Avian Roosting Behavior and Vector-Host Contact Rates for West Nile Virus Hosts

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by

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ABSTRACT

AVIAN ROOSTING BEHAVIOR AND VECTOR-HOSTCONTACT RATES FOR WEST NILE VIRUS HOSTS

by

WILLIAM M. JANousek

Transmission of vector-borne disease is driven by contact rates between vectors and hosts. However, little is known about what drives fine-scale variation in mosquito host seeking behavior and the resulting consequences for contact patterns between mosquitoes and their hosts. We examined the roosting behavior of seven avian hosts of West Nile virus (WNV) and patterns of mosquito abundance among communal roost and non-communal roost sites and at different heights where birds roosted. We found some variation in roosting height among avian species coupled with increases in host-seeking mosquito densities higher in the canopy suggesting avian species experience differing vector contact rates influenced by their preferred roosting height. Prior research suggests host-seeking mosquito abundance increase with host group size, however in contrast to a priori predictions, we found significantly fewer host-seeking *Culex* mosquitoes at American robin communal roosts than non-communal roost sites, and far lower per capita biting mosquitoes and vector-host ratios at roost sites. Focusing specifically on American robins, the preferred host of *Culex* mosquitoes, our results suggest communal roosting behavior may reduce mosquito-biting rates on roosting individuals. Changes in American robin roosting behavior may partly explain previously observed seasonal changes in feeding...
patterns of *Culex* mosquitoes, which has direct implications for the transmission of WNV among birds and humans.
ACKNOWLEDGEMENTS

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I would like to thank the Smithsonian Migratory Bird Center for providing laboratory facilities, as well as residents and Neighborhood Nestwatch participants from Takoma Park, M.D. and Foggy Bottom, D.C. for allowing us to conduct research on their property. We had many field technicians working hard to ensure the success of this project. A special thanks to T. Austin, M. Bouboulis, G. Jones, E. Perryman, E. Piller, L. Reifel for assistance in the field, and R. Reitsma for logistical support. Costly field and laboratory work was supported by the National Science Foundation and the National Institute of Health.

My devoted parents, Lynn and James Janousek, introduced me to the wonders of our natural world and I cannot imagine completing this thesis without their continued support. In closing, I dedicate this thesis in the memory of William K. Janousek, my grandfather, who instilled in me the desire to pursue my dreams wherever they take me.
INTRODUCTION

The behavioral ecology of hosts can play a significant role in determining pathogen transmission dynamics. For diseases where transmission is direct, host foraging ecology, habitat preference, and even social organization including mating strategy, are all factors that can increase the probability of contact with an infected host or environment (Johnson et al 2009; Venesky et al 2011; Altizer et al 2003). Few studies, however, have examined the consequences of host behavior in a vector-borne disease system where contact rates between vectors and hosts govern the dynamics of pathogen transmission (Moore 2008). The majority of studies exploring the influence of host behavior on vector contact rates are generally focused on the effects of human host behavior on diseases such as malaria, dengue fever, and Chagas disease (Stoddard et al 2009; Cohen & Gürtler 2001; Martens & Hall 2000). In order to combat emerging diseases of economic, conservation, and human health concern, it is imperative that we expand our understanding about the consequences of wildlife host behavior on vector contact rates and determine what influence wildlife behavior may have in driving fine-scale variation in vector abundance.

The formation of communal groups by animals is now commonly accepted as a behavioral mechanism for the protection from predators by cooperative defense and through a dilution effect by which the probability of predation is shared amongst members of a group and thus is lower than the risk for an individual living alone (Hamilton 1971). It has also been argued that some aspects of social grouping may be behavioral adaptations to avoid biting insects and ultimately the pathogens they may
carry (Mooring & Hart 1992). While parasitism is one of the major costs associated with sociality in birds, some evidence suggests infection intensity of endo- and ectoparasites decrease with increasing host group size across a wider range of taxa (Cote & Poulinb 1995). Identifying the influence communal groups have on the transmission of vector-borne disease is an essential step in understanding patterns of exposure observed among wildlife species to emerging pathogens such as West Nile virus in North America (Ladeau et al 2008).

