Research

Oikos 118: 1139–1147, 2009
doi: 10.1111/j.1600-0706.2009.17342.x,
© 2009 The Author. Journal compilation © 2009 Oikos
Subject Editor: Kenneth Schmidt. Accepted 8 January 2009

Does attraction to conspecifics explain the patch-size effect? An experimental test

Robert J. Fletcher, Jr.

R. J. Fletcher, Jr. (robert.fletcher@ufl.edu), Dept of Wildlife Ecology and Conservation, PO Box 110430, 110 Newins-Ziegler Hall, Univ. of Florida, Gainesville, FL 32611-0430, USA.

Recent theory suggests that attraction to conspecifics during habitat selection can be one potential, yet untested, mechanism for animal sensitivity to habitat fragmentation. The least flycatcher *Empidonax minimus*, a highly territorial migratory bird, has previously been shown to be attracted to conspecifics and sensitive to patch size by avoiding small patches of riparian forest in Montana, USA. I used a large-scale field experiment in this region to test the conspecific attraction hypothesis for explaining sensitivity to patch size, and I supplemented this experiment by estimating whether vegetation structure, nest predation, or nest parasitism rates could better explain patterns of sensitivity to patch size. Vegetation structure did not vary consistently with patch size, based on a random sample of patches across 150 km of the Madison and Missouri Rivers, Montana. Nest predation and parasitism rates by brown-headed cowbirds *Molothrus ater* also did not vary with patch size during the experiment. However, when conspecific cues were simulated across a gradient of patch sizes, flycatchers settled in all patches – and their sensitivity to patch size vanished – providing strong support for the conspecific attraction hypothesis. These results provide the first experimental evidence that attraction to conspecifics can indeed help explain area sensitivity in nature and highlight how understanding the role of animal behavior in heterogeneous landscapes can aid in interpreting pressing conservation issues.

Many organisms show consistent sensitivity to habitat loss and fragmentation. Although animals can show fragmentation sensitivity in many ways, sensitivity in patterns of distribution with patch size are common, where animals are less likely to occur (per unit area) or occur at lower densities as patch size declines (e.g. 'area sensitivity' or negative patch-size effects; Bender et al. 1998, Connor et al. 2000). Meta-analyses suggest that negative patch-size effects on animal distribution are indeed common in a variety of taxa, particularly birds and insects (Bender et al. 1998, Connor et al. 2000), whereas positive effects of patch-size are less often reported. From a conservation perspective, area sensitivity is relevant because such patterns can increase the likelihood of population persistence in fragmented landscapes (Donovan and Lamberson 2001). While there is a growing awareness of the commonality of these patterns, much less emphasis has been placed on interpreting the mechanisms driving such patterns (Fletcher et al. 2007).

A variety of hypotheses can potentially explain fragmentation sensitivity (Connor et al. 2000, Brotons et al. 2003, Fletcher et al. 2007). Until recently (with the addition of landscape-context hypotheses; Brotons et al. 2003), two general hypotheses have been developed and tested to explain patch-size effects: the resource concentration and the enemies hypotheses (Root 1973, Risch 1981). The resource concentration hypothesis states that larger areas contain a greater amount or diversity of resources, thereby allowing higher densities of individuals. Resources commonly considered include variation in habitat structure and diversity, because these measures are thought to reflect important resources, such as food and/or breeding sites (Ambuel and Temple 1983, Blake and Karr 1987; the habitat hypothesis hereafter). The enemies hypothesis states that predators are more abundant or more effective in smaller areas of habitat, such that prey either avoid small patches or have greater predation rates in small patches, leading to lower densities or occurrence as patch size declines (Root 1973, Risch 1981). Currently, there is some support for each of these hypotheses generating patch-size effects, although nearly all of this evidence is confounded by the potential for edge effects driving purported area effects (Fletcher et al. 2007).

More recently, a third alternative hypothesis that invokes social behavior has been developed to explain patch-size effects: if individuals are attracted to conspecifics, attraction can emerge as patterns of area sensitivity across patchy landscapes (the conspecific attraction hypothesis; Bourque and Desrochers 2006, Fletcher 2006). Conspecific attraction occurs when animals use social cues (or 'location' cues; Danchin et al. 2004) as positive proximate stimuli in decision-making, including foraging, movement, and settlement decisions (Stamps 1988). This behavior may evolve when conspecifics act as an indirect indicator of resource quality or through Allee effects, such as aggregative behavior

increasing the likelihood of finding mates (Stamps 1988). Recent modeling confirms that this type of 'social information use' (Danchin et al. 2004) during search (movement) and/or settlement decisions could generate significant fragmentation sensitivity in animals, where animals exhibiting conspecific attraction are less likely to occur in small patches or near edges (Fletcher 2006). Correlative data on forest birds further support this possibility (Bourque and Desrochers 2006). While conservation biologists have long noted that conspecific attraction may explain patterns of fragmentation sensitivity in animal distribution (Verner 1992, Reed and Dobson 1993), to date this potential has not been experimentally examined. Yet if patterns of sensitivity are driven by attraction alone, then fragmented habitats may not be of lower habitat quality as would be the case under the resource concentration and enemies hypotheses. Furthermore, each hypothesis suggests different foci for potential conservation strategies. Understanding mechanisms for fragmentation sensitivity will thus be crucial for interpreting the consequences of ongoing habitat loss and fragmentation.

