PATCH COLONIZATION DYNAMICS IN CAROLINA CHICKADEES (*POECILE CAROLINENSIS*) IN A FRAGMENTED LANDSCAPE: A MANIPULATIVE STUDY

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ABSTRACT.—Habitat and landscape features that influence the rate of interpatch movement and colonization may determine the likelihood that a species will persist in fragmented landscapes. We simulated patch extinction by removing Carolina Chickadees (*Poecile carolinensis*) from woodland fragments in an Ohio agricultural landscape in January 2002. We then monitored the woodlands to determine their dates of reoccupation and subsequent use for breeding by the birds. All woodlots were eventually reoccupied, regardless of size or degree of isolation, but woodlots in less-forested landscapes connected to other woodland by habitat corridors were reoccupied sooner than unconnected woodlots. Reoccupation was more likely to occur during periods of mild wind chill. Following reoccupation, individual Carolina Chickadees were more often temporarily absent from smaller woodlots, which suggests that they may have used woodlots that insufficiently met foraging or breeding requirements. Carolina Chickadees were more likely to remain to breed in larger woodlots. Results indicate that habitat connectivity may affect the tendency of this species to move through a fragmented landscape. Habitat corridors may be important management tools for maintaining movement of animals between patches. *Received 13 February 2005, accepted 4 January 2006.*

Key words: Carolina Chickadee, colonization, corridor, fragmentation, *Poecile carolinensis*, wind chill.

Dinámica de Colonización de Parches en *Poecile carolinensis* en Paisajes Fragmentados: Un Estudio de Manipulación

RESUMEN.—Las características del hábitat y del paisaje que influencian la tasa de movimiento y colonización entre parches puede determinar la probabilidad de que una especie determinada persista en pasajes fragmentados. Simulamos la extinción en parches mediante la remoción de individuos de *Poecile carolinensis* en fragmentos de bosque en un paisaje agrícola en Ohio en enero del 2002. Posteriormente monitoreamos los fragmentos para determinar las fechas de reocupación y el uso posterior para reproducción por parte de las aves. Todos los fragmentos fueron reocupados eventualmente, independientemente de su tamaño o grado de aislamiento, pero los fragmentos que se encontraban en paisajes con menor cobertura de bosque pero conectados por corredores a otros fragmentos fueron reocupados antes que los fragmentos no conectados. La reocupación fue más probable durante periodos con vientos moderados fríos. Posterior a la reocupación, en fragmentos pequeños los individuos de *P. carolinensis* presentaron más ausencias temporales, lo que sugiere que éstos usaron fragmentos que no cumplían los requerimientos

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mínimos para el forrajeo o la reproducción. Los individuos de *P. carolinensis* tuvieron una mayor probabilidad de continuar reproduciéndose en los fragmentos de mayor tamaño. Los resultados de este estudio indican que la conectividad del hábitat puede afectar la tendencia de esta especie a moverse a través de un paisaje fragmentado. Los corredores de hábitat pueden ser herramientas de manejo importantes para mantener el movimiento de animales entre parches.

The ability of individual organisms to move through a landscape and recolonize a patch after a patch-level extinction event may play an important role in maintaining species within a landscape (Burkey 1989, Gonzalez et al. 1998). Theoretical models suggest that recolonizations of habitat patches in which extirpations have occurred can be critical for the long-term survival of metapopulations (Fahrig and Merriam 1994). Observational studies (Pettersson 1985) and experimental studies (Gonzalez et al. 1998, Tewksbury et al. 2002) support these findings. We performed a manipulative study methodologically similar to that of Middleton and Merriam (1981), who entirely removed their study species, white-footed mouse (*Peromyscus leucopus*), from a single woodlot. Our study was designed to determine the relative importance of patch and landscape variables in affecting the probability of patch colonization by the Carolina Chickadee (*Poecile carolinensis*). Such information may shed light on factors that influence interpatch movement and allow for models that incorporate added degrees of realism in predicting the persistence of threatened species that currently live in fragmented habitats.

