

Consequences of rainfall variation for breeding wetland blackbirds

Robert J. Fletcher, Jr. and Rolf R. Koford

Abstract: Annual variability in abiotic factors can be pronounced, especially in systems that rely on precipitation, such as arid regions and prairie potholes. We report how annual variation in precipitation from 1999 to 2002 in the Prairie Pothole Region of Iowa, USA, affected both density and reproduction of two interspecific competitors: yellow-headed blackbirds, *Xanthocephalus xanthocephalus* (Bonaparte, 1826), and red-winged blackbirds, *Agelaius phoeniceus* (L., 1766). During dry years, yellow-headed blackbirds, an obligate wetland-breeding species, showed a marked reduction in density and a complete reproductive failure in which none of the nests we monitored fledged young. The reproductive failure was attributed primarily to nest predation, which was negatively correlated with water levels in wetlands. Conversely, red-winged blackbirds, a facultative wetland-breeding species, showed little variation in density and nest success. Both species exhibited similar patterns of reduced clutch size and later nest initiation dates in dry years, measures often tied to bottom-up effects of food availability and (or) age of individuals. Yet top-down effects of nest predation had a stronger influence, because lower clutch size did not result in fewer young fledged per successful nest. Incorporating how rainfall variation can affect wetland songbird demography will be critical for understanding population and community dynamics in changing environments.

Résumé : La variabilité annuelle des facteurs abiotiques peut être importante, particulièrement dans les systèmes qui dépendent des précipitations, tels que les régions arides et les étangs (« fondrières ») des prairies. Nous décrivons comment la variation annuelle des précipitations de 1999 à 2002 dans la région des fondrières des prairies de l'Iowa, États-Unis, a affecté tant la densité que la reproduction de deux compétiteurs interspécifiques, le carouge à tête jaune (*Xanthocephalus xanthocephalus* (Bonaparte, 1826)) et le carouge à épauettes (*Agelaius phoeniceus* (L., 1766)). Les années sèches, le carouge à tête jaune, qui se reproduit obligatoirement dans les terres humides, subit une réduction marquée de sa densité et rate complètement sa reproduction, car aucun des nids que nous avons observés n'a produit de petits prêts à l'envol. L'échec de la reproduction est attribué principalement à la prédation qui est en corrélation négative avec le niveau de l'eau dans les terres humides. En revanche, le carouge à épauettes, qui se reproduit de façon facultative dans les terres humides, subit peu de variation de sa densité et du succès de sa reproduction. Les années de sécheresse, les deux espèces réduisent de façon semblable la taille de leurs couvées et retardent la date de leur nidification, des mesures souvent reliées aux effets ascendants de la disponibilité de la nourriture et (ou) de l'âge des individus. Néanmoins, les effets descendants de la prédation au nid ont une influence prépondérante, parce que la taille réduite de la couvée n'entraîne pas de diminution du nombre de petits prêts à l'envol dans les nids où la reproduction est réussie. L'incorporation du rôle des précipitations dans la démographie des oiseaux chanteurs est d'importance capitale pour comprendre la dynamique des populations et des communautés dans les environnements changeants.

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Introduction

The relative importance of abiotic and biotic processes in regulating populations and structuring communities has been the subject of long-standing debate in ecology (e.g., Davidson and Andrewartha 1948; MacArthur 1958; Martin 2001). In particular, the role of climate and climate variation has attracted renewed interest in light of global climate change (e.g., Root et al. 2003). Recent evidence suggests

that climate variation can have both direct and indirect effects on primary productivity, behavior, species distribution, population dynamics, species interactions, and natural selection (Post et al. 1999; Inouye et al. 2000; Sæther et al. 2000; Knapp and Smith 2001; Martin 2001; Grant and Grant 2002). Climate variation is thought to play a pivotal role in population and community dynamics in arid regions (Polis et al. 1997; Grant et al. 2000; Morrison and Bolger 2002), wetlands (Weller 1999), and other systems constrained by

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R.J. Fletcher, Jr.^{1,2} Iowa Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Science Hall II, Iowa State University, Ames, IA 50011, USA.

R.R. Koford. US Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Science Hall II, Iowa State University, Ames, IA 50011, USA.

¹Corresponding author (e-mail: robertjfletcherjr@yahoo.com).

²Present address: Avian Science Center, Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA.

either precipitation or temperature (e.g., Inouye et al. 2000; Sæther et al. 2000). Identifying the direct and indirect effects of climate variation on biotic processes will be critical for understanding the dynamics of populations and communities and their potential responses to global climate change (Martin 2001; Root et al. 2003).

Interannual variability in precipitation affects wetland conditions by altering both water levels and habitat structure (e.g., Weller 1999). This, in turn, can affect both habitat selection and fecundity of wetland-nesting birds. Some species, such as yellow-headed blackbirds (*Xanthocephalus xanthocephalus* (Bonaparte, 1826)), may not settle to breed in areas of poor wetland condition that occur because of low precipitation (Weller and Fredrickson 1974). Furthermore, fecundity may be compromised for at least two reasons: (1) variation in life-history parameters, in which certain parameters tied to fecundity, such as clutch size, are negatively affected by shallow water levels, and (2) variation in nest success, in which nest predation is positively affected by shallow water levels (Picman et al. 1993). Variation in reproductive life-history parameters has been correlated with “bottom-up” effects of food availability for many songbirds (Arcese and Smith 1988; Rodenhouse and Holmes 1992; Turner and McCarty 1998; but see Arnold 1992), and food availability has been linked to variable water levels in wetlands (Turner and McCarty 1998; Murkin and Ross 2000). However, “top-down” effects of predation are generally thought to be the primary factor responsible for nest success and fecundity in songbirds (Ricklefs 1969), and predation rates can vary relative to water depth and wetland conditions (Robertson 1972; Picman et al. 1993; Beissinger and Snyder 2002). Understanding the relative role of these potential forces with climate variation will be critical for interpreting the long-term viability of wetland populations constrained by climate.