I report on a large-scale experiment designed to test the conspecific attraction hypothesis for patch-size effects to explain the distribution of the least flycatcher *Empidonax minimus*, a highly territorial, migratory bird. In the western US, this species is confined to breeding in riparian forest habitats, which comprise less than 1% of total land area (Knopf et al. 1988), and has experienced significant population declines across North America, based on the Breeding Bird Survey (Sauer et al. 2006). The least flycatcher has been shown to be attracted to conspecifics (Fletcher 2007; Fig. 1a) and sensitive to patch width in riparian habitats of Montana (Fletcher and Hutto 2008), which is highly correlated with patch size. Re-analysis of data from Fletcher and Hutto (2008) highlights that flycatchers show strong sensitivity to patch size in the region (Fig. 1b). Taken together, these data suggest that conspecific attraction may indeed help explain area sensitivity of flycatchers; here I provide an experimental test. I also supplement this experiment with information on vegetation structure, nest predation, and nest parasitism rates as a function of patch size to determine if potential habitat or enemies could better explain these patterns of sensitivity.

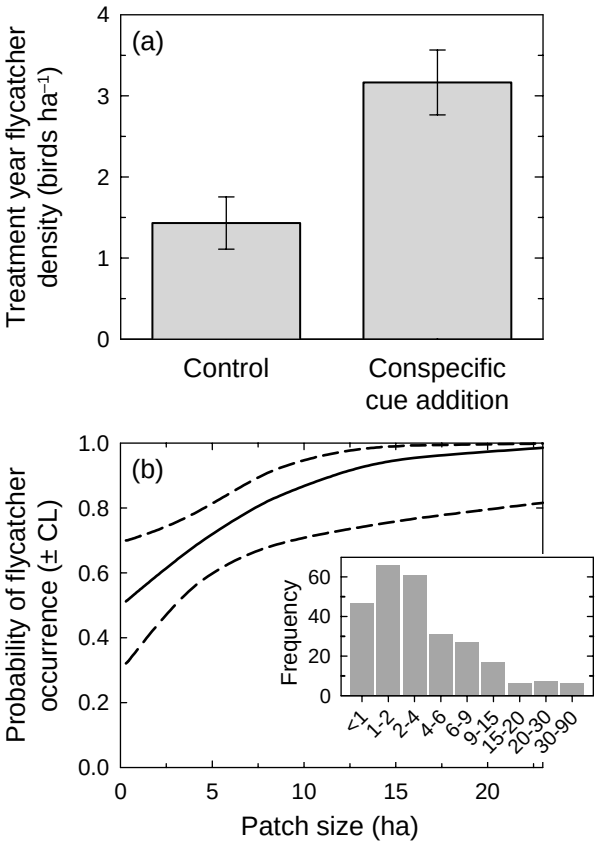

Figure 1. The least flycatcher uses conspecific attraction in habitat selection and shows sensitivity to patch size in riparian habitats, Montana, 2003–2005. (a) Least squares estimates ($\bar{x} \pm$SE) of density for plots with added flycatcher cues ($n = 7$) and controls (no added cues; $n = 11$), controlling for pre-treatment densities (modified from Fletcher 2007), shows that flycatchers increase in density two times with the addition of conspecific cues (ANCOVA testing for treatment effect: $p = 0.003$). (b) In the study region, the probability of occurrence (per unit area) increases with patch size ($p = 0.0069$). Analysis based on 50-m point counts from a random sample of 51 patches in this region ($n = 99$ points) and analyzed using generalized linear mixed models that considered points within patches as correlated sampling units (Fletcher and Hutto 2008). In this analysis, occurrence was not corrected for detection probability, because estimates of detection probability were very high based on a modified removal model ($p = 0.99$; Fletcher unpubl.). Inset shows the distribution of patch sizes in the study region for all riparian patches, highlighting that most riparian patches are < 4 ha.

Methods

Study area

The study occurred within deciduous riparian patches in Montana along approximately 150 km of the Madison and Upper Missouri Rivers, during May–July, 2004–2006. Riparian areas were dominated by narrowleaf cottonwood *Populus angustifolia* and a variety of willow species (e.g. *Salix amygdaloides*). Other tree and shrub species included water birch *Betula occidentalis*, mountain alder *Alnus incana*, juniper *Juniperus scopulorum*, rose *Rosa* spp. and snowberry *Symphoricarpos albus*.

The habitat hypothesis

To address the habitat hypothesis, I used an extensive database from a larger investigation on avian communities and vegetation in riparian habitats (Fletcher and Hutto 2008). From this database, flycatchers consistently avoided small patches (Fig. 1b). I used habitat measurements collected in these patches to test for variation in vegetation structure and diversity as a function of patch size that could help explain flycatcher distribution. Measures of vegetation structure and diversity are often thought to reflect potential resources regarding nest-sites and/or food availability, based

on associations of vegetation with nest-site selection and breeding fitness components (Martin 1998, Chalfoun and Martin 2007), and the common correlations of vegetation with other resources, such as food (Smith and Shugart 1987, Burke and Nol 1998).

In 2004 and 2005, my assistants and I surveyed birds using 50-m point counts across a random sample of 51 patches in the study region where flycatcher conspecific attraction was documented (Fletcher 2007, Fletcher and Hutto 2008). For each patch selected, we identified the maximum number of potential sampling locations available within the patch, with the constraint that samples were 150 m apart. We did so by overlaying a 150×150 m grid, parallel to the main axis of the riparian patch, where the center of each grid cell was considered a potential sampling unit. We sampled all potential locations within each patch (1–4 points patch^{-1}) to ensure adequate sampling across the entire area (99 points sampled across 51 patches). At each point-count location, we measured vegetation to determine if habitat structure or diversity changed as a function of patch size. Vegetation was measured within 5 m and 11.3-m radii at four equally spaced sampling locations in each point-count area. Within the 5-m radius, we visually estimated shrub cover (by species) and ground cover (<1 m) structure. Ground cover categories included woody, grass, forb, litter and bare ground. Within the 11.3-m radius, we counted the total number of trees (by species) and snags by three diameter breast height (dbh) size categories: 8–23, >23–38 and >38 cm. We also measured canopy height, using a clinometer, and estimated canopy cover, by averaging four readings from a densiometer in each sampling location.

