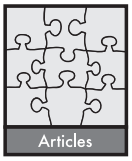

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The role of territory settlement, individual quality, and nesting initiation on productivity of Bell's vireos *Vireo bellii bellii*

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Variation in habitat quality among territories within a heterogeneous patch should influence reproductive success of territory owners. Further, territory settlement order following an ideal despotic distribution (IDD) should predict the fitness of occupants if territory selection is adaptive. We recorded settlement order and monitored nests in territories occupied by individually marked Bell's vireos *Vireo bellii bellii* across a range of shrubland habitats in central Missouri, USA. We used an information theoretic approach to evaluate multiple hypotheses regarding the relationship between territory settlement order and seasonal territory productivity (productivity), which we define as the number of young fledged from all nest attempts in a territory. Territory settlement order and arrival date were not analogous and later arriving males displaced early settlers in 13 of 49 territories. Settlement order and lay date together were the best predictors of a territory's productivity; productivity decreased 2.08 young from earliest to latest settlement rank and lay date. Males that defended the same territory in successive years occupied territories with earlier settlement dates, but we found little evidence that age or prior ownership influenced productivity. Territory selection by male Bell's vireos was adaptive because males preferred to settle in territories that had high seasonal offspring production, but even though settlement rank was linked to territory quality, high productivity was only realized on high quality territory when also linked to early nest initiation date. While settlement rank was related to territory quality, obtaining a high quality territory had to be combined with early nest initiation to maximize productivity. We found support for the IDD hypothesis because the highest quality territories, (i.e. most productive), were settled earlier. Research that identifies high quality habitat by linking individual fitness with habitat characteristics may elucidate the importance of habitat quality, individual experience and temporal factors to productivity of Bell's vireos.

Individuals generally select habitat to maximize fitness (Fretwell and Lucas 1970, Francis and Cooke 1986). The ideal despotic distribution (IDD) model of habitat selection predicts that fitness varies with habitat quality because individuals limit population density through territoriality and select territories in order of habitat quality (Fretwell and Lucas 1970). Individuals of many migratory bird species defend breeding territories and preference can be inferred from spatio-temporal patterns in annual territory selection (Krebs 1971, Arvidsson and Neergaard 1991, Robertson and Hutto 2006). Variation in habitat quality among territories should influence reproductive success of territory owners if habitat quality influences fitness. Thus, the IDD should result in territory settlement order predicting fitness of occupants if territory selection is adaptive.

Early territory settlement is linked to higher reproductive success (Lozano and Perreault 1996, Smith and Moore 2005b, Choi and Lee 2010), but this relationship may be driven by factors other than territory quality. Early settlement increases the length of an individual's breeding season, allowing earlier breeding or time for more nest attempts, both of which can increase seasonal productivity (Lanyon and Thompson 1986, Forstmeier 2002, Wilson and Arcese 2003, Grzybowski and Pease 2005, Cooper et al. 2011). Nest predation rates may also be lower early in the season, so territories with earlier nests may have higher seasonal productivity (Öberg et al. 2013). However, variation in nest predation and brood parasitism rates between populations may offset benefits of early breeding (Wilson and Arcese 2006). Settlement order and lay date are often used interchangeably in species where later arriving males do not displace original settlers (Aebischer 1996, Marra et al. 1998, Brown and Roth 2002, Robertson and Hutto 2006, Chalfoun and Martin 2007). However, settlement order may not determine the lay date in species where territory fidelity or dominance results in owner turnover after initial settlement (Lanyon and Thompson 1986, Forstmeier 2002).