We compare how interannual variation in precipitation in the Prairie Pothole Region of Iowa, USA, affected both density and reproduction of two wetland-breeding species, the yellow-headed blackbird, an obligate wetland breeder, and the red-winged blackbird (*Agelaius phoeniceus* (L., 1766)), a facultative wetland breeder. These species are related members of the family Icteridae (Lanyon and Omland 1999) that exhibit strong interspecific competition (Orians and Willson 1964), which is thought to be related to the vast overlap of their food resources and their preferences for similar nesting substrates (Orians and Willson 1964; Voigts 1973). Both species have recently declined in the Midwest, but yellow-headed blackbirds have declined at a greater rate than red-winged blackbirds (Fletcher and Koford 2003). In addition, we also untangle the importance of wetland conditions for direct and indirect forces that influence breeding birds by addressing diverse measures of reproductive output closely tied to predation and food limitation.

Methods

Study area

Our study area was located in Hancock and Winnebago counties, north-central Iowa, USA (43°N 94°W), as part of a larger study on the effects of habitat restoration on bird populations (Fletcher and Koford 2002, 2003). The study area

encompassed approximately 162 km² and contained a complex of federal waterfowl production areas (WPAs) and state wildlife management areas (WMAs) in an agricultural landscape. We focused on all WPAs and WMAs within the area that contained wetland potholes, totaling 10 restored wetland complexes, all of which also contained restored grassland surrounding wetland habitat. We considered wetland complexes as independent units and defined them as the total of all seasonal, semipermanent, and permanent wetlands (as defined in Cowardin et al. 1979) within a WPA or WMA (sensu Fairbairn and Dinsmore 2001). See Fletcher and Koford (2003) for detailed descriptions of restoration techniques for grassland and wetland habitat. Dominant wetland vegetation included cattails (*Typha* spp.), bulrush (*Scirpus* spp.), and reed canary grass (*Phalaris arundinacea* L.). Potential nest predators included raccoons (*Procyon lotor* (L., 1758)), striped skunks (*Mephitis mephitis* (Schreber, 1776)), mink (*Mustela vison* Schreber, 1777), plains garter snakes (*Thamnophis radix* (Baird and Girard, 1853)), American crows (*Corvus brachyrhynchos* Brehm, 1822), marsh wrens (*Cistothorus palustris* (Wilson, 1810)), and common grackles (*Quiscalus quiscula* (L., 1758)) (Sawin et al. 2003).

Bird surveys

From 1999 to 2002, we surveyed breeding birds using a standard protocol for wetlands (cf. Delphey and Dinsmore 1993; Ralph et al. 1995; Naugle et al. 1999). Each restored wetland complex was surveyed three times during the breeding season: 15 May to 5 June, 6–22 June, and 23 June to 5 July. We conducted wetland bird surveys using 8-min, 20-m fixed-radius point counts. Because wetland habitats are relatively small and narrow, a 20-m radius was used to reduce habitat heterogeneity within the surveyed area (see also Delphey and Dinsmore 1993; Naugle et al. 1999). Point-count locations were ≥ 75 m apart. Surveys were conducted between sunrise and 4 h after sunrise and were not conducted during windy conditions (wind velocity ≥ 20 km/h) or during precipitation. During surveys, observers recorded the following data for all birds seen or heard: how the individual was detected (song, visual, or call), sex, and distance from the center point. We did not include birds flying over points in our analyses. Distances (metres) to birds seen were estimated using a range finder.

Count locations were selected using a geographic information system (see Fletcher and Koford 2003 for details). We randomly selected three locations within each wetland complex using infrared aerial photographs taken in 1999 that were georeferenced and digitized using the geographic information system ($n = 8$ complexes; 2 complexes were not surveyed owing to small size but were used for monitoring of breeding biology; see below). Points were centered in the emergent vegetation zone or at the water's edge when no emergent vegetation was present (Delphey and Dinsmore 1993). We repeated surveys at each point-count location during each period ($n = 72$ points/year). Although wetland conditions varied among years (see Results), the same count locations were surveyed each year.

Breeding biology

In 1999, we systematically searched five of the wetland complexes for wetland bird nests; in 2000–2002, we system-

atically searched all wetland complexes ($n = 10$). We visited nests every 2–4 days to determine their fate. To minimize problems of assigning uncertain nest fates (Manolis et al. 2000), we considered a nest successful if at least one host nestling remained in the nest at day 7–8 (approximately 1 day before the earliest known fledging date for these species; Twedt and Crawford 1995; Yasukawa and Searcy 1995). Because we often found nests after the onset of incubation, we estimated the nest initiation date, defined as the first day of incubation, for each nest by estimating the age of eggs (using candlers; Lokemoen and Koford 1996) or nestlings (using descriptive accounts from known-aged nests). We defined the clutch size as the maximum number of host eggs observed in nests during the incubation stage. We initially analyzed clutch size for all nests, but we also analyzed only nonparasitized nests to determine whether patterns were consistent, because parasitism events could have reduced clutch sizes of parasitized nests. We defined the number of fledglings per successful nest as the number of host nestlings that remained in the nest on the final visit (day 7–8). We did not include nests that were abandoned because of observer activity in any analyses (red-winged blackbirds, $n = 11$; yellow-headed blackbirds, $n = 8$). We considered nests abandoned because of observers if the nest was abandoned on the first nest-monitoring visit after the nest had been found.