The conspecific attraction hypothesis

In 2006, I used a song playback experiment to test the conspecific attraction hypothesis. Manipulating songs of flycatchers to change social cues within plots is a powerful and appropriate method because flycatchers sing often and breed in forests with substantial sub-canopy structure in this region (Fletcher unpubl.), which limits the availability of visual cues. This hypothesis predicts that by adding social cues to smaller patches, the probability of occupancy should no longer decline with decreasing patch size (Fletcher 2006). I focused on occupancy rather than density because theoretical modeling predictions are specifically for occupancy rather than density and density is also thought to be influenced by social cues in highly nonlinear ways (Fletcher 2006), which has been demonstrated in this species (Fletcher 2007).

The experimental design entailed testing for patch-size effects on the occurrence of flycatchers across a stratified random sample of patches as a function of patch size (<1 ha, 1–5, 5–10, 10–20, >20 ha). Treatments were applied to a random sample of patches in each size class ($n = 8$ patches: 2, 2, 2, 1, 1 for each size class, respectively) and were compared to a random sample of unmanipulated controls ($n = 22$ patches: 6, 6, 5, 4, 1, for each size class, respectively). Treatment patches used in Fletcher (2007) were considered unavailable for random selection for this experiment, thereby limiting any potential for carry-over effects from a previous playback experiment in this region. Control playbacks were not used (Ward and Schlossberg 2004, Hahn and Silverman 2006, Fletcher 2007, Betts et al. 2008), but another behavioral playback experiment on least flycatchers showed that playbacks did not have general effects (Martin et al. 1996). In stratifying sampling effort, I placed more effort on smaller patches because most patches in this system are <5 ha and variation in flycatcher occurrence is most pronounced in small patches (Fig. 1b). Overall, patch sizes used in this experiment averaged 6.14 ha, ranging from 0.66 ha to 21.96 ha (controls: 5.99 ± 5.92 SD; treatments: 6.56 ± 6.96 SD), and the percent of riparian habitat surrounding patches within 1 km was similar between treatments (mean $\pm$ SD: $11.7 \pm 7.3\%$) and controls (13.5 ± 6.0; $t = 0.66$, $DF = 11$, $p = 0.53$).

I used individual, fixed-width transects (50×150 m; 0.75 ha) in different riparian patches (transects hereafter) as the sampling unit. For this experiment, I used fixed-width transects instead of point counts to improve sampling areas surrounding playbacks and to better sample riparian patches, which are typically linear in shape. Nonetheless, I also did conduct point counts at the center of these transects using the same approach as Fletcher and Hutto (2008; Fig. 1b), which provided identical results on occupancy, highlighting that the methods were effectively comparable for estimating occupancy of flycatchers. Least flycatchers generally have small territories (~ 0.13 ha, range 0.01–0.38 ha; Briskie 1994), such that the size of transects could potentially accommodate >1 territory. To limit potential confounding of habitat edge as a function of patch size (Fletcher et al. 2007), all transects were placed adjacent to the edge of patches, parallel to the river. All plots were >500 m apart.

Each treatment consisted of two playback stations located 25 m from the ends of transects (100 m apart), with each station pointed toward the center of the transect. Playbacks commenced on 1 May and continued daily until 1 June, when flycatchers had settled in the area and begun breeding (Fletcher 2007). Each playback station consisted of a portable stereo mounted 1–2 m up a tree or shrub, wired to a timer and a deep-cycle marine battery. Stereos broadcasted songs of local dialects recorded in Montana at full volume (approximately 90 dB) from a CD during 04:00–10:00 each day (Ward and Schlossberg 2004). Each CD contained 60 min of song tracks and 5 min of silent tracks in a random order, with timers shutting down the system for 5 min between broadcasts of the entire CD (Fletcher 2007, 2008).

To estimate flycatcher occupancy, flycatchers were surveyed along transects four times during the breeding season, between 1 June–10 July, with each survey being separated by at least one week. To survey birds, an observer randomly picked one end of the transect as a starting point. A single observer slowly walked the transect at a consistent pace, with each transect being surveyed for approximately 10 min. During surveys, observers recorded all flycatchers seen or heard, including estimating the distance and direction to each detection. To ensure accurate delineation

of birds within or outside plots, distances to birds were estimated using a laser rangefinder. To limit any potential observer biases, two observers rotated surveying for flycatchers between visits, with each observer surveying each transect twice.

The enemies hypothesis

The enemies hypothesis predicts that smaller patches have higher predation and/or parasitism rates than larger patches, thereby leading to lower densities of prey in smaller patches. To address this hypothesis, my assistants and I measured nest predation and parasitism rates as a function of patch size using a subset of patches considered for the experimental test of the conspecific attraction hypothesis outlined above. Nest predation is known to be a major factor influencing nest success in migratory birds (Martin 1993, Schmidt and Whelan 1999), and brood parasitism by brown-headed cowbirds *Molothrus ater* is also known to have substantial effects on reproductive success (Robinson et al. 1995). As such, focus on nest predation and parasitism rates to address the enemies hypothesis is warranted.

My assistants and I searched for nests on 14 control and 7 treatment patches across the gradient of patch sizes (see Conspecific attraction hypothesis) throughout the 2006 breeding season (25 May–31 July). Nests were primarily found by following individual flycatchers and noting behaviors. We monitored nests every 2–3 days until nests terminated. We attempted to find all nests within these patches throughout the breeding season. Nest predation was inferred if nests failed and there was no evidence for other sources of failure (e.g. weather).