Landscape variables appear to influence movement in species that are ecologically and phylogenetically similar to the Carolina Chickadee. Bélisle et al. (2001) found that experimentally displaced Black-capped Chickadee (*P. atricapillus*) males were less likely to return to their breeding territories, and males that successfully returned required more time to do so in landscapes with less forest cover. Desrochers and Hannon (1997) and St. Clair et al. (1998) found that, where possible, Black-capped Chickadees generally avoided crossing habitat gaps, and instead traveled longer distances through woodland to reach mobbing-call play-backs. Finally, Lens and Dhondt (1994) found that forest fragments received first-brood dispersing Crested Tit (*Parus cristatus*) immigrants later than nearby continuous wooded areas and

were occupied by proportionally more second-brood immigrants, which suggested that the fragments did not represent optimal habitat.

Here, we examine the hypothesis that the rate at which habitat patches are reoccupied decreases with increased local habitat fragmentation (Wiens 1997). If this hypothesis is correct, the amount of forest and the presence of woodland habitat corridors in the landscape surrounding a woodlot from which Carolina Chickadees have been removed should be negatively associated with the length of removal–reoccupation intervals. If the reverse is correct (i.e., that the rate at which habitat patches are reoccupied increases with increased local habitat fragmentation), then the amount of forest and presence of habitat corridors should be positively correlated with the amount of time after removal until patch reoccupation and colonization. This latter situation is plausible if a low number of patches in a local landscape promotes a greater frequency of visits by dispersers per woodlot than a less fragmented landscape. We further hypothesized that for a small homeotherm, reoccupation events in winter are more likely to occur during periods of relatively mild wind chill, when thermoregulation and interpatch movement have lower metabolic costs. From this hypothesis, we predicted that we would be more likely to detect new immigrants during or immediately following periods of relatively mild wind chill.

Methods

From January to May 2002, we studied Carolina Chickadees within 25 privately owned woodlots in central Ohio (Delaware, Union, Madison, and Marion counties; Fig. 1). The study began during winter flocking and ended with mated-pair territories. All habitat patches used were between 1 and 12 ha and, though all were located within a 2,840-km^2 area, none was closer than 5 km to any other. We believe that >5 km between study woodlots effectively
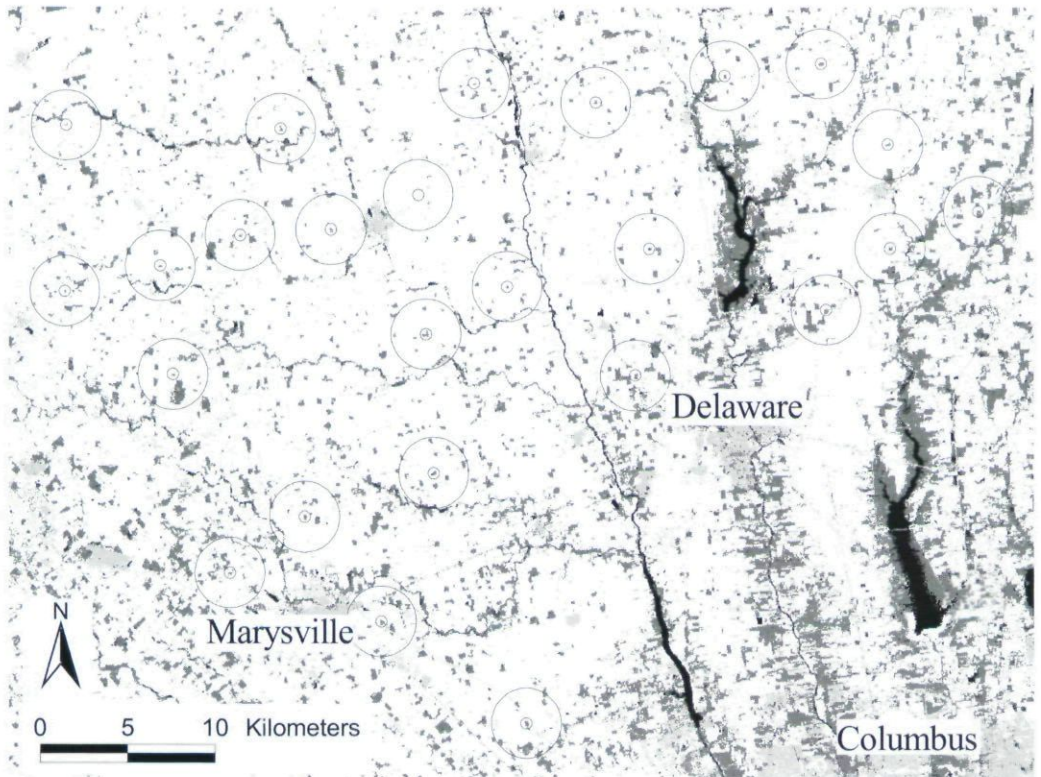
Fig. 1. Location of 25 study woodlots northwest of Columbus, Ohio. Light gray areas are urban, dark gray indicates wooded regions, water is represented by black, and agriculture is white. Study woodlots lie within the small circles and are additionally buffered by 2-km-radius circles.