West Nile virus (WNV) was first detected in North America in 1999 (Nash et al 2001), and is primarily maintained between avian hosts and mosquito vectors. Crepuscular-feeding mosquitoes of the genus Culex, specifically Cx. pipiens and Cx. restuans, feed primarily on avian hosts and are believed to be the most important enzootic vectors of WNV in urban and residential areas in North America (Turell et al 2005; Kilpatrick et al 2005). Although over 200 species of birds have been shown to be infected with WNV, mounting evidence from the mid-Atlantic, Northeast and Midwestern USA, as well as Colorado suggest that a single species, American robin (Turdus migratorius), is a preferred host of Culex mosquitoes and likely responsible for infecting the majority of WNV-infectious mosquitoes (Kilpatrick et al 2006a; Kent et al 2007; Hamer et al 2009; Molaei et al 2006; Kilpatrick et al 2010). Nonetheless, the mechanisms leading to preferential feeding on this species are unknown and several other bird species make up a substantial portion of Culex bloodmeals.
We sought to evaluate whether variation in avian roosting behavior and patterns in host-seeking behavior in *Culex* mosquitoes could contribute to patterns of feeding behaviors exhibited by WNV vectors in the mid-Atlantic region of the United States (Kilpatrick *et al* 2006b). Two previous studies suggested communal roosts of American robins and house sparrows (*Passer domesticus*) in Connecticut and Colorado respectively, attracted larger numbers of mosquitoes and increased WNV transmission (Kent *et al* 2009;Duik-Wasser *et al* 2010). In contrast, a study in Illinois found no significant associations between American robin communal roosting behavior and WNV-infected mosquitoes (Benson *et al* 2012). One critical aspect needed to resolve whether avian communal roosts act to amplify WNV transmission is to determine the number of mosquitoes feeding on each individual bird within a communal roost rather than simply the number of mosquitoes within a roost as a whole.

Previous studies have suggested host-seeking *Culex* abundance increases with height in the canopy and with host group size (Brown & Sethi 2002; Drummond *et al* 2006; Savage *et al* 2008). We compared differences in roosting height and roost aggregation size for hatch-year individuals from seven avian species including American robins with mosquito abundance data. We focused on hatch-year birds because they appear to play a key role in the amplification and transmission of WNV (Hamer *et al* 2008). We hypothesized avian species roosting higher in the canopy and/or in larger groups would have higher contact rates with host-seeking mosquitoes resulting in preferential feeding by mosquitoes on those species.
We also experimentally assessed whether large aggregations of birds could affect the trapping effectiveness of mosquito traps and ultimately mosquito abundance estimates at trapping sites. A potentially confounding factor in previous studies on avian communal roosting behavior and WNV transmission is that host-seeking mosquitoes could be drawn away from mosquito traps by the presence of additional hosts around traps and this could result in mosquito abundance estimates at communal roosting sites to be biased low. Prior research has shown insect traps placed centrally within ungulate herds catch significantly fewer biting flies than traps placed on the perimeter of the herds (Helle & Aspi 1983). We conducted a similar study to test whether the number of avian hosts around a mosquito trap may influence the number of host-seeking mosquitoes caught in a trap by placing mosquito traps within simulated communal roosts.

METHODS

Study Sites

Our study was conducted at three sites in Maryland and Washington, DC. Sites included an urban area in Foggy Bottom, DC, just north of the Watergate Hotel, a residential area in Takoma Park, MD, near Spring Park, and a predominantly forested area, Rock Creek Regional Park (Rockville, MD). Data on avian roosting behavior and host-seeking mosquito abundance were collected from August through September 2010. Mosquito abundance data were collected in August and September of 2010 and 2011.
Radio Telemetry

We attached transmitters (Lotek Wireless Inc. Newmarket, Ontario) weighing less than 5% of an individual’s weight (Cochran 1980) to seven species of bird: American robin (transmitter weight: 2.8 g), Northern cardinal (*Cardinalis cardinalis*, 1.5g), tufted titmouse (*Baeolophus bicolor*, 0.7g), gray catbird (*Dumetella carolinensis*, 1.4g), mourning dove (*Zenaida macroura*, 2.8g), European starling (*Sturnus vulgaris*, 2.8g), and house sparrow (0.7g). Birds were taken from nests (American robins and Northern cardinals), or captured using passive mist-netting, and were banded, radio-tagged, and released. We attached transmitters using a figure-8 shaped two-loop harness design that slid over the legs of the bird and allowed the transmitter to rest on the synsacrum (Rappole & Tipton 1991). Harness loops were made from clothing elastic, which has been shown to work as a durable but less-constrictive material for short-term attachments of transmitters to birds (Amlaner et al 1978; Wanless et al 1991). Harness size was adjusted to individual body size and fixed with super glue to prevent unraveling.