Variation in territory owner quality may also drive differences in productivity among territories. Productivity may be higher for individuals who are older and more experienced (Greaves 1987, Budnik et al. 2000, Brown and Roth 2002), larger (Francis and Cooke 1986, Greaves 1987),

arrive with more fat (Smith and Moore 2003, 2005a), have more pronounced sexually selected characteristics (Møller 1994), sing more frequently (Arvidsson and Neergaard 1991), or arrive in better body condition (Marra et al. 1998, Smith and Moore 2005a). Territory fidelity may provide advantages as territory faithful males, those who return to the same territory as the previous breeding season, may be physically dominant (Marra 2000) or may have an advantage due to knowledge of the territory or social dominance (Lanyon and Thompson 1986, Forstmeier 2002). Also, later arriving, higher quality territory faithful males may displace males who arrive and settle earlier (Lanyon and Thompson 1986, Forstmeier 2002). When previous ownership, not just arrival time, affects who obtains high quality territories, arrival order alone would not predict individual or territory quality. Finally, settlement order may be confounded with individual experience if first year breeding males, who tend to have lower reproductive success, may settle territories later (Marra et al. 1998, Brown and Roth 2002). However, the relationship between male quality and productivity can by examined by evaluating both age and territory fidelity of males (Forstmeier 2002).

Territory settlement order may not always predict the quality of the occupant or temporal factors important to productivity, but settlement order should reflect habitat preference and quality if selection of territories follows the IDD hypothesis. Our objectives were to determine the relationship between territory productivity and settlement order, lay date, and male age and territory fidelity. We studied populations of individually marked Bell's vireos *Vireo bellii bellii* across a broad range of shrubland habitats in central Missouri, USA to separate fitness consequences of territory settlement date from individual male quality and lay date. We assumed that the order of territory establishment indicated its perceived quality by the population and that territory faithful males had a reproductive advantage over non-territory-faithful males and males in their first breeding season.

Methods

Study species

The central Bell's vireo subspecies *Vireo bellii bellii* is a shrub nesting Neotropical migrant songbird that breeds in a variety of open shrubland habitats in the central United States and winters along the Pacific coast of Mexico and Guatemala. In Missouri, males arrive and begin defending territories during the last week of April by frequently and conspicuously singing from perches along territory boundaries; females arrive up to two weeks later (Kus et al. 2010). Bell's vireo are generally territory faithful, but 22 and 28% are reported to have returned to the same study site but selected a different territory (Greaves 1987, Budnik et al. 2000). Males typically remain within a territory throughout the breeding season, but females may switch territories one or more times within a breeding season (Greaves 1987, Joos unpubl.).

Field data collection

We conducted this study between April and August of 2008–2011 at eight sites across Callaway, Boone, Cooper and Howard counties in central Missouri. Study sites were an average of 40.8 km apart (range 1.9–81.2 km) and chosen to cover a wide range of Bell's vireo breeding habitat and included Missouri River floodplain, native prairie, restored prairie, old-field, agricultural land, and a restored strip mine consisting of early successional oak savanna. See Joos (2013) for a detailed description of habitat and locations of each site.

Beginning in 2008 and throughout all years of the study, we banded birds with unique combinations of three plastic color bands and a U.S. Geological Survey numbered aluminum band to allow visual identification of individuals. We lured males into mist nests using playbacks of Bell's vireo or by strategically placing nets in flight paths or around nests during building or after completion of laying. No nests were abandoned due to banding activities. Starting in 2010, we aged individuals based on plumage when possible (Pyle et al. 1997). We refer to males in their first breeding season as second year (SY) individuals. All males older than SY were grouped as after second year (ASY) individuals. As we did not age birds in 2009, we only included banded returns as ASYs.

We searched sites for arriving birds every 1–5 d (mean 2.95 ± 1.3), depending on weather and time constraints, beginning 26 April 2009, 26 April 2010 and 16 April 2011. We excluded territories with search intervals of > 5 d before the first detection to ensure we did not miss the first nest attempt, as this is the shortest time interval observed for a male to obtain a mate and initiate a nest (Kus et al. 2010). We searched for newly arrived males in suitable habitat encompassing territories from previous years. We are confident that we detected newly arrived males because Bell's vireos sing frequently and respond strongly to playbacks. We recorded date, time and location of detections (± 5 m) with handheld global positioning systems (GPS). Following Lanyon and Thompson (1986) and Arlt and Pärt (2007) we defined settlement day for a territory as the first day we detected a territorial male and considered males territorial if we observed them singing from perches, responding to playbacks, or counter singing with neighbors. However, the male that first settled a territory was not necessarily the male that ultimately bred there.