Climate variation

We compared the effects of precipitation at different scales. To examine density at the scale of the wetland, we measured water depth (centimetres) at point-count locations after each survey at four locations within the point-count area: one at the center of the point and three at locations 10 m from the center, at 0° , 120° , and 240° . To examine breeding success at local scales within wetlands, we measured water depth directly beneath nest sites when nests were initially found and when nests were terminated (2000–2002 only). These two measures were highly correlated ($r = 0.98$) and thus for analyses we used only water depth at the time of nest termination.

To examine the effects of precipitation at a larger temporal scale, we compared precipitation for each year during our study with long-term precipitation patterns gathered from 1932 to 2002 at a standard National Oceanic and Atmospheric Administration (NOAA) weather observation station located 7.5–23 km from the study sites (National Climate Data Center 2003). For analyses, we defined a “bioyear” as August of the preceding year to July of the current year (sensu Rotenberry and Wiens 1991; Morrison and Bolger 2002). To better interpret settlement patterns, we compared the amount of precipitation occurring from August of the preceding year to April of the current year, just prior to the onset of breeding in the species investigated (i.e., prebreeding season precipitation; sensu Morrison and Bolger 2002).

Statistical analyses

We calculated bird density (number of males or females/ha) for each species using the program Distance (Buckland et al. 2001). Distance uses distances from the center point to individuals to calculate detection functions and subsequently corrects for detectability when estimating

density. Density was estimated for each site in each year using a global detection function across years (see Fletcher and Koford 2002 for more details). Using these density estimates, we then tested for among-year differences in male and female densities (birds/ha) using a mixed-model analysis with site as a random effect and year as a repeated measure (Littell et al. 1996). This repeated measure was modeled by specifying four potential covariance structures: variance components, autoregressive order one, compound symmetric (exchangeable), and unstructured covariance (Littell et al. 1996, pp 93–102). We then selected the most parsimonious covariance structure using Akaike’s Information Criterion adjusted for small sample sizes (AIC_c ; Littell et al. 1996; Burnham and Anderson 1998). Density was log transformed ($\ln(x + 1)$) to improve normality and homogeneity of variance, but we report untransformed estimates for better interpretation. We tested for among-year differences in water depth measured at point-count locations using a similar repeated measures framework.

To untangle the effects of abiotic factors on reproduction, we tested two reproductive measures tied to top-down forces and four measures independent of top-down forces that are more closely tied to bottom-up effects due to food availability. Top-down parameters included nest parasitism from brown-headed cowbirds (*Molothrus ater* (Boddaert 1783)) and nest predation, both of which can have severe effects on fecundity (e.g., Pease and Grzybowski 1995). Other parameters included nest initiation date, clutch size, nestling survival rate within a nest, and the number of fledglings per successful nest. These parameters, particularly clutch size and nest initiation date, are commonly tied to food availability (reviewed in Arcese and Smith 1988). We considered nestling survival to be influenced by habitat quality based on food availability rather than predation pressure (see also Rodenhouse and Holmes 1992; Morrison and Bolger 2002). Clutch size and nestling survival, in turn, directly affect the number of fledglings per successful nest.

We tested for year effects on nest initiation dates using Kruskal–Wallis nonparametric tests (Rodenhouse and Holmes 1992). We tested for differences in clutch size and the number of fledglings per successful nest using a mixed-model analysis similar to that used for surveys. For clutch size, we also included nest initiation date (Julian date) as a covariate in models because clutch size can decline over time within breeding seasons (Arnold 1992).

We tested for year effects on partial brood loss by estimating individual nestling survival rates within nests using a modified Mayfield model that accounts for a lack of independence among nestlings within a nest by considering each nest as a clustered sampling unit (Flint et al. 1995). We right-censored data when nests terminated, either from fledging or failing, to focus on nestling mortality in the absence of predation pressure. We tested for year effects using the program CONTRAST (Hines and Sauer 1989; Flint et al. 1995).

We estimated daily predation rates (DPR) for nests using the Mayfield method (Mayfield 1975; Johnson 1979). We used the midpoint assumption for estimating failure dates between nest visits (Johnson 1979). We focused on DPR instead of daily survival rates (Johnson 1979) to isolate effects of predation, because some nests failed for reasons other

than predation (e.g., weather; see Results). We used CONTRAST (Hines and Sauer 1989; Sauer and Williams 1989) to test for differences in DPR among years for the incubation and nestling stages and for the entire nesting cycle. To further evaluate whether nest predation is directly linked to wetland water conditions, we developed models to explain the probability of nest predation for each species using generalized linear mixed models with a logit link function (Littell et al. 1996). Explanatory variables included year and water depth beneath nests. All possible combinations (including interactions) were compared with an intercept only model ($n = 5$ models), and the most parsimonious model was selected using AIC_c (Burnham and Anderson 1998). Because brown-headed cowbirds parasitized only four nests with >1 egg, we also tested for differences in the probability of brood parasitism among years using generalized linear mixed models with a logit link function, similar in structure to the mixed models described above.

Finally, we estimated overall nest productivity, NP , for each site each year as $NP = DSR^n F$, where DSR is the daily survival rate (which includes all sources of nest failure; Mayfield 1975; Johnson 1979), n is the number of days in the nesting cycle (red-winged blackbirds, 24 days; yellow-headed blackbirds, 25 days; Twedt and Crawford 1995; Yasukawa and Searcy 1995), and F is the number of host fledglings produced per successful nest. Nest productivity should not be confused with seasonal fecundity (or the number of young fledged per female each season), which requires estimates of renesting effort (Pease and Grzybowski 1995).