maintained statistical independence, given that Black-capped Chickadee dispersers in a similarly fragmented landscape settled a median of 1 km from natal sites (Weise and Meyer 1979). Two woodlots were considered the same patch if they were <30 m apart (Villard et al. 1995) or if there was a vegetated corridor wider than 10 m connecting them.

Between 2 and 22 January, we captured Carolina Chickadees from occupied woodlots with feeder traps or with mist nets surrounding caged decoys and vocalization playback equipment. A woodlot was considered empty of Carolina Chickadees if none responded to postcapture playback, and none was seen or heard within resident mixed-species flocks. Carolina Chickadee removal required 1.5–5 h, depending on woodlot size and the number of resident Carolina Chickadees. We wished to avoid altering the value of woodlots for potential immigrants, so we removed feeders after removing residents.

We banded Carolina Chickadees slated for removal with U.S. Fish and Wildlife Service (USFWS) bands and transported them to and released them within the suburban "birdfeeder belt" of Columbus, Ohio (minimum distance: 23 km). All birds were released within 10 h of capture unless sunset was <1 h away—in which case, birds were held overnight and released at dawn. During transport, all birds were housed in individual containers with adequate ventilation and *ad libitum* sunflower seeds, *Tenebrio molitor* larvae, and water.

After removing all Carolina Chickadees from a woodlot, we visited at three-day intervals to determine whether immigrants had arrived in the interim. We searched for colonist Carolina Chickadees by broadcasting playbacks throughout the woodlots (assuming a 50–75 m detection radius) and by examining the composition of resident mixed-species flocks. If immigrants had reoccupied the woodlot, a feeder was briefly redeployed to capture them. In 24 woodlots,

all initial immigrants were banded with USFWS bands, individually marked with colored streamers, and then released on site. In the remaining woodlot, only one of the two initially reoccupying Carolina Chickadees could be marked. After immigrant Carolina Chickadees in a woodlot had been marked with streamers, feeder traps were removed.

We were unable to determine the age or sex of resident individuals at the time of capture. Apparently, in our Ohio study areas, some juvenile Carolina Chickadees grow new rectrices during the first prebasic molt, such that rectrix-tip angle is not an unambiguous indicator of juvenile or adult status (T. C. Grubb, Jr., pers. obs.) We putatively assigned sex to marked immigrants according to the individual vocal response to playbacks, "males" being those that sang the *"fee-bee, fee-bay"* song and "females" being those that did not. The vocal response of individual birds marked with streamers remained consistent over the course of the study.