We observed post-banding movements of tagged individuals to insure attached transmitters were fitted properly and nestlings were fed by their parents. Some adult N. cardinals reacted unfavorably to the presence of transmitters on nestlings. Adverse behavior often consisted of tugging and/or biting the transmitters’ antennae with enough intensity to negatively affect the wellbeing of the nestlings. When aggressive adult behavior was observed transmitters were removed from nestlings.
Biotracker scanning receivers in combination with three-element folding yagi antennas (Lotek Wireless Inc. Newmarket, Ontario) were used to locate birds fitted with radio transmitters. To record nightly roosting behaviors of tagged birds, bearings were taken simultaneously from two or more points for triangulation. Once the approximate location of a bird was discovered we used ToughCam thermal imaging cameras (Infrared Cameras Inc. Beaumont, Texas) in tandem with radio receivers to determine the exact roosting location and height of individuals. We estimated the height of the bird using a clinometer, a 50m tape, and the bird’s location. Several large communal roosts were found and roost aggregation size at these locations was determined by counting the number of birds arriving from the four cardinal directions at dusk and by counting all birds within the roost’s contiguous vegetation area with a thermal imaging camera. When a bird was found roosting solitarily, not in association with a large communal aggregation, and in a patch of vegetation with an area greater than 10m² we searched within a ~10m radius circle of the bird using a thermal imaging camera to determine if additional hosts were roosting in close proximity. We assumed 10m to be the maximum distance between hosts that could strongly influence a foraging mosquito. If a bird was roosting solitarily in an area less than 10m² we searched the entire patch of vegetation as previously described.

**Host-seeking Mosquito Abundance**

We measured host-seeking mosquito abundance using 2 - 6 CDC light traps baited with CO₂ at each of two non-communal and two communal roosting sites in Takoma Park, MD. Non-communal roosting sites were part of a long-term study of
WNV transmission, and were the location where birds were initially banded. Communal roosting sites consisted of large robin aggregations discovered while radio-tracking tagged robins. All four sites (2 communal and 2 non-communal) were within a circular area approximately 2 km radius circle and consisted of relative similar residential areas with small (e.g. <2 Ha) green spaces along stream corridors.

**Simulated Roost Experiment**

We tested the hypothesis that the density of avian hosts around a mosquito trap influences the number of host-seeking mosquitoes caught in a trap. We compared mosquitoes caught in CDC light traps baited with a single 2/3 Gallon Igloo cooler full of dry ice with traps surrounded by 4 additional dry ice filled coolers spaced evenly around the trap in a spiral staircase pattern at a distance of 0.5 – 1.0 m from the light trap with one in each cardinal direction. The experimental setup was designed to mimic the host densities observed around mosquito traps at actual communal roosting sites. We ran traps for one night as described and then alternated the location of the additional coolers of dry ice. We replicated this experiment across four trapping locations for a total of 32 trap nights. In total, we estimate the four additional coolers produced the same amount of CO\textsubscript{2} per hour as 372.4 ± 24.8 additional hosts, based on estimated field metabolic rate (FMR) of American robins (hereafter robin) (Nagy *et al* 1999). We chose FMR over basal metabolic rate because birds at communal roosts were active throughout the night, vocalizing and flying between perches, and did not exhibit behaviors indicative of a resting metabolic rate.
Vector-Host Ratios

We calculated vector-host ratios (i.e. the number of mosquitoes per bird) for robins at communal roosts by dividing mosquito abundance estimates for communal roosts by the number of birds at roost sites. Vector-host ratios at sites not used for communal roosting were calculated assuming host abundance equal to a single individual robin in order to estimate the influence of communal roosting on vector-host ratios.

Adjusting Mosquito Abundance Estimates and Vector-Host Ratios at Communal Roosts

We attempted to correct for the influence nearby hosts likely have on mosquito trapping efficacy by increasing mosquito abundance estimates at communal roost sites based on the results from the artificial roosting experiment. We calculated the ratio of roost sizes of communal roosts and the number of robins that would give off the same amount of CO₂ as our artificial roost experiment and multiplied this ratio by the percent reduction in mosquito capture rate observed in the artificial roost experiment. We then increased mosquito abundance estimates using this correction to calculate the amount of mosquitoes we would expect to catch at a communal roost site if nearby birds did not affect trapping success. Finally, we estimated corrected vector-host ratios at communal roosts by dividing the adjusted mosquito abundance estimates at communal roosts by the number of birds at roost sites.