Statistical analyses

To address the habitat hypothesis, I tested for an overall effect of variation in vegetation structure and diversity as a function of patch size using canonical correlation analysis (CCA), a multivariate analysis that allows for multiple response variables and continuous explanatory variables (e.g. patch size). This analysis also estimated a canonical variate that was a linear combination of vegetation variables, such that the correlation between vegetation and patch size was maximized. I focused on vegetation metrics reflecting variation in shrub and tree/canopy structure and diversity, based on known habitat associations and nest-site locations of flycatchers. Least flycatchers in this area nest in cottonwoods, birch, alder, willow and occasionally juniper (Fletcher unpubl.). Accordingly, response variables for the CCA included total shrub cover, shrub diversity (Simpson index), canopy height, canopy cover, tree diversity (Simpson index), the density of deciduous trees (total number of trees ha^{-1}), and the density of conifer trees averaged across point counts within patches.

To test the conspecific attraction hypothesis, I used occupancy modeling (MacKenzie et al. 2002), which controls for variation in detection probability, to compare models explaining variation in occupancy as a function of patch size and treatment (and their interaction) based on 2006 transect data. For this experimental design, occupancy refers to whether a transect was occupied as a function of patch size and/or treatment, which controls for the random sampling hypothesis for area sensitivity (Fletcher et al. 2007). I used occupancy modeling that corrects for imperfect detection because the playback treatment could potentially alter the detectability of flycatchers (e.g. via counter-singing) without altering their actual occupancy. Note, however, that comparing logistic regression models without adjusting for detection probability led to the same conclusions because of consistently high detection probabilities of this species (Fletcher 2007). I compared models using Akaike's information criterion, adjusted for sample size (AIC_c) and AIC_c weights (Burnham and Anderson 1998). With this experimental design, the conspecific attraction hypothesis predicts a significant interaction between patch size and the addition of conspecific cues, where occupancy should increase as a function of patch size in controls but such sensitivity should disappear in treatments. Thus, I compared a global model that included a treatment × patch size interaction for occupancy and a treatment effect on detection probability to reduced models for explaining occupancy and detection probability (Table 1).

Nest predation rates were analyzed using logistic-exposure models that extend generalized linear models (GLMs) to accommodate variation in exposure (monitoring) days between nests (Shaffer and Thompson 2007). Nest parasitism by brown-headed cowbirds was analyzed by testing for the probability of nest parasitism using GLMs that assumed a binomial error distribution and used a logit link function. Based on this experimental design, the enemies hypothesis predicts an increase in nest predation or parasitism as patch size declines for control patches, which explains area sensitivity by flycatchers. Because social cue manipulation can increase flycatcher densities to levels above that observed in unmanipulated areas (Fletcher 2007), tests for the effects of enemies in treatment patches as a function of patch size may confound patch-size effects and density-dependent effects on reproductive success. However, it is also crucial to interpret whether treatment patches experience general differences predation and parasitism rates. Consequently, I tested for patch-size effects in control patches only, but I also compared five candidate models using data from treatments and controls to better interpret effects of patch size and treatment on predation and parasitism rates: intercept only (constant rates), patch

Table 1. A comparison of models testing for area (patch size) and treatment effects (trt; control versus conspecific cue additions) on the occupancy of least flycatchers, 2006. Table includes the number of parameters estimated in each model (K), Akaike's information criterion, adjusted for sample size (AIC_c), and the relative model weights. In model descriptions, p = detection probability, and (.) = constant parameter.

Model	K	AIC_c	ΔAIC_c	AIC_c weight
Occupancy(area × trt)p(.)	5	106.41	0.00	0.36
Occupancy(area × trt)p(trt)	6	106.83	0.41	0.29
Occupancy(area)p(.)	3	108.46	2.04	0.13
Occupancy(area)p(trt)	4	108.87	2.46	0.10
Occupancy(.)p(.)	2	110.96	4.55	0.04
Occupancy(.)p(trt)	3	111.19	4.78	0.03
Occupancy(trt)p(.)	3	111.47	5.06	0.03
Occupancy(trt)p(trt)	4	111.89	5.48	0.02

size, treatment, patch size + treatment, and a patch size × treatment model.

Results

Across the random sample of 51 patches surveyed in 2004–2005, I found no strong evidence for vegetation structure and diversity varying with patch size (Wilk's Λ: 0.846, $F_{7,42} = 1.09$, $p = 0.38$), although there was a slight trend for the canonical variate increasing with patch size (Fig. 2). The canonical variate explaining variation in vegetation structure was positively correlated with tree diversity ($r = 0.75$), the number of coniferous ($r = 0.61$) and deciduous ($r = 0.47$) trees, and canopy height ($r = 0.38$). Results from CCA suggested that vegetation structure was more variable among small patches (larger spread in canonical variate values across small patches; Fig. 2); however, flycatchers were absent (i.e. not detected) in patches across this entire vegetation gradient (Fig. 2).

Comparing control patches to those with added social cues across a gradient of patch sizes, however, caused area sensitivity to disappear (Fig. 3). There was strong support for occupancy being influence by patch size, but the effect was conditional on treatment, where the top two models considered both included a patch size × treatment interaction (Table 1). Based on model-averaged estimates of the top competing models ($\Delta AIC_c < 2$; Burnham and Anderson 1998), control plots showed similar patterns of occupancy to surveys conducted in 2004–2005 (cf. Fig. 1b and Fig. 3), but all treatment plots were occupied (Fig. 3). As with the point count sampling design of Fletcher (2007) and Fletcher and Hutto (2008), estimated detection probabilities of flycatchers were very high ($p = 0.99$ for the four visits), such that analyses based on uncorrected estimates of occurrence provided identical results (Fletcher unpubl.).