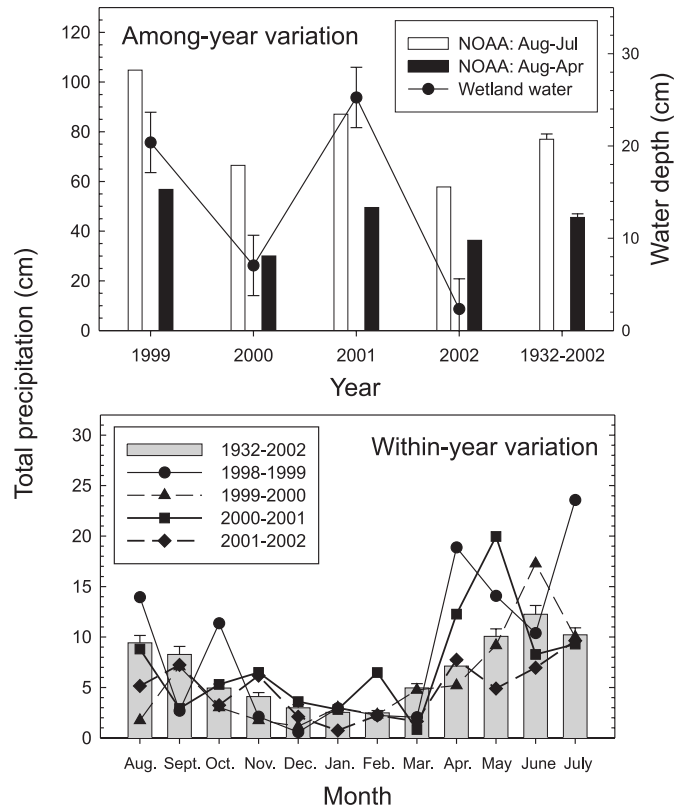
Prior to all analyses, we identified three orthogonal contrasts to interpret year effects on density, water depth, and reproduction: (1) contrasts between 1999 and 2001 (wet years hereafter; see Fig. 1), (2) contrasts between 2000 and 2002 (dry years hereafter), and (3) contrasts between the average of wet years and the average of dry years. We expected precipitation to govern any year effects and thus expected no evidence for differences between wet years or between dry years (contrasts 1 and 2), but we expected evidence for differences between the average of wet years and the average of dry years (contrast 3).

Results

Climate conditions

Water depth at point-count locations varied among years ($F_{[3,21]} = 25.64$, $P < 0.001$), with water depth being shallower in 2000 and 2002 than in 1999 and 2001 (Fig. 1). Based on contrasts, 1999 and 2001 did not differ ($F_{[1,21]} = 1.26$, $P = 0.275$), and 2000 and 2002 did not differ ($F_{[1,21]} = 1.18$, $P = 0.289$); however, water depth differed between wet years and dry years ($F_{[1,21]} = 67.68$, $P < 0.0001$). From NOAA data, estimates of bioyear (August–July) and prebreeding season (August–April) precipitation for 2000 and 2002 were lower than the 71-year average (1932–2002), whereas the estimates for 1999 and 2001 were above the 71-year average (Fig. 1). In each case, annual precipitation estimates were >2 standard errors above or below the long-term average. Total precipitation for the prebreeding season and for the bioyear was highest in 1999, compared with the other 3 years (Fig. 1). In 2000, conditions were dry prior to breed-

ing, but rainfall increased in June, increasing water levels within wetlands. In 2001, precipitation was high in May and then dropped off in June and July. In 2002, precipitation was low during the entire year, causing total bioyear precipitation to be the lowest over the 4 years (Fig. 1). Water depth in wetlands was more closely correlated with bioyear precipitation ($r = 0.88$) than with prebreeding season precipitation ($r = 0.83$).



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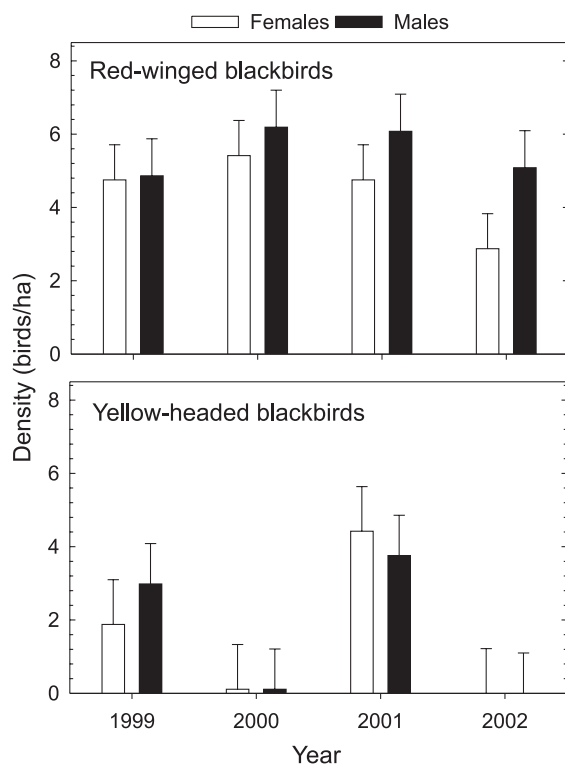
Bird density

Red-winged blackbirds were more commonly observed during point counts ($n = 385$ detections) than yellow-headed blackbirds ($n = 136$ detections). There was no evidence that red-winged blackbird density differed among years ($F_{[3,21]} < 0.68$, $P > 0.57$; Fig. 2). However, density of both male and female yellow-headed blackbirds varied among years ($F_{[3,21]} > 3.43$, $P < 0.036$; Fig. 2). Based on contrasts, yellow-headed blackbird density did not differ between wet

Table 1. Daily predation rates (DPR; mean \pm SE) for red-winged blackbird (*Agelaius phoeniceus*) and yellow-headed blackbird (*Xanthocephalus xanthocephalus*) nests in restored wetlands, northern Iowa, 1999–2002.