Statistical Analyses

We compared differences in host-seeking mosquito abundance at communal
and non-communal roosting sites, and variation in avian host roosting behavior using
generalized mixed models formulated with the \texttt{glmer} and \texttt{lmer} functions in the \texttt{lme4}
package in R (v 2.15). For the mosquito abundance estimates we treated each
individual mosquito trap and trapping period as random effects, and roost type
(whether collection site was used as an avian communal roost) as a fixed effect.
Mosquito trap height did not confer a significant effect and was not included in the
final model. To determine variation in roosting height among avian species each
individual bird was treated as a random effect and species was treated as a fixed
effect. In assessing variation in roost aggregation size among avian species each
individual bird was treated as a random effect with species and the interaction terms
of species by Julian date and species by the square root of Julian date were included
as fixed effects. We selected the best fitting mixed models using Akaike’s
information criterion (AIC) (Akaike 1974).

We also examined how roosting height might influence mosquito feeding
preferences by using data from a previous field study (Kilpatrick \textit{et al} 2006a) at the
same field sites. We used a generalized linear model to compare the preference for a
species (the fraction of blood meals from a species divided by it’s relative abundance)
to the average roosting height for that species. Our analyses focus on the behavior of
hatch-year birds and we were not able to capture enough hatch-year E. starlings to
include in this analysis.
RESULTS

Avian Roosting and Mosquito Host-seeking Behavior

We collected roosting data on seven species, American robins (N=23), northern cardinals (N=31), house sparrows (N=10), morning doves (N=5), gray catbirds (N=11), European starlings (N=7), and tufted titmice (N=5). All birds except one robin and six of the E. starlings were hatch-year birds. Roosting height did not differ among sites ($\chi^2=0.602$, df=2, P=0.74) but differed among species (Figure 1; mixed-effects model with individual bird as a random effect, $\chi^2=36.59$, df=6, P<0.001) with tufted titmice roosting highest in the canopy (Figure 1). All other species roosted at similar heights except that American robins roosted significantly higher than house sparrows (Figure 1). As in previous studies (Drummond et al 2006; Savage et al 2008), we found that host-seeking mosquito abundance increased with trap height in the canopy (Figure 2, generalized linear mixed-effects model with Poisson distribution and log-link, $\chi^2=24.51$, df=2, P<0.001). In addition, we found evidence that mosquito host feeding preference also increased with increasing roosting height (F=5.02, p=0.025), where avian species roosting higher in the canopy were fed upon more frequently than would be expected by their abundance.

Roost size differed among species (generalized linear mixed-effects model with a Poisson distribution and a log-link, $\chi^2=107.89$, Df=6, P<0.001) with American robin roosts being largest, followed by European starlings and house sparrows. Roost sizes of three of the seven species, American robins, European starlings, and house
sparrows, increased from August to September (Figure 3, Table 1). Mourning doves also roosted communally, although aggregations for these species were much smaller than other communal roosting species (Figure 4). Gray catbirds, northern cardinals, and tufted titmice had the smallest roost size and often roosted individually or in pairs (Figure 4).

Host-seeking mosquito abundance varied among the four sites (generalized linear mixed-effects model with log-link, $\chi^2=9.85$, Df=3, P=0.02) and robin communal roosting sites had significantly fewer mosquitoes than non-communal roosting areas (Figure 5; generalized linear mixed-effects model with log-link, $\chi^2=4.03$, Df=1, P=0.04). We calculated the vector-host ratios at communal roost sites to be $0.001 \pm 0.0004$ mosquitoes per robin per night between our two communal roost sites. In contrast at a non-communal roost site there were $2.62 \pm 0.52$ mosquitoes per robin per trap night. Thus, the vector-host ratio of a single robin in a communal roosting is on average 2620 times lower than a robin roosting solitarily.

**Trapping Bias - Effect of Hosts Near Traps**

Additional coolers of CO$_2$ reduced the number of mosquitoes caught by 57% ± 12% at artificial roost assemblages compared to traps run independently (Figure 6; generalized linear mixed-effects model with a Poisson distribution and a log-link, $\chi^2=298.04$, Df=1, P<0.001).

