin to assess this assumption we first have to understand how the availability of various bird species changes

TABLE 3. Trends in the Breeding Bird Survey and associated variances 1967–2007 and 1978–2007 for the state of Alabama, as well as the change in the number of detections (Δ detections) per survey calculated as the difference between area under curves of observed availability and curves shifted 1 week later to estimate past availability[a].

Species	1967–2007	Variance	1978–2007	Variance	Δ Detections
Great Blue Heron	5.52***	1.25	5.37***	1.59	0
Red-shouldered Hawk	1.07	1.94	0.28	0.58	0
Mourning Dove	−1.38**	0.14	−2.41***	0.15	0
Yellow-billed Cuckoo[b]	−2.31***	0.04	−3.00***	0.08	0
Red-bellied Woodpecker	−0.04	0.14	−0.46	0.16	0
Downy Woodpecker	−1.83**	0.25	−2.09**	0.42	0
Pileated Woodpecker	1.35*	0.39	1.16	0.47	−0.08
Eastern Wood Pewee[b]	−2.35***	0.16	−2.26**	0.39	0
Acadian Flycatcher[b]	0.63	0.27	1.13*	0.21	−0.29
Great Crested Flycatcher[b]	1.58***	0.13	1.4**	0.17	−0.22
White-eyed Vireo[b]	0.76*	0.10	0.5	0.13	0.05
Yellow-throated Vireo[b]	0.58	0.77	1.56	0.71	0
Red-eyed Vireo[b]	1.23*	0.24	0.8	0.17	−0.14
Blue Jay	−2.38***	0.14	−1.78**	0.22	−0.04
Fish Crow	−1.10	1.53	−1.19	2.05	0
American Crow	0.29	0.95	1.04**	0.07	0
Carolina Chickadee	−1.95***	0.16	−3.01***	0.48	0
Tufted Titmouse	0.41	0.20	0.72	0.15	−0.09
Carolina Wren	0.33	0.09	0.65	0.11	0
Blue-gray Gnatcatcher	0.48	0.40	−0.34	0.64	0
Northern Parula[b]	1.15	1.06	0.44	0.79	−0.02
Prothonotary Warbler[b]	−3.79***	0.19	−3.63**	0.84	−0.34
Pine Warbler	0.37	0.19	−0.72	0.35	−0.10
Louisiana Waterthrush[b]	−0.29	2.48	−1.52	2.45	−0.06
Common Yellowthroat	0.03	0.68	0.58	0.54	0
Hooded Warbler[b]	2.28***	0.29	1.35*	0.27	0
Eastern Towhee	−0.86**	0.07	−0.51	0.13	0
Summer Tanager[b]	0.01	0.19	−0.5	0.13	−0.01
Northern Cardinal	−0.63**	0.04	−0.28	0.06	0
Indigo Bunting[b]	−0.67	0.13	−0.23	0.08	0.08
Red-winged Blackbird	−4.46***	0.26	−5.71***	0.22	−0.09

[a] Probabilities: *$P < 0.05$, **$P < 0.01$, ***$P < 0.0001$
[b] Migrant.

within a breeding season. By analyzing intervals of bird songs recorded through the breeding season in southern Alabama, we were able to show that the availability of many species varies seasonally. Furthermore, the availability of migrants changed more within a breeding season than did the availability of residents. These patterns likely reflect the synchrony of breeding of migratory birds being greater than that of residents (Spottiswoode and Møller 2004). Greater synchrony leads to the population-wide availability of migratory species during the breeding season being more distinct than that of residents (Slagsvold 1977).

Many resident birds begin breeding before the period that we monitored in this study (Haggerty 2009), which may explain why we failed to observe a peak in detection for some species—for these species detection likely peaked before we began our observations. Resident birds may also defend territories year round, resulting in a more constant song rate and availability (Best 1981). Our results suggest that although some residents' availability varies seasonally, change in availability through the breeding season is more characteristic of migratory species.

Our observations of systematic changes in the availability of some species support the prediction that a shift in peak availability would cause a change in the availability of many species on the BBS. As a group, migrants showed a stronger effect of date on availability, and for most migrants the outcome of the change in availability was reduced detections. Such declines in the availability of species could resemble