Year	No. of nests	No. of successes	Incubation cycle		Nestling cycle		Entire cycle	
			DPR	Exposure days	DPR	Exposure days	DPR	Exposure days
Red-winged blackbird								
1999	35	13	0.044 \pm 0.013	248.0	0.074 \pm 0.024	121.0	0.055 \pm 0.012	381.0
2000	72	21	0.062 \pm 0.012	436.0	0.090 \pm 0.020	200.0	0.074 \pm 0.010	650.5
2001	54	24	0.078 \pm 0.016	294.0	0.036 \pm 0.014	168.0	0.061 \pm 0.011	479.0
2002	67	27	0.065 \pm 0.014	321.5	0.064 \pm 0.017	202.0	0.071 \pm 0.011	538.5
Total	228	85	0.063 \pm 0.007	1299.5	0.067 \pm 0.009	691.0	0.066 \pm 0.005	2049.0
Yellow-headed blackbird								
1999	17	10	0.009 \pm 0.009	111.5	0.056 \pm 0.024	89.5	0.029 \pm 0.012	208.0
2000	1	0	—*	1.5	—	0.0	—	1.5
2001	72	40	0.011 \pm 0.004	649.0	0.034 \pm 0.010	352.0	0.019 \pm 0.004	1027.0
2002	14	0	0.105 \pm 0.038	66.5	0.417 \pm 0.142	12.0	0.148 \pm 0.038	88.0
Total	104	50	0.020 \pm 0.005	828.5	0.046 \pm 0.010	453.5	0.030 \pm 0.005	1324.5

*Not estimable: only 1 nest was found, which was depredated after 1.5 exposure days.

Fig. 2. Annual density estimates (birds/ha; mean \pm SE) for male and female red-winged blackbirds (*Agelaius phoeniceus*) and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) in restored wetlands, northern Iowa, 1999–2002.

years or between dry years ($F_{[1,21]} \leq 1.97$, $P \geq 0.17$), but densities were considerably higher in wet years than in dry years ($F_{[1,21]} > 8.30$, $P < 0.009$). Overall, yellow-headed and red-winged blackbird densities were weakly negatively correlated (Spearman's coefficient of rank correlation: $\rho = -0.294$, $n = 32$, $P = 0.10$).

Reproduction

Between 1999 and 2002, we monitored 228 red-winged

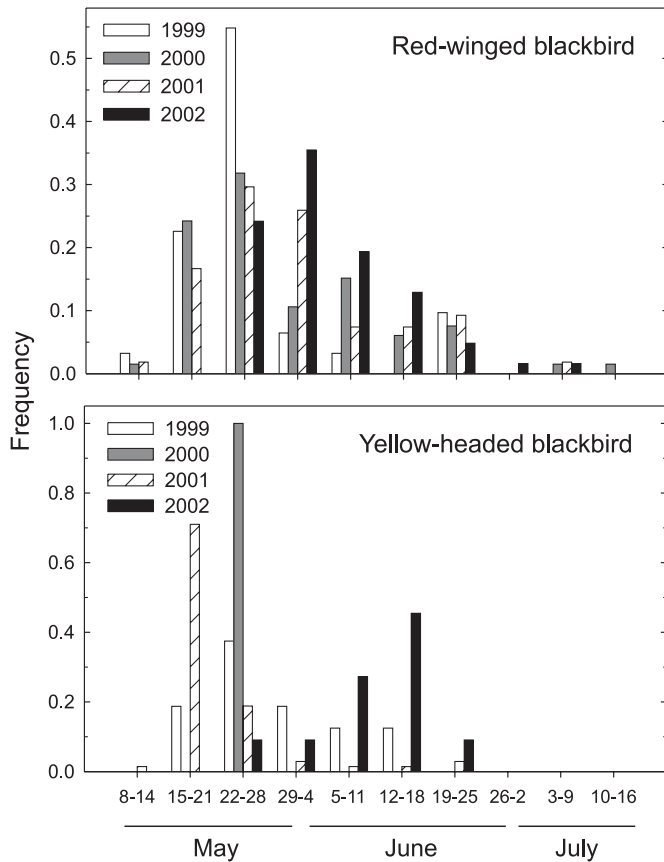
and 104 yellow-headed blackbird nests (Table 1). Red-winged blackbirds bred at all 10 sites, whereas yellow-headed blackbirds bred at only 4 sites. Nest initiation dates varied among years for both red-winged blackbirds ($\chi^2 = 25.50$, $df = 3$, $P < 0.0001$) and yellow-headed blackbirds ($\chi^2 = 39.27$, $df = 3$, $P < 0.0001$; Fig. 3). Nest initiation dates for red-winged blackbirds tended to be later in 2002 than in other years (Fig. 3). For yellow-headed blackbirds, nest initiation dates were later in both dry years than in the wet years, but only one nest was found in 2000, limiting inference for that year. However, in 2002 there was a dramatic shift in initiation dates in which the peak initiation occurred approximately 3 weeks later than peak initiation dates in wet years (Fig. 3).

When we controlled for clutch size variation as a function of Julian date, clutch size varied among years for red-winged blackbirds ($F_{[3,19]} = 3.92$, $P = 0.025$), with size being lower in dry years than in wet years ($F_{[1,19]} = 7.24$, $P = 0.015$; Fig. 4A), although size did not differ between wet years or between dry years ($F_{[1,19]} \leq 1.09$, $P \geq 0.310$). This relationship was also observed when only nonparasitized nests were analyzed ($F_{[3,19]} = 3.21$, $P = 0.046$). Yellow-headed blackbirds showed similar patterns in clutch size estimates (Fig. 4A), but patterns were not significant and were based on few sites, so inference is limited ($F_{[3,1]} = 2.30$, $P = 0.443$). Clutch size declined with Julian date in red-winged blackbirds ($F_{[1,161]} = 8.52$, $P = 0.004$) but showed little decline in yellow-headed blackbirds ($F_{[1,82]} = 2.72$, $P = 0.103$).