We mapped territory boundaries by marking location coordinates (± 5 m) of males with handheld GPS units. We defined the territory as the area used during breeding, and based boundaries on locations of males recorded from the onset of breeding to the end of the last nest attempt. We visited territories 3–5 times per week until the end of the breeding season and marked 1–3 locations each visit (median 1, range 1–14). The median number of territory visits was 21 (range 10–42) and the median number of points used for mapping was 37 (range 19–90). We recorded locations that represented the total extent of the area used during breeding and avoided repeatedly marking frequently used perches and locations near the nest. Behaviors at these locations included foraging, song perches, gathering nest material, feeding fledglings or following mates. Paired males were not observed outside of the area defended by song perches or other territorial behavior (Joos unpubl.). We outlined territory polygons using GPS coordinates and the most recent aerial imagery available in Google Earth

(<www.google.com/earth/index.html>). We chose a priori not to use minimum convex polygons (MCP) to define territory boundaries as boundaries typically followed the edges of shrub patches containing a male's locations and MCPs would have included large areas of unavailable land cover, such as row crops and roads. We categorized males as non-territory faithful ASY, territory faithful ASY, or SY. Non-territory faithful males were unbanded ASY males that occupied a territory previously occupied by a banded male or banded males that returned to a different territory at the same site. Territory faithful males occupied a territory that overlapped his previous territory by ≥50% or included a previous year's nest site (Currie et al. 2000, Howlett et al. 2003). When later arriving males replaced the original settler, we categorized territories by the age/fidelity class of the permanent owner that ultimately bred in the territory, not the class of the original settler.

We located and monitored nests May through August starting in 2009 to document territory lay date and productivity (total number of young fledged per territory). We located nests via systematic searches and observing parental behavior and monitored each nest thereafter every 1–5 d, with more frequent visits within 3 d of fledging to determine nest fate and number of young fledged. Nest monitoring followed Martin and Geupel (1993) to limit disturbance at the nest and avoid creating a visible path to the nest. We counted a nest as fledged if we observed fledglings in the territory, feces on the nest rim or in nearby foliage combined with highly agitated parents, and/or parents carrying food to multiple locations (Kus et al. 2008). We considered a nest depredated if it was found empty prior to possible fledge date, torn from substrate, empty within possible fledge dates but with no evidence of fledglings, or if parents were building a new nest shortly after failure. We used the number of chicks present at 1–2 d before fledging as the number of chicks fledged.

Data analysis

We used settlement date as an index for territory preference and ranked settlement day for all territories across all sites within years to remove the temporal effect of date and refer to this as settlement order. We tested for a linear relationship between ranked settlement order and lay date using simple regression to determine if lay date was driven by settlement order. We also tested for a difference in ranked settlement order and lay date between fidelity/age classes using a one-way analysis of variance (ANOVA) followed by Tukey's post hoc multiple comparison procedure and report least squared means ± standard error.