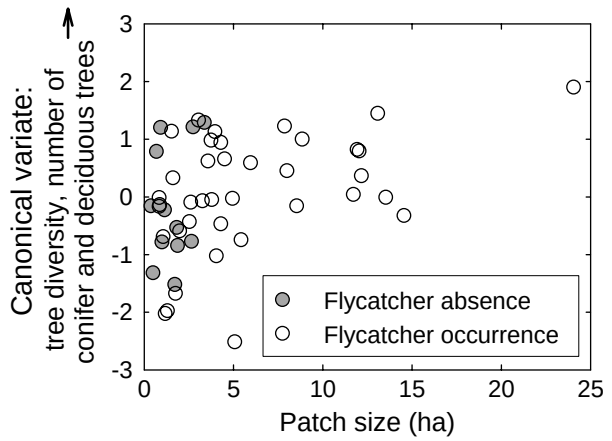

Figure 2. Results from canonical correlation analysis testing for overall changes in vegetation structure and diversity as a function of patch size, Montana, 2004–2005. Shown is the canonical variate derived from the analysis for explaining variation in vegetation, with patches where least flycatchers were detected (occurrence) or not detected (absence) noted.

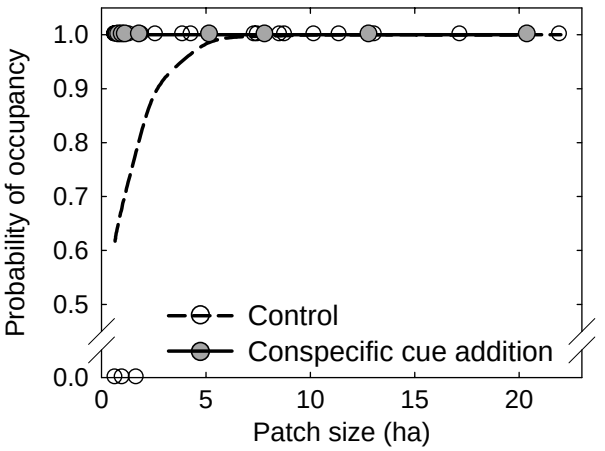

Figure 3. Predicted occupancy from model-averaged estimates describing variation in least flycatcher occupancy as a function of treatment and patch size, 2006. Symbols show presence/absence of flycatchers in treatments and controls.

Although model selection criteria provided strong support for differences in occupancy between treatments and controls as a function of patch size (Table 1), it is possible that the power to detect a lack of an area effect in treatments, as predicted from the conspecific attraction hypothesis, was relatively low given the sample size and observed occupancy patterns in unmanipulated areas (Fig. 1b, 3). When contrasting patterns between treatment and control plots in 2006, the differences in occupancy occurred in patches < 2 ha (Fig. 3), where all four treatment plots were occupied, whereas 5 of 8 (62%) of control plots were occupied. In the larger sample of unmanipulated patches surveyed in 2004–2005 (Fig. 1b), 8 of 19 (42%) plots were occupied in patches < 2 ha. Using predicted occupancy from unmanipulated patches in 2004–2005 (Fig. 1b) to predict observed patterns in 2006 (Fig. 3), the probability of observing occupancy patterns in treatment patches < 2 ha was 0.09, providing marginal evidence that treatments increased occupancy above average rates of occupancy in unmanipulated areas. The probability of observed occupancy in control patches < 2 ha was 0.25, suggesting that control patches were similar in occupancy to patterns from 2004–2005. Indeed, when pooling all unmanipulated data from 2004–2006, there was no evidence for year effects ($p = 99$) or year × area effects ($p = 0.34$). Thus, I pooled all unmanipulated data from 2004–2006 to estimate the average occupancy for patches < 2 ha; based on this estimate (0.48), the probability of all treatment plots < 2 ha in size being occupied was 0.053 (using 2004–2005 data only: 0.03; 2006 only: 0.14). Taken together, the likelihood of observing the lack of effect in treatments, given that a null hypothesis derived from unmanipulated areas is true, is low.

We found and monitored 87 flycatcher nests from 15 patches, 40 in treatments and 47 in controls, 36 of which suffered predation and 7 of which were parasitized by cowbirds. Based on control plots, there was no evidence for nest predation rates or brood parasitism rates varying with patch size (predation: $\chi^2 = 1.94$, DF = 1, $p = 0.16$; parasitism: $\chi^2 = 0.04$, DF = 1, $p = 0.85$). When comparing among

Table 2. A comparison of nest predation and parasitism models testing for effects of patch size (area) and treatment (trt) on least flycatcher reproductive performance, 2006. Table includes the number of parameters estimated in each model (K), Akaike's information criterion, adjusted for sample size (AIC_c), and the relative model weights.

Model	K	AIC_c	ΔAIC_c	AIC_c weight
Nest predation				
Constant	1	270.74	0.00	0.38
Trt × Area	4	271.72	0.98	0.23
Trt	2	272.17	1.42	0.18
Area	2	272.70	1.96	0.14
Trt + Area	3	274.14	3.40	0.07
Nest parasitism				
Constant	1	50.75	0.00	0.48
Trt	2	52.46	1.71	0.21
Area	2	52.47	1.72	0.21
Trt + Area	3	54.46	3.72	0.08
Trt × Area	4	56.33	5.58	0.03

models that tested for treatment and patch-size effects, the best model for both nest predation and parasitism was a constant model, though in both cases, there was moderate support for models that included treatment and patch size (Table 2). Based on model-averaged estimates of models with some support ($\Delta AIC_c < 2$; see Shaffer and Thompson 2007 for estimation methods), there were no strong patterns of nest predation or parasitism rates changing with patch size (Fig. 4). However, I note that in treatment plots, we did not find nests in patches <5 ha (Fig. 4), even though birds settled in these patches (Fig. 3).

Discussion

When animals are attracted to conspecifics, such behaviors can emerge on landscapes as patterns of sensitivity to patch size. This pattern in distribution arises from the aggregative nature of conspecific attraction and the geometric fact that, even simply by chance, there are fewer opportunities for social cues to guide settlement in smaller patches because of limited availability of habitat where such cues could occur (Fletcher 2006). Experimental results provided here, together with other recent work on least flycatchers in this region (Fletcher 2007, Fletcher and Hutto 2008), provide strong evidence that flycatcher sensitivity to patch size is driven, at least in part, by attraction to conspecifics. While this possibility has been noted for years by conservation biologists (Verner 1992, Reed and Dobson 1993), and has been confirmed recently with theoretical modeling (Fletcher 2006), to my knowledge this is the first experimental test of this hypothesis.