Partial brood loss from nestling mortality did not differ among years for red-winged blackbirds ($\chi^2 = 3.14$, $df = 3$, $P = 0.37$), but mortality differed among years for yellow-headed blackbirds ($\chi^2 = 59.03$, $df = 2$, $P < 0.001$; Table 2). For yellow-headed blackbirds, survival rates were lower in 2001 than in 1999 ($\chi^2 = 8.45$, $df = 1$, $P = 0.0037$), but survival rates could not be compared between wet and dry years because of the small sample size in dry years (5 nests, each of which was depredated after the first monitoring visit during the nestling stage).

In red-winged blackbirds, nest predation and abandonment accounted for 95.1% and 2.8% of nest failures, respec-

Fig. 3. Distribution of nest initiation dates (i.e., first day of incubation) for red-winged and yellow-headed blackbirds in restored wetlands, northern Iowa, 1999–2002.



tively. In yellow-headed blackbirds, predation and abandonment accounted for 74.1% and 24.1% of nest failures, respectively. DPR for red-winged blackbirds did not differ among years for the entire nesting cycle ($\chi^2 = 2.011$, $df = 3$, $P = 0.570$) or for either the incubation or the nestling stages ($\chi^2 < 5.58$, $df = 3$, $P > 0.13$). In 2000 and 2002, yellow-headed blackbirds experienced a complete reproductive failure in which all of the nests we monitored failed (Table 1). In these dry years, predation accounted for 93% of nest failure. DPR for yellow-headed blackbirds differed among years for the entire nesting cycle (2000 not included because only one nest was found: $\chi^2 = 11.86$, $df = 2$, $P = 0.003$) and for both the incubation and the nestling stages ($\chi^2 > 6.14$, $df = 2$, $P < 0.047$). For each stage and for the entire cycle, DPR for yellow-headed blackbirds did not differ between wet years ($\chi^2 < 0.72$, $df = 1$, $P > 0.42$) but was much higher in dry years than in wet years ($\chi^2 > 6.14$, $df = 1$, $P < 0.014$). Daily survival rates, which included all sources of nest failure, showed similar patterns (see Fletcher 2003).

The best model to explain the probability of predation for red-winged blackbirds included only water depth beneath nests ($\text{logit}(y) = 0.57 - 0.01(\text{nest})$; nest, $F_{[1,176]} = 2.13$, $P = 0.15$), but precision for parameter estimates in this model was low (Fig. 5). Likewise, the best model to explain the probability of predation for yellow-headed blackbirds included only the water depth beneath nests ($\text{logit}(y) = 2.78 - 0.06(\text{nest})$; nest, $F_{[1,69]} = 8.80$, $P = 0.004$; Fig. 5). There was

no evidence that parasitism rates for red-winged blackbirds differed among years (Fig. 4B; $F_{[3,19]} = 1.46$, $P = 0.256$). Contrasts revealed weak evidence for higher parasitism rates in dry years than in wet years ($F_{[1,19]} = 3.31$, $P = 0.084$) but no evidence that parasitism rates differed between wet years or between dry years ($F_{[1,19]} \leq 0.87$, $P \geq 0.361$). None of the 104 yellow-headed blackbird nests were parasitized by brown-headed cowbirds.

The number of red-winged blackbird nestlings fledged per successful nest did not differ among years ($F_{[3,16]} = 1.94$, $P = 0.163$; Fig. 4C). For yellow-headed blackbirds, the number of nestlings fledged per successful nest tended to be lower in 2001 than 1999, but inference is limited because patterns were based on few sites (Fig. 4C). Finally, although overall nest productivity tended to be lower for both species during dry years, particularly for yellow-headed blackbirds (Fig. 4D), nest productivity did not differ across years for red-winged ($F_{[3,19]} = 1.94$, $P = 0.791$) or yellow-headed blackbirds ($F_{[3,3]} = 1.5$, $P = 0.374$).

Discussion

Abiotic variation among years had pronounced effects on both density and reproduction of yellow-headed blackbirds breeding in restored wetland potholes of northern Iowa, yet red-winged blackbirds exhibited only limited variation in their reproduction. The influence of water levels on wetland birds has been extensively investigated (e.g., Robertson 1972; Murkin et al. 1997; Beissinger and Synder 2002; Gawlik 2002), but we provide a unique comparative sketch of how interannual variation in water levels influences both habitat use and diverse measures of reproductive output in two avian competitors. Although effects on density and reproduction were stronger for yellow-headed blackbirds, red-winged blackbirds also exhibited variation in some reproductive measures. Why were effects more severe for yellow-headed blackbirds? The two species prefer similar nesting areas in wetlands (Orians and Willson 1964; Miller 1968), exhibit marked overlap in foraging preferences (Orians and Willson 1964; Voigts 1973), and are closely related phylogenetically (Lanyon and Omland 1999). However, yellow-headed blackbirds are considered obligate wetland breeders, being closely tied with distinct wetland conditions having emergent vegetation over deep water (Miller 1968), whereas red-winged blackbirds are more opportunistic, breeding in a variety of habitats (e.g., Miller 1968; Yasukawa and Searcy 1995). Differences in plasticity were exemplified by red-winged blackbirds breeding at all sites, whereas yellow-headed blackbirds bred at fewer than half (40%) of the sites investigated. The relative plasticity in these preferences between species may help explain differences in both density and reproduction (see below) because water levels are closely tied to both nest-site availability (Lederer et al. 1975) and predation risk (Robertson 1972; Picman et al. 1993).