We evaluated support for relationships between territory productivity and settlement order, lay day, and fidelity/age with generalized linear models programmed in the GLIMMIX procedure in SAS ver. 9.2 (SAS Inst. 2008). Our response variable was the number of chicks fledged per territory (productivity); we compared Gaussian and Poisson distributions for the response and selected Poisson because it had the lowest Akaike's information criteria (AIC_c) value and overdispersion parameter ($\hat{c}$) closest to 1. We evaluated support for 11 a priori candidate models that we considered biologically meaningful (Table 1). We included individual territory owner as a random effect. Based on a likelihood ration test ($\chi^2 = 0.01$, $p = 0.5$), site was not supported as a random effect. We included year as a fixed effect in all models as territory settlement order was ranked by year, and to account for annual variation in productivity and lay date that are likely influenced by factors such as weather. We did not treat annual observations as repeated measures on territories because territory boundaries and habitat characteristics changed between years due to habitat management activities. Prior to fitting models we calculated tolerance values for all continuous covariates in a global model and found no support for multicollinearity (Allison 1999; all values ≥0.9). We used an information-theoretic framework (Burnham and Anderson 2002) and ranked models by Akaike's information criteria for small sample sizes (AIC_c) and reported the difference between the top model and other candidate models (ΔAIC_c) and Akaike weights (w_i) to assess relative support for each model. We first examined the global model for evidence of lack of fit by determining if $\hat{c}$ was close to 1, and if so proceeded with model selection (Burnham and Anderson 2002). We evaluated the predictive ability of the top supported model using k-fold validation (Boyce et al. 2002) where we fit the model while withholding 10 observations (12%) and compared predicted and observed values for these observations, and repeated this 5 times. We generated model-averaged predictions and unconditional confidence intervals based on models with $\Delta AIC_c < 2$ for a range of covariate values that were representative of our sample (Burnham and Anderson 2002).

Table 1. Support for models predicting productivity of Bell's vireo territories (n = 84). All models included year as a fixed effect and individual as a random effect. The global model included all covariates and two-way interactions and models with interaction effects also included main effects. K is the number of parameters in each model including the intercept, ΔAIC_c is the difference between each model and the lowest AIC_c value, and w_i represents the relative support for each model.

Model	k	AIC_c	ΔAIC_c	w_i
Lay date + Rank	6	325.9	0.0	0.33
Lay date × Rank	7	326.2	0.2	0.30
Lay date	5	327.3	1.3	0.17
Rank	5	328.7	2.7	0.09
Fidel/age + Lay date	7	331.0	5.0	0.04
Null	4	331.5	5.6	0.02
Fidel/age + Rank	7	332.1	6.1	0.02
Fidel/age × Lay date	9	332.6	6.6	0.02
Fidel/age	6	334.2	8.1	0.01
Fidel/age × Rank	9	336.1	10.2	0.00
Global	13	339.7	13.8	0.00

Lay date = date the first egg was laid in a territory, Rank = territory settlement rank, Fidel/age = fidelity/age class described in text.

Results

Of the 382 territories followed, 84 had banded male owners and complete data on productivity, settlement day, lay day, and male fidelity/age. We excluded one territory as an outlier due to an extreme settlement day caused by a rare

late season territory switch. These 84 territories were occupied by 63 males, of which we followed 44 for one year, 17 for two years, and two for three years. Four of the males that we followed for more than one season were site but not territory faithful and 12 were territory faithful; both males followed for three seasons used the same territory for two years and a different territory at the same site for one year. This resulted in 25 territories with the same male for two years and 59 territories that had a different male each year. Return rate in the population as a whole was 60% (Joos 2013); however, this data set was limited by which territories we obtained complete data for this analysis. We observed three incidences of double brooding and all produced five fledglings, the same as the largest fledged clutch. However, these territories were not included in analyses due to missing data.

We detected the first territorial male on 29 April 2009, 27 April 2010, and 1 May 2011. We back-dated arrival based on progress of nest building for two males who were paired and had partially constructed nests on the first detection day (Kus et al. 2010). Males settled territories over 20 d from 28 April–23 May with a median date of 7 May. Pairs initiated first clutches over 46 d from 14 May to 29 June with a median of 25 May. Site but not territory faithful males, territory faithful males, and first year breeders occupied 33.3, 55.9, and 10.7% of territories, respectively (Fig. 1). We determined if one banded male continuously occupied a territory, or owner turnover occurred within a season (i.e. did a banded male replace an unbanded male, an unbanded male replace a banded male, or a banded male replaced another banded male) in 48 territories. Of these 48, later arriving males replaced the original settler in 13 territories.