When addressing other alternatives for patch-size effects, I found no major support for vegetation structure explaining the patch-size effect of flycatchers. Although habitat structure showed no strong variation with patch size and flycatcher distribution spanned this entire vegetation gradient (Fig. 2), some critical resource may have remained unmeasured that varied consistently with patch size (food or another habitat parameter; Burke and Nol 1998). For example, in riparian habitats in Japan, Iwata et al. (2003) found that flycatcher abundance was correlated with emergent insects, but showed no correlations with vegetation

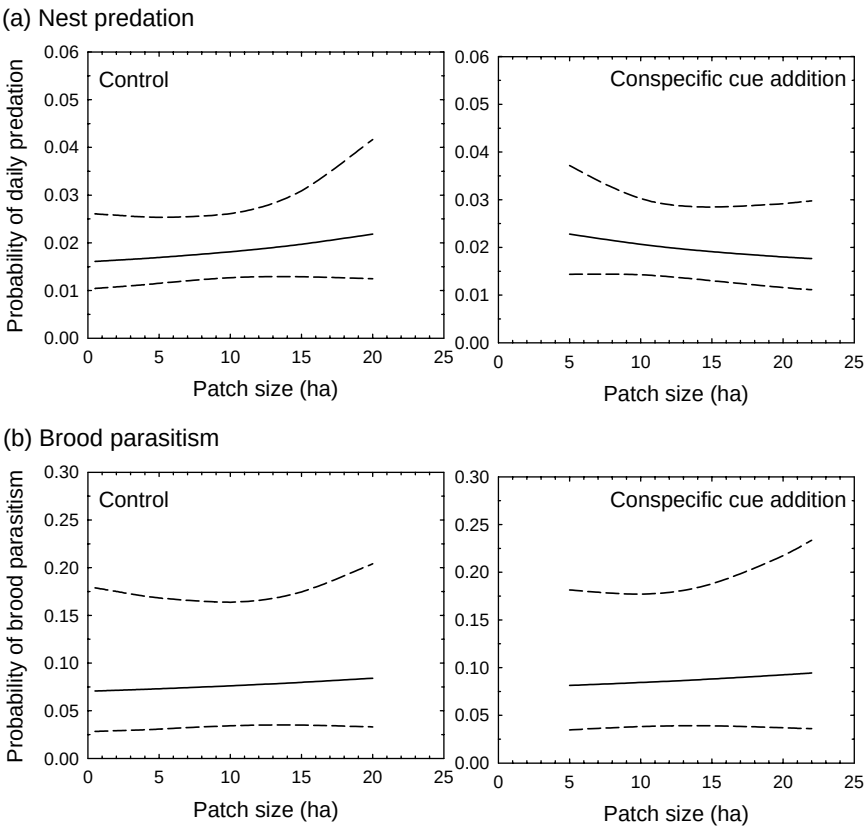

Figure 4. Model-averaged predictions (±95% CL) for (a) the probability of daily nest predation and (b) the probability of brood parasitism of least flycatcher nests as a function of patch size in treatments and controls, 2006.

structure. Furthermore, vegetation structure was only measured across the 51 patches used to initially infer a patch-size effect (Fig. 1b), vegetation was not measured in patches used in the playback experiment, and vegetation was not manipulated. As a consequence, it is not possible to interpret the potential for vegetation driving effects observed in the experiment, nor the relative role of vegetation versus conspecifics. Two lines of evidence do provide some further inference into flycatcher area sensitivity, habitat, and conspecific attraction. First, in another playback experiment, Fletcher (2007) found that flycatchers settled in treatments with conspecific cues greater than controls in this region, even though vegetation structure was similar between plot types, suggesting that flycatchers use conspecific cues independent of habitat. Second, Fletcher and Hutto (2008) also found that while vegetation structure helped explain flycatcher distribution in this region, patch width indeed explained independent variation (after controlling for vegetation effects) in occurrence of flycatchers, suggesting that patch size/width may influence flycatcher distribution beyond variation in habitat. These results and other recent studies (Nocera et al. 2006, Betts et al. 2008) highlight the need to quantify the relative roles of habitat and social cues in driving patterns of animal distribution. In addition, other measures of reproductive performance, such as nestling growth rates (Forsman et al. 2008), could provide a richer view regarding the role of resource limitation in small fragments as a mechanism for area sensitivity.

Overall nest predation and parasitism rates also showed no strong patterns with patch size that could explain flycatcher distribution, and rates were generally low in this system (cf. Tewksbury et al. 1998). A lack of variation in nest parasitism rates as a function of patch size was not surprising, because least flycatchers are generally thought to be less susceptible to nest parasitism than other migratory birds (Briskie 1994). However, numerous investigations have shown strong gradients of nest predation as a function of habitat loss and fragmentation (Robinson et al. 1995). Nest predation rates can be highly variable across years (Chalfoun and Martin 2007) and because nest predation rates were only estimated in one year, stronger patterns of predation effects could manifest with a longer study duration in this system (Stephens et al. 2004). Other research in cottonwood forests of the western United States, however, has not found strong evidence for year effects or patch-size effects on nesting success rates (Tewksbury et al. 1998, Davidson and Knight 2001). Nonetheless, Perry and Andersen (2003) did document higher vigilance rates inside least flycatcher clusters than outside of clusters in Minnesota, and Perry et al. (2008) estimated that nest predation rates toward the interior of flycatcher clusters were lower than for flycatchers on the edges of clusters. While neither of these investigations was attempting to test the enemies hypothesis for patch-size effects, both suggest that flycatcher aggregations may generally facilitate predator deterrence. Results from Perry and colleagues and those presented here suggest the possibility that patch-size effects could emerge from conspecific attraction behavior regardless of actual predation risk, but conspecific attraction may be ultimately used to reduce predation risk in general (regardless of patch size; see below). Alternatively, the enemies hypothesis could manifest from variation in predation risk on adults rather than on nests, which was not considered during the experiment. In any case, future attempts to better interpret the potential for nest predation and adult predation risk varying with patch size could provide stronger inference regarding the enemies hypothesis and area sensitivity in flycatchers.