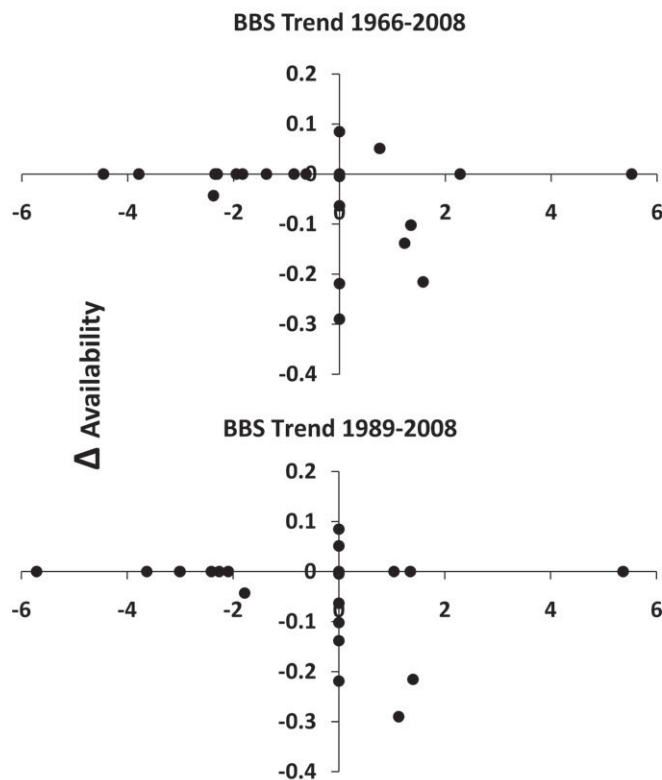## BBS Trend 1966–2008

BBS Trend 1989–2008

FIGURE 3. Scatterplot of population trends according to the Breeding Bird Survey (BBS) and the assumed changes in availability for each species analyzed.

declines in abundances if counts taken on the same date each year were compared. Thus the pattern of decline in neotropical migrants with respect to resident birds is consistent with the hypothesis that such changes are due to changes in a species' availability rather than to true population declines.

We tested this hypothesis by looking for correlations between predicted changes in the number of detections and the population trends observed in the BBS dataset. We found that the shifts in availability were not correlated with observed trends in BBS data in Alabama. Interestingly though, since the 1970s, the mean date on which BBS routes are run within the state of Alabama has moved forward by roughly 7 days (Sauer et al. 2008). This 7-day change in count date may offset the 7-day change in bird phenology. The reason for the change in count date is unknown, but we can speculate that the birders who run the routes may be compensating for the phenologies of breeding birds shifting earlier. Whether there has been such a shift in count dates beyond Alabama remains to be assessed.

This study shows seasonal changes in the availability of several species of birds while controlling for weather, time of day, and observer effects. By using sound recordings we were able to examine each survey thoroughly, thus controlling for bias due to observer effects or misidentification. However, the use of audio recordings allowed for accurate detection (or nondetection) at the species level only because individuals could not be accurately counted or tracked. We believe that the use of presence/absence data to address the utility of programs used to estimate trends in abundance is valid because the availability of a species during surveys is a function of the availabilities of individuals of that species (Royle and Nichols 2003). This study was designed to assess broad changes in the availability of birds, regardless of habitat. Our estimates of availability are likely higher than those encountered during BBS surveys because of our longer count period (Dawson et al. 1995, Thompson and Schwalbach 1995, Dettmers et al. 1999). However, because availability is a function of song rate, and thus phenology, we expect the seasonal changes of availability during BBS surveys to mirror our estimates. We believe that our availability estimates approximate availability during BBS surveys within Alabama and that the relationship between seasonal bird availability and BBS trends should hold for the BBS in general.

The timing of breeding of other taxa such as amphibians and butterflies is also shifting in accordance with climate change (reviewed in Parmesan 2007). Many of these species are monitored by large-scale, annual surveys that may also be affected by changes in availability due to climate change (Weir et al. 2005, Kéry and Plattner 2007), reinforcing calls for all monitoring programs to incorporate the probability of detection into population estimates (e.g., Anderson 2001, Weir et al. 2005, Kéry and Plattner 2007). Furthermore, other bird-monitoring programs, such as the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante 1992), that use survey methods other than point counts are also susceptible to changes in bird phenology because the data are collected within fixed dates every year.

Because song rate is correlated with nesting stage (Best 1981, Best and Petersen 1982, Wilson and Bart 1985) and pairing status (Sayre et al. 1980, Hayes et al. 1986, Gibbs and Wenny 1993), we can make inferences about the breeding phenology of migratory species based on availability at our study site (Slagsvold 1977). For instance, in the Louisiana Waterthrush song rate peaks prior to pair formation (Craig 1981), so the falling availability curve that we observed for the Louisiana Waterthrush suggests that most male waterthrushes on our study site had paired prior to the beginning of our surveys. Similarly, the Acadian Flycatcher's song rate decreases after the young hatch (Wiley 2005), and the falling availability curve that we observed for the Acadian Flycatcher indicates that most of the young had hatched by June. Inferences about nesting stage deduced from availability curves must be made cautiously but may be useful when logistical constraints prohibit intensive nest searching and monitoring.

Our results suggest that, if global warming is causing birds to breed earlier, the availability of migratory species will decline during June. A change in availability over time may induce trends within data recorded between fixed dates every year. However, this decrease in availability is not inducing the

current trends in bird abundance observed in BBS data within the state of Alabama. The effects of changing phenology may have been offset in Alabama by survey dates shifting earlier within June. The effect of shifting phenology on bird availability and hence on trends in bird abundance should be tested in other regions of North America and on other sets of long-term data recorded within fixed dates.

ACKNOWLEDGMENTS

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