Bird density and climate variation

Interannual variation in precipitation affected habitat use of yellow-headed blackbirds, which tended not to settle in the study area during dry years. Although the selection of point locations during a wet year (1999) could have pro-

Fig. 4. Annual estimates (mean + SE) of (A) clutch size, (B) brood parasitism rate (probability of parasitism), (C) number of fledglings per successful nest, and (D) nest productivity for red-winged and yellow-headed blackbirds in restored wetlands, northern Iowa, 1999–2002.

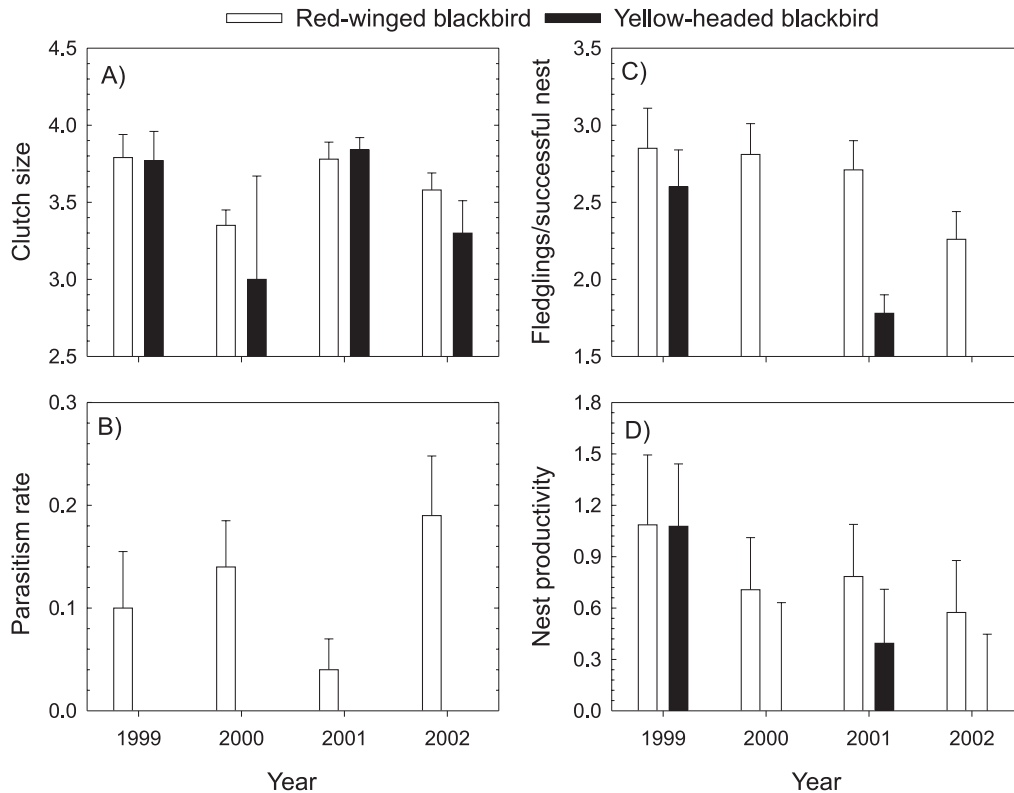


Table 2. Daily nestling survival rates within nests (DSR; mean \pm SE) for red-winged blackbird and yellow-headed blackbird nests in restored wetlands, northern Iowa, 1999–2002.

Year	No. of nests	No. of nestlings	Nestling mortality	Exposure days	DSR*
Red-winged blackbird					
1999	23	71	2	338	0.994 \pm 0.006
2000	36	115	7	524	0.987 \pm 0.005
2001	30	92	11	495	0.978 \pm 0.008
2002	36	95	8	449	0.982 \pm 0.007
Total	125	373	28	1806	0.984 \pm 0.003
Yellow-headed blackbird					
1999	17	36	5	215	0.977 \pm 0.012
2000	0	0	0	0	— [†]
2001	72	161	52	777	0.933 \pm 0.009
2002	5	11	0	14	1.000 \pm 0.000 [‡]
Total	104	208	57	1006	0.943 \pm 0.007

Note: Nests were right-censored for nest termination (failure or success) to isolate partial brood loss.

*Modified Mayfield estimates of DSR are based on considering nestlings within a nest as a clustered sampling unit (Flint et al. 1995).

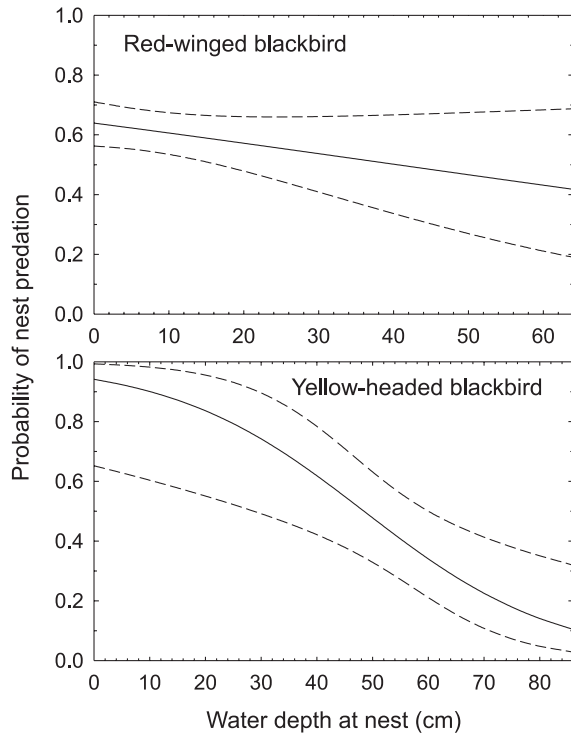
[†]Not estimable: only 1 nest was found, which was depredated during incubation.