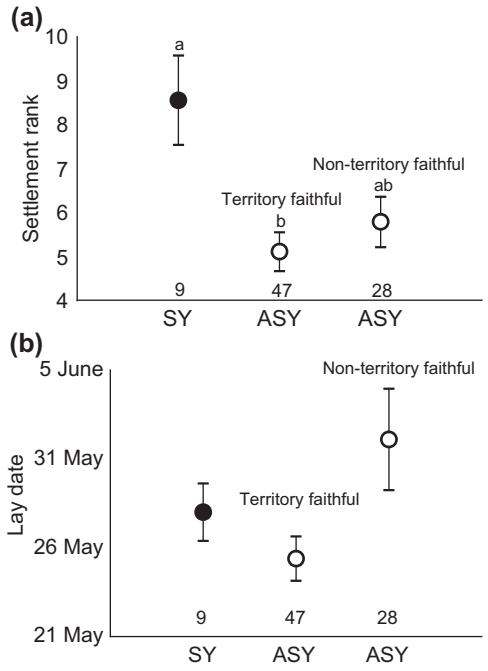

Figure 1. Comparison of mean ± standard error ranked settlement order (a) and lay date (b) for Bell's vireos in central Missouri categorized by age and territory fidelity. Means with different letters in (a) indicate significant pairwise comparisons based on Tukey's post hoc test ($p < 0.05$). Letters below categories indicate sample sizes.

We were able to measure distances between year and year-1 territories for 14 site faithful but not territory faithful males as we followed them for multiple years but were not able to include all years in this dataset due to missing data. The mean distance between year and year-1 territory centroids was 305 m (range 42–1523) and only two of these territories overlapped between years.

Settlement order of the territory varied with the fidelity/age class of the permanent occupant ($F = 4.94_{2,82}$ $p = 0.01$; Fig. 1a). Territories occupied by SY males were settled later than territories occupied by territory faithful ASY males, but not non-territory faithful ASY males. Lay date tended to vary with fidelity/age class following the same pattern as settlement rank, but this trend was not significant at the 0.05 level ($F = 2.81_{2,82}$ $p = 0.07$; Fig. 1b). We found little support for a relationship between settlement rank and lay date (Fig. 2).

There was no evidence of lack of fit for our global model predicting productivity ($\hat{c} = 1.21$), therefore we proceeded with model selection. We found nearly equal support for the interactive and additive models for the relationship of productivity with settlement rank and lay day (Table 1). Parameter estimates and SE for all models within 2 ΔAICc show settlement rank to have the largest effect size, but only when considered additively with lay date (Table 2). As the two top models have different mathematical properties it was not appropriate to generate model averaged parameter estimates. There was little evidence for an effect of age/fidelity class on productivity. Our k-fold validation of the most supported model indicated a strong positive correlation between predicted and observed productivity (mean $r = 0.595$, 95% CI = 0.50–0.69), and hence good fit. Productivity declined similarly with lay date regardless of the territory settlement rank (Fig. 3). Predicted productivity decreased by 2.08 fledglings from the territory with the earliest settlement rank and earliest lay date to the territory with the latest of each, (Fig. 3). When holding settlement rank constant at 5, the number of fledglings per territory decreased by 1.27 as lay date increased from 17 May and 16 June (Fig. 3). Comparatively, the number of fledglings decreased by 1.05 from settlement rank 1 to settlement rank 12 with lay dates of 14 May and 15 May, respectively (Fig. 3). If two territories had the same lay date, but different settlement ranks, the territory settled earlier would have greater productivity.

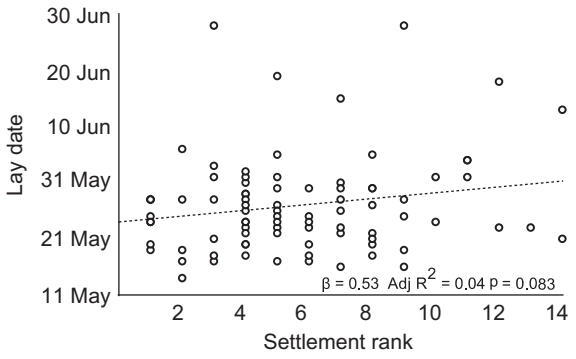

Figure 2. Relationship between ranked territory settlement order and lay date of Bell's vireos breeding in central Missouri, USA.