A variety of ultimate factors have been invoked to explain why attraction may evolve (Stamps 1988). Increased mating success is often used to explain attraction at moderate to low densities in many species, and some evidence suggests that least flycatchers may have 'hidden leks', where males settle in aggregations due to extra-pair copulatory behaviours (Tarof et al. 2005, Fletcher and Miller 2006). Mating success in this system may indeed play a role in conspecific attraction: while social cues attracted birds to all treatment plots, I did not find flycatcher nests in plots <5 ha, which likely occurred from lower pairing success in these plots (Fletcher unpubl.). Such a pattern is consistent with the female preference model of hidden-lek evolution (Fletcher and Miller 2006). Indeed, reduction in pairing success is the most common demographic pattern observed in songbirds exposed to increased habitat loss and fragmentation (Lampila et al. 2005). Yet Fletcher (2007) found that similar patterns of attraction by flycatchers were seen with heterospecific cues from a subordinate competitor (the American redstart, *Setophaga ruticilla*), suggesting that other factors may at least partly explain the use of social cues in settlement by this species. Another alternative that might help explain the consistent attraction by flycatchers to both conspecific and heterospecific cues includes individuals using conspecifics or heterospecifics as indirect cues of habitat quality (Stamps 1988, Mönkkönen et al. 1990). For example, there is some evidence in other birds that younger individuals are more likely to use social cues for settlement (Ward and Schlossberg 2004, Nocera et al. 2006; but see Hahn and Silverman 2006), which could occur because older birds are an indicator of habitat quality (but see Fletcher and Miller 2006 for similar predictions from hidden-lek models). Alternatively, other potential Allee effects, such as group-size effects as a means of predator deterrence (Stamps 1988), could drive conspefic attraction behavior. Perry and colleagues (Perry and Andersen 2003, Perry et al. 2008) have recently provided some evidence suggesting that deterrence from both adult and nest predators could be greater in least flycatcher clusters. Because none of these hypotheses are mutually exclusive, it is possible that all of these alternatives play a role in the evolution of conspecific attraction.

Much of the evidence for patch-size effects on animal distribution is confounded by edge effects, because sampling designs for patch-size studies tend to sample further from the edge as patch-size increases (Parker et al. 2005, Fletcher et al. 2007). Results from this experiment, where I limited the potential for edge effects driving purported area effects via sampling design, show that patch-size effects do indeed occur on flycatcher distribution independent of edge effects. This makes sense, because while some hypotheses for patch-size effects can also explain edge effects (e.g. resources, enemies), the conspecific attraction hypothesis is

one of the few hypotheses fundamentally tied to patch-size per se rather than edge (Fletcher et al. 2007).

The species-area relationship is one of the few laws in ecology (Lawton 1999). In this region, the least flycatcher avoids small patches in a way that should have consistent impacts on species–area relationships in riparian habitats, although for a different mechanism than commonly assumed (Fletcher et al. 2007). However, such behaviorally driven avoidance of small patches could disrupt the species-area relationship in this system, because the least flycatcher is a dominant community member that other migrants avoid. Fletcher (2008) showed that migrant species richness declines with increasing densities of flycatchers. Consequently, small patches of riparian habitat in this region could have disproportionately high diversity because of reduced probability of occurrence of flycatchers. Such potential feedbacks from conspecific attraction via heterospecific avoidance of dominant competitors could provide an alternative mechanism for deviations from the species-area law and should be tested to better interpret the consequences of social information use.

Conclusions

Animal behavior can have emergent consequences at landscape scales. Results presented here highlight that social behavior can help explain large-scale patterns of distribution in a migratory bird. Social information use could have other large-scale influences, such as potentially altering functional connectivity and the costs and benefits of moving through landscapes (Sieving et al. 2004, Fletcher 2006). Because conspecific attraction has been experimentally documented in a wide variety of taxa (Stamps 1988), and recent investigations suggest that some species aggregate across heterogeneous landscapes (Bourque and Desrochers 2006), this behavior could help explain widespread patterns of sensitivity to fragmentation observed in many animals.

Acknowledgements – Thanks to T. Smucker, A. Peterson, J. Csoka, B. Robertson, E. Wellington, and R. Baylout for their hard field work and to the numerous landowners that allowed bird songs to be broadcasted from their properties. PPL-Montana, the Bureau of Land Management and the US Dept of Agriculture provided support for this project. Thanks to S. Schlossberg for advice on playback stations. A. Chalfoun, C.W. Miller, J. Nocera and K. Schmidt provided helpful and constructive reviews of previous drafts of this manuscript.

References

Ambuel, B. and Temple, S. A. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. – Ecology 64: 1057–1068.

Bender, D. J. et al. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. – Ecology 79: 517–533.

Betts, M. G. et al. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. – Proc. R. Soc. Lond. B 275: 2257–2263.

Blake, J. G. and Karr, J. R. 1987. Breeding birds of isolated woodlots: area and habitat relationships. – Ecology 68: 1724–1734.

Bourque, J. and Desrochers, A. 2006. Spatial aggregation of forest songbird territories and possible implications for area sensitivity. – Avian Conserv. Ecol. 1: 3.

Briskie, J. V. 1994. Least flycatcher (*Empidonax minimus*). – In: Poole, A. and Gill, F. (eds), The birds of North America, No. 99. Acad. Natl Sci., Philadelphia; Am. Ornithol. Union, Washington, DC.