[‡]All five nests were depredated after the first nestling visit, so inference is limited.

duced a negative bias for density estimates during dry years, we also found very few nests of yellow-headed blackbirds during dry years, indicating that yellow-headed blackbird density was indeed substantially lower during dry years. Yellow-headed blackbirds tend to settle for breeding in areas with high rates of emergence of odonates, a primary prey

item for feeding nestlings (Orians and Wittenberger 1991). Emergence and abundance of odonates and other aquatic insects are closely tied with water levels in wetlands (Turner and McCarty 1998; Murkin and Ross 2000), providing a link between annual abiotic variation and food supply in wetlands. However, yellow-headed blackbirds also prefer rela-

Fig. 5. Estimates (solid lines) and 95% confidence intervals (broken lines) of the best logistic models (based on Akaike's Information Criterion adjusted for small sample sizes) to explain the probability of predation on red-winged and yellow-headed blackbird nests, northern Iowa, 1999–2002. For both species, the best model included only the water depth directly under nests.



tively high emergent vegetation density when selecting nest sites (Miller 1968; Orians and Wittenberger 1991; Murkin et al. 1997), which can also vary with interannual variability in precipitation (Lederer et al. 1975). Although it is unclear whether the settlement patterns we observed were tied to insect emergence rates or habitat structure, this pattern was clearly linked with annual variation in precipitation.

Reproduction and climate variation

Two life-history parameters independent of predation risk changed among years with climate variation: clutch size and nest initiation date. Red-winged blackbirds had lower clutch sizes during dry years and yellow-headed blackbirds showed similar patterns, although sample size was low in dry years because of their reduced density. Nest initiation dates for each species also varied among years; initiation dates were later in 2002 (a dry year) than in other years. Arcese and Smith (1988) reviewed food supplementation experiments on birds and found that the life-history parameters most often influenced by food were nest initiation dates and clutch size. Yet in some migratory species (including red-winged and yellow-headed blackbirds), evidence suggests that clutch size and nest initiation dates can also be influenced by the age of the female: older females initiate nests earlier and lay larger clutches than younger individuals (Crawford 1977). If this occurred in our system, age structure likely varied across years, with dry years having a higher proportion of younger, less experienced females, which would be consis-

tent with ideal despotic habitat selection (sensu Fretwell and Lucas 1970). Although variation in annual precipitation apparently influenced clutch size and nest initiation dates, the net effect on populations was limited because reduced clutch size did not result in a reduced number of fledglings per successful nest, a measure ultimately tied to seasonal fecundity (Pease and Grzybowski 1995).

Annual variation in precipitation influenced top-down forces: nest predation rates were particularly high during dry years. However, predation rates were generally high for red-winged blackbirds during all years of the study. For both species, predation rates were negatively correlated with water levels beneath nests (see also Robertson 1972; Shipley 1979). Differences in predation pressure between species might be explained by at least two factors related to nest-site selection and antipredatory behaviors. Red-winged blackbirds have greater plasticity in nest-site selection based on microhabitat structure (Twedt and Crawford 1995; Yasukawa and Searcy 1995), which could increase variation in predation rates even in areas of high predation risk, such as at the water's edge. In Iowa, red-winged blackbirds are also more aggressive toward intruders at nest sites than are yellow-headed blackbirds (R. Fletcher, personal observation).

Variation in precipitation is often thought to lead to bottom-up effects on populations by reducing food availability (e.g., Meserve et al. 2001). Numerous studies have documented strong correlations between precipitation, food availability, and measures of reproductive output tied to food availability (e.g., Rotenberry and Wiens 1991; Turner and McCarty 1998; Grant et al. 2000; Morrison and Bolger 2002). However, top-down effects (nest predation) swamped other effects on yellow-headed blackbirds in our system. These top-down effects can arise either from changes in the predator community (Picman et al. 1993) or from changes in predator behavior (Post et al. 1999). In wetlands, water levels can directly affect the predator community. Picman et al. (1993) found that as water depth increased in wetlands in Ontario, the diversity of the nest predator community declined to essentially one species, the marsh wren. Although in this respect wetlands and other systems constrained by climate are disparate, Morrison and Bolger (2002) also found evidence that top-down effects of predation governed fecundity dynamics with rainfall variation in certain years for populations of rufous-crowned sparrows (*Aimophila ruficeps* (Cassin, 1852)) in arid, coastal sage scrub habitat of California.

Temporal dynamics and conservation

The variability in wetland conditions and its implications for density and reproduction illustrate the dynamic nature of wetland communities. In the short term, these areas may have detrimental effects on populations when conditions are poor, but these effects might be dissipated in the long term, particularly if habitat selection is adaptive (Orians 1980; Beletsky and Orians 1994). Indeed, Beletsky and Orians (1994) argued that yellow-headed blackbirds have likely adapted to highly unstable interannual wetland conditions based on variable precipitation. The relative consistency and periodicity of climate variability across years in the long term will ultimately be critical in determining the stability of these populations.

Much of the historical wetland habitat in the Prairie Pothole Region of the United States has declined in the past two centuries (Dahl 1990), and conservationists have responded by restoring wetlands throughout the United States (e.g., Bishop et al. 1998). Recently, spatial and landscape scales have been emphasized for conserving wetland bird populations (Naugle et al. 1999; Fairbairn and Dinsmore 2001). However, at local scales managers can actively alter water levels in restored potholes using a variety of techniques (Bishop et al. 1998; Weller 1999). Actively managing wetland conditions is nonetheless constrained by the total amount of water available for diversion into and out of wetlands, limiting the possible options for mitigating precipitation effects on wetland birds. Although we found positive correlations between water depth and the breeding biology of these species, these effects are probably nonlinear. Years of extremely high precipitation and water depth likely lead to a lower emergent vegetation to open water ratio, thus reducing the density of potential breeding sites (Lederer et al. 1975; Murkin et al. 1997). Conservation of wetland birds will require adaptive management of both landscape and local conditions that vary temporally.

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