Table 2. Parameter estimates and standard error (SE) for all parameters included in models within 2 ΔAICc of the most supported model. Model averaging parameter estimates was not appropriate due to the difference in mathematical properties of the additive and interactive models.

Model parameter	Lay date + Rank		Lay date × Rank		Lay date	
	β	SE	β	SE	β	SE
Intercept	2.371	0.637	1.493	0.859	2.261	0.656
Year 2009	−0.417	0.287	−0.304	0.297	−0.359	0.291
Year 2010	0.096	0.169	−0.093	0.218	0.135	0.171
Lay date	−0.025	0.012	−0.005	0.017	−0.029	0.012
Rank	−0.054	0.028	0.084	0.101		
Lay date × Rank			−0.002	0.001		

Lay date = date the first egg was laid in a territory, Rank = territory settlement rank.

Discussion

Bells vireos that occupied earlier settled territories had greater productivity than those in territories that had a similar lay date, but were settled later. We found support for one IDD prediction because the highest quality territories, as determined by productivity, were selected (i.e. settled) first (Fretwell and Lucas 1970). Territory faithful males occupied territories settled earlier than SY males and tended to have earlier lay dates as well. While age or territory fidelity may have enabled higher quality males to occupy higher quality territories and initiate breeding earlier, we found little support for a relationship between productivity and age/fidelity status of males, even when we controlled for settlement date in our age/fidelity and settlement date additive model. We suggest lay date combined with territory characteristics (i.e. habitat structure), instead of individual experience, drove territory productivity.

While both settlement rank and lay date predicted productivity of territory occupants, these covariates were weakly correlated, which differs from previous findings (Fretwell and Lucas 1970, Chalfoun and Martin 2007, Cooper et al. 2011). This weak correlation may be explained by weather and territory owner turnover. Severe weather early in the breeding season often destroyed early nest attempts throughout the entire study area during building and limited when nesting could begin (Joos unpubl.). Further, when owner turnover occurs, lay date should be related to the arrival of the breeding male or related to female arrival date or date of pairing. Therefore, the decoupling of settlement date and lay date may be explained by later arriving males displacing original settlers in 31% of the territories for which we had the data to detect this. Consequently, lay date may be more closely tied to the arrival date of the breeding male than the initial territory settlement date.

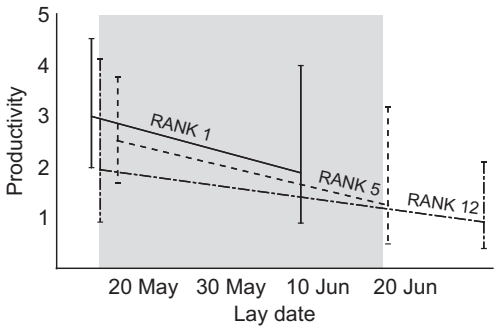

Figure 3. The relationship between productivity and lay date and ranked territory settlement order for Bell's vireo territories in central Missouri. Rank 1, 5, and 12, represent the 5, 50, and 95% percentiles of settlement order and the shaded area represents 95% of lay date observations.

Temporal factors associated with nest success may explain the importance of an early lay date. Early nest initiation should increase territory productivity if a longer breeding period allows for more nest attempts (Lozano and Perreault 1996, Grzybowski and Pease 2005, Smith and Moore 2005b, Choi and Lee 2010) and/or early nests have higher nest survival due to lower rates of nest predation or brood parasitism (Krebs 1971, Burhans et al. 2002, Grant et al. 2005, Robertson and Hutto 2006). However, in Bell's vireos, avoidance of brood parasitism is unlikely to explain increased productivity in early nesters, as they arrive on the breeding grounds after brown-headed cowbirds *Molothrus ater*. Our population abandoned 82% of parasitized nests during laying (Joos unpubl.), suggesting brood parasitism was similar to nest predation as it resulted in near immediate re-nesting. Bell's vireos in general quickly re-nest after nest failure (Kus et al. 2010), therefore a longer breeding season would allow more re-nest attempts and increase territory productivity (Martin 1995, Anders and Marshall 2005, Grzybowski and Pease 2005). More information on how productivity is related to temporal factors associated with nest survival may elucidate how lay date influences productivity.