We corrected for the effect of additional hosts near mosquito traps at communal roost sites by incorporating the results from our artificial roost experiment. This increased mosquito abundance estimates from $1.23 \pm 0.4$ to $3.6 \pm 1.1$ mosquitoes
per trap night at communal roosts. With these adjusted estimates, there is no longer a significant difference in mosquito abundance between communal roosts and non-communal roosting areas (Figure 5, generalized linear mixed-effects model with a Poisson distribution and a log-link, $\chi^2=0.0372$, Df=1, P=0.85). However, vector-host ratios using adjusted mosquito abundance at roosts were still more than 850 times lower at communal roost sites (0.003 ± 0.001 mosquitoes per robin per night) than at sites not used for communal roosting (2.62 ± 0.52 mosquitoes per bird).

DISCUSSION

The purpose of this study was to investigate patterns in avian roosting behavior and mosquito host-seeking abundance to determine how those patterns may influence vector-host contact rates. Host-seeking mosquito abundance was on average nearly four times larger at mid-level traps and six times larger at high-level traps compared to low-level (1.5 m) traps. These results suggest contact rates between vectors and hosts would be greatest for host species roosting higher in the canopy. Tufted titmice roosted significantly higher than all other species in the study and were the only species to roost at heights similar to high-level mosquito traps. By roosting at heights where increased numbers of mosquitoes are foraging, Tufted titmice may be contacting more WNV-infected mosquitoes. Increased vector contact rates could therefore result in more WNV-transmission and this may partly explain population declines recorded for this species after the discovery of WNV in North America (Ladeau et al 2007). In contrast, by roosting at lower heights, house sparrows may
experience reduced mosquito contact rates providing a potential explanation for why house sparrows were fed upon nearly eight times less often than would be expected based on their abundance (Kilpatrick et al. 2006a). While we found little variation in roosting height among other species under investigation, we found some evidence of a correlation between mosquito feeding preference and avian roosting height, which suggests species roosting higher in the canopy may be fed upon preferentially over species roosting at lower heights.

American robins, European starlings, and house sparrows all joined communal roosts in late summer and fall, as observed in other studies (Kent et al. 2009; Diuk-Wasser et al. 2010; Benson et al. 2012; Morrison & Caccamise 1990). Social grouping is thought to confer fitness benefits through protection from predators, and serve as centers for sharing foraging information (Ward & Zahavi 1973). Our results suggest social grouping may also reduce per capita contact rates with biting insects that can transmit lethal pathogens (Mooring & Hart 1992). We expected large aggregations of hosts to provide a substantial CO$_2$ signature that would attract host-seeking mosquitoes and elevate mosquito densities within communal roosts. We actually trapped significantly fewer mosquitoes at communal roosting areas and found no significant differences in mosquito abundance between site type after correcting for the reduced trapping efficiency of traps within communal roosts. More importantly, even if we attempt to account for the effect additional hosts have on mosquito capture rate, traps at communal roost sites would have to catch roughly 870 times more mosquitoes on average to have vector-host ratios equivalent to areas
not utilized for communal roosting (see Results section). It is possible that robins choose to roost communally at sites where mosquito abundances are lower to avoid the risk of being bitten by disease carrying vectors. However the ability of robins to assess mosquito abundance and adjust roost locations accordingly has not been empirically studied. The results from our artificial roost experiment, showing the addition of hosts around a mosquito trap can lower a trap’s capture rate, support the hypothesis that American robins benefit from roosting communally by reducing the risk of being bitten by mosquitoes due to lower vector-host ratio at roosting sites.

Feeding of *Cx. pipiens* on their preferred avian host, American robins, decreases in the fall (Kent *et al* 2009; Hamer *et al* 2009; Molaei *et al* 2006; Savage *et al* 2007) and this decrease has been associated with an increase in human feeding and human cases of WNV (Kilpatrick *et al* 2006b). This was hypothesized to result from the late-summer dispersal and migration of robins following breeding. Our results suggest that the dispersal of robins to nocturnal communal roosts observed in this and other studies might account for reduced feeding on robins in many areas (Kent *et al* 2007; Molaei *et al* 2006; Kilpatrick *et al* 2006b). Our results suggest that the availability of robins to host-seeking mosquitoes becomes highly spatially variable in the fall and the per capita feeding rates on robins at communal roost sites may be significantly lower.