Brotons, L. et al. 2003. Are fragments islands? Landscape context and density–area relationships in boreal forest birds. – Am. Nat. 162: 343–357.

Burke, D. M. and Nol, E. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. – Auk 115: 96–104.

Burnham, K. P. and Anderson, D. R. 1998. Model selection and inference: a practical information-theoretic approach. – Springer.

Chalfoun, A. D. and Martin, T. E. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. – J. Appl. Ecol. 44: 983–992.

Connor, E. F. et al. 2000. Individuals–area relationships: the relationship between animal population density and area. – Ecology 81: 734–748.

Danchin, E. et al. 2004. Public information: from nosy neighbors to cultural evolution. – Science 305: 487–491.

Davidson, A. S. and Knight, R. L. 2001. Avian nest success and community composition in a western riparian forest. – J. Wildlife Manage. 65: 334–344.

Donovan, T. M. and Lamberson, R. H. 2001. Area-sensitive distributions counteract negative effects of habitat fragmentation on breeding birds. – Ecology 82: 1170–1179.

Fletcher, R. J., Jr. 2006. Emergent properties of conspecific attraction in fragmented landscapes. – Am. Nat. 168: 207–219.

Fletcher, R. J., Jr. 2007. Species interactions and population density mediate the use of social cues for habitat selection. – J. Anim. Ecol. 76: 598–606.

Fletcher, R. J., Jr. 2008. Social information and community dynamics: nontarget effects from simulating social cues for management. – Ecol. Appl. 18: 1764–1773.

Fletcher, R. J., Jr. and Miller, C. W. 2006. On the evolution of hidden leks and the implications for reproductive and habitat selection behaviours. – Anim. Behav. 71: 1247–1251.

Fletcher, R. J., Jr. and Hutto, R. L. 2008. Partitioning the multi-scale effects of human activity on the occurrence of riparian forest birds. – Landscape Ecol. 23: 727–739.

Fletcher, R. J., Jr. et al. 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? – Can. J. Zool. 85: 1017–1030.

Forsman, J. T. et al. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. – Behav. Ecol. 19: 539–545.

Hahn, B. A. and Silverman, E. D. 2006. Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. – Biol. Lett. 2: 337–340.

Iwata, T. et al. 2003. Stream meanders increase insectivorous bird abundance in riparian deciduous forests. – Ecography 26: 325–337.

Knopf, F. L. et al. 1988. Conservation of riparian ecosystems in the United States. – Wilson Bull. 100: 272–284.

Lampila, P. et al. 2005. Demographic responses by birds to forest fragmentation. – Conserv. Biol. 19: 1537–1546.

Lawton, J. H. 1999. Are there general laws in ecology? – Oikos 84: 177–192.

MacKenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. – Ecology 83: 2248–2255.
Martin, P. R. et al. 1996. Response of American redstarts (suborder Passeri) and least flycatchers (suborder Tyranni) to heterospecific playback: the role of song in aggressive interactions and interference competition. – Behav. Ecol. Sociobiol. 39: 227–235.
Martin, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. – Am. Nat. 141: 897–913.
Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? – Ecology 79: 656–670.
Mönkkönen, M. et al. 1990. Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities? – Oecologia 85: 218–225.
Nocera, J. J. et al. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. – Proc. R. Soc. Lond. B 273: 349–355.
Parker, T. H. et al. 2005. Edge and area effects on the occurrence of migrant forest songbirds. – Conserv. Biol. 19: 1157–1167.
Perry, E. F. and Andersen, D. E. 2003. Advantages of clustered nesting for least flycatchers in north-central Minnesota. – Condor 105: 756–770.
Perry, E. F. et al. 2008. Reduced predation at interior nests in clustered all-purpose territories of least flycatchers (*Empidonax minimus*). – Auk 125: 643–650.
Reed, J. M. and Dobson, A. P. 1993. Behavioral constraints and conservation biology: conspecific attraction and recruitment. – Trends Ecol. Evol. 8: 253–256.
Risch, S. J. 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. – Ecology 62: 1325–1340.
Robinson, S. K. et al. 1995. Regional forest fragmentation and the nesting success of migratory birds. – Science 267: 1987–1990.
Root, R. B. 1973. Organization of a plant arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). – Ecol. Monogr. 43: 95–124.
Sauer, J. R. et al. 2006. The North American Breeding Bird Survey, results and analysis 1966–2005. Ver. 6.2.2006. – USGS Patuxent Wildlife Res. Center.
Schmidt, K. A. and Whelan, C. 1999. The relative impacts of nest predation and brood parasitism on seasonal fecundity in songbirds. – Conserv. Biol. 13: 46–57.
Shaffer, T. L. and Thompson, F. R., III. 2007. Making meaningful estimates of nest survival with model-based methods. – Studies Avian Biol. 34: 84–95.
Sieving, K. E. et al. 2004. Heterospecific facilitation of forest boundary-crossing by mobbing understory birds. – Auk 121: 738–751.
Smith, T. M. and Shugart, H. H. 1987. Territory size variation in the ovenbird: the role of habitat structure. – Ecology 68: 695–704.
Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. – Am. Nat. 131: 329–347.
Stephens, S. E. et al. 2004. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. – Biol. Conserv. 115: 101–110.
Tarof, S. A. et al. 2005. Are least flycatcher (*Empidonax minimus*) clusters hidden leks? – Behav. Ecol. 16: 207–217.
Tewksbury, J. J. et al. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. – Ecology 79: 2890–2903.
Verner, J. 1992. Data needs for avian conservation biology: have we avoided critical research? – Condor 94: 301–303.
Ward, M. P. and Schlossberg, S. 2004. Conspecific attraction and the conservation of territorial songbirds. – Conserv. Biol. 18: 519–525.