Early settled territories with early lay dates had higher productivity, but not always for the original male settler, as later arriving males displaced some original settlers. This finding differs from American redstarts *Setophaga ruticilla*, where increased productivity was generally predicted by an individual's early arrival on the breeding grounds, facilitated by their superior physiological condition, which was the result of occupying high quality habitat on wintering grounds (Marra et al. 1998, Tonra et al. 2011). Individual experience did appear to play a role in obtaining higher quality territories, as older males, regardless of territory fidelity, bred in earlier settled territories than younger males. However, if productivity was more related to individual experiences than territory quality, then age/fidelity models, which represented qualities of the territory breeder but not the settler, would have received more support. Our observational results are similar to those of McKeller et al. (2013), where early settled territories with late lay dates had higher productivity than territories where late breeding was a result of late settlement. Further, McKeller et al. (2013) found that the productivity of early arriving males with artificially delayed settlement was similar to late settled territories, and, further, that late arriving males that obtained vacated early settled territories had similar productivity as non-manipulated early settled territories. These findings, combined with our poor support for age/fidelity models, support the interpretation that increased productivity in earlier settled territories was due to quality of the territory and not just the experience of the occupant (Aebischer 1996, Currie et al. 2000, Robertson and Hutto 2006, Chalfoun and Martin 2007).

Due to replacement of early settlers by later arriving males and the poor relationship between settlement rank and lay date, there was not a guaranteed temporal advantage for males to arrive and settle early. There may be reduced selection pressure for early arrival in this system if dominant males can arrive late and obtain high quality territories without delaying breeding. Conversely, early arriving lower quality males who settle high quality territories early and remain unchallenged may obtain a high quality territory. This could result in increased lifetime productivity if territory fidelity results in greater likelihood of obtaining high quality territories in subsequent years, as shown in painted buntings *Passerina ciris* (Lanyon and Thompson 1986, Grzybowski and Pease 2005, Cooper et al. 2011). This may be the case in our population; of the later arriving males who replaced the original settlers, six were territory faithful and eight were site faithful but still displaced unbanded original settlers. Of the replaced original settlers, 13 were unbanded on arrival, and two banded ASY males returned to their previous year's territory after being replaced by later arriving owners from the previous year. If first year males, and males with poor territories, had a greater benefit from early arrival we would expect them to arrive earlier than males returning to high quality territories. However, this was outside the scope of our study, as not all males were banded on arrival. Further research on how arrival time varies by age, the previous year's reproductive success, and territory quality is necessary to clarify how individual experience influences arrival order and territory selection patterns.

We found that territory settlement order when combined with lay date predicted one measure of fitness, supporting that territory selection by Bell's vireos in Missouri is adaptive. Even without including information typically linked with reproductive success of migratory songbirds (e.g. nest survival rates or physiological condition of owners), territory settlement order and lay date together were more strongly related to productivity than male age and territory fidelity. The lack of strong relationship between settlement rank and lay date, combined with strong support for lay date in combination with settlement rank predicting productivity, suggests that settlement rank was a predictor of territory quality, instead of a temporal advantage due to early onset of breeding. However, obtaining a high quality territory must be combined with the temporal advantage of early nest initiation to maximize productivity of the territory. Nest success, and therefor territory productivity, of forest and grassland breeding songbirds in the Midwest is related to habitat structure and characteristics at multiple scales, from concealment at nest sites to the proportion of forest cover within the landscape. Bell's vireo populations would benefit from similar multi-scale habitat analyses that quantify high quality breeding habitat by linking fitness with species specific habitat characteristics.

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