The effect large aggregations of robins have on the spatial distribution of WNV-infected mosquitoes is unresolved. Diuk-Wasser (2010) found a higher proportion of WNV-infected mosquitoes at communal robin roost sties than non-
communal roosting areas, while Benson (2012) conducted a similar study and found no significant relationships between communal roosts and spatial patterns of WNV-positive mosquitoes. Use of different mosquito trap types between these studies is believed to have contributed to the differing conclusions (Benson et al 2012). The effect of trap placement at communal roosts sites may provide an alternative explanation for the differences in the Diuk-Wasser (2010) and Benson (2012) studies, however trap locations were not explicitly discussed in either of these studies. Our artificial roost experiment suggests that hosts near mosquito traps within communal roosts can decrease trapping efficacy. Traps placed outside of communal roosts, where host densities are lower, may catch more mosquitoes than traps placed within communal roosts. The placement of mosquito traps could result in drastically different conclusions about mosquito abundances at communal roosts. Future studies estimating host-seeking mosquito abundances and WNV-infection rates of mosquitoes must account for potential biases resulting from trap placement at communal roost sites.

In sum, we found variation in roosting height among avian species coupled with increases in host-seeking mosquito densities higher in the canopy suggesting avian species experience differing vector contact rates influenced by their preferred roosting height. Surprisingly, in contrast to a priori predictions, we found significantly fewer host-seeking Culex mosquitoes at robin communal roosts than non-communal roost sites. After correcting for the reduced trapping efficiency of traps within communal roosts we found no significant differences in mosquito
abundance across sites and vector-host ratios at communal roost sites were over 850 times lower than areas not utilized as communal roosts sites. Reduced vector-host ratios of this nature may confer a reduction in per capita feeding rates on robins in communal roosts and ultimately suggests robin communal roosting behavior may contribute to the observed late-summer shift in mosquito feeding patterns and resulting increase in human cases of WNV infection.
Figure 1. The roosting height of seven bird species in Maryland and Washington DC. Bold crossbars indicate the mean, boxes encompass ± 1 SE of the mean, and dashed lines represent 95% confidence bounds around the mean. Letters designate significant differences. Points represent raw data and different levels of opacity indicate number of observations for a given roosting height.
Figure 2. Mean number of host-seeking *Cx. p. p. p.* and *Cx. restuans* mosquitoes collected per trap night at three traps along a single trap line at four trapping locations (separated by vertical bars) in Foggy Bottom, DC.
Figure 3. Temporal patterns of roost size for American robins (A), European starlings (B), and House sparrows (C). Individual American robins (A) and house sparrows (C) observed more than three times are represented by different symbols (individuals observed less than three times are represented by closed circles). Points for Robins are jittered slightly to facilitate presentation.
Figure 4. Roost size of species with no associated temporal pattern. Bold crossbars indicate the mean, boxes encompass ± 1 SE of the mean, and dashed lines represent 95% confidence bounds around the mean. Points represent raw data and different levels of opacity indicate number of observations for a given roost size.
Figure 5. Mean number of host-seeking *Cx. pipiens* and *Cx. restuans* collected per trap night from August through September 2010 across (A) two non-communal roosting sites and (B) two American robin communal roosts. Adjusted mosquito abundance estimates for communal roost sites (C) account for the effect hosts have on mosquito trapping efficacy.
Figure 6. Mean number of host-seeking *Cx. pipiens* and *Cx. restuans* trapped at normal trap setup locations and at locations with traps surrounded by four coolers full of dry ice to simulate communal roosts.
Table 1. Results of a generalized linear mixed-effects model analysis of the differences in avian roosting size across time for seven species of bird. American robin is the reference level against which other effects are compared.

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<tr>
<td>Julian date^{.05} (A.robin)</td>
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<td>T. titmouse:Julian date^{.05}</td>
<td>-58.1</td>
<td>78.9</td>
<td>-2.48</td>
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<td>E. starling:Julian date^{.05}</td>
<td>85.1</td>
<td>19.1</td>
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<td>G. catbird:Julian date^{.05}</td>
<td>28.5</td>
<td>30.8</td>
<td>-3.54</td>
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<td>H. sparrow:Julian date^{.05}</td>
<td>66.5</td>
<td>22.5</td>
<td>-3.17</td>
<td>0.002</td>
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<td>M. dove:Julian date^{.05}</td>
<td>-109.4</td>
<td>39.6</td>
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<tr>
<td>N. cardinal:Julian date^{.05}</td>
<td>13.0</td>
<td>17.4</td>
<td>-7.16</td>
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LITERATURE CITED