Woodlots with marked Carolina Chickadees were observed every five days to determine their length of stay. To determine instances of colonization, we followed marked individuals until it was evident that they were initiating breeding (courtship feeding observed or female begging calls detected, or both) or until 3 May, by which time the breeding season of Carolina Chickadees is well underway in Ohio (Grubb and Bronson 2001). Villard et al. (1995) validated absences of birds in woodlots by broadcasting playback tapes of conspecific vocalizations. We censused woodlots throughout the study using this method. We used only playbacks of Carolina Chickadee calls, not the characteristic *"fee-bee, fee-bay"* song, to avoid simulating the presence of a resident territorial male. Otherwise, we might have risked triggering behavioral responses by neighboring Carolina Chickadees, enhancing or dampening their probability of moving into the study woodlot. We used an Aiwa CSD-A120 portable CD player to broadcast Carolina Chickadee calls. During each visit, in the absence of response, we broadcast playbacks throughout the woodlot.

Once we detected the presence of Carolina Chickadees, we ceased broadcasting the playback. We noted the number of Carolina Chickadees detected and resightings of individual marked birds. We also looked for USFWS

bands, in case relocated birds had managed to return to their original woodlot.

We related the amount of time between induced extinction and subsequent reoccupation to patch area, distance to nearest adjacent patch, total woodland area within 2 km of the habitat patch, and presence of fencerows connecting the focal patch to other patches in the landscape. Ten of the 25 woodlots were connected to other local woodlots by fencerows. We defined a patch as a cluster of trees >10 m in height, with an overlapping canopy covering >1 ha. Whereas fencerow connectivity was determined from aerial photographs, the other variables were determined by analyzing U.S. Geological Survey Landsat Thematic Mapper 2000 data with ARCGIS, version 8.1 (ESRI, Redlands, California), and FRAGSTATS, version 3.2 (see Acknowledgments).

The three response variables of interest were whether a patch was reoccupied, the length of time from patch extinction to patch reoccupation, and whether a reoccupied patch was subsequently colonized. Immigrant pairs that arrived at an empty patch during the winter but disappeared before the beginning of the breeding season were not considered colonists, because they did not attempt to breed in that patch.

We used linear regression for analyses involving continuous response variables (i.e., time from extinction to reoccupation), and we addressed incidence of woodlot colonization using logistic regressions. All independent variables were transformed to correct for non-normal residual distributions.

We used an information-theoretic approach with the linear regression models. Nested model sets were constructed *a priori* and compared using Akaike's Information Criterion (AIC; Burnham and Anderson 1998). Models were evaluated by comparing ΔAIC values and the number of model parameters (K). The best models were those with ΔAIC < 2 and the fewest parameters (most parsimonious). Because the relative best models may not explain much variance, we additionally report P values and r^2 values to enable assessment of individual model fit.

Potential habitat-patch quality for Carolina Chickadees was measured using vegetation sampling *sensu* Grubb and Bronson (2001). We quantified nine variables: average diameter at breast height (DBH) of trees; average DBH of the largest 10% of trees; average DBH of the largest 20% of

trees; percentage of shrub cover; and densities of saplings, snags, logs, trees, and trees with poison ivy (*Rhus radicans*) vines. Poison ivy berries are an important winter food of Carolina Chickadees (T. C. Grubb, Jr., pers. obs.). We condensed vegetation data with principal component analysis (PCA) and employed PCA scores as independent variables in analyses incorporating vegetation data. Vegetation variables that violated normality assumptions were log transformed (Anderson-Darling normality test; D'Agostino 1986). The nine vegetation variables entered into the PCA are detailed in Table 1. We used the first three principal components (PC1, PC2, PC3) in our analysis, because their eigenvalues were greater than those generated by the broken-stick model (Jackson 1993). Principal component 1 was positively related to size of trees, PC2 was positively related to density of logs (Logs) and snags (Snags), and PC3 was positively related to the average densities of both poison ivy (Ln_PI) and percentage of shrub cover (Ln_Shrub).

We did not determine whether repopulation was related to average daily temperature or wind speed alone, because wind chill (i.e., the interaction of the two) was more likely to affect vagile homeothermic organisms (Grubb

1978). Weather data were averaged from daily weather summaries recorded at The Ohio State University Airport in Columbus and the Marion County Airport (data for 2003 from National Climatic Data Center; see Acknowledgments), sites that bracketed the locations of the study woodlots. We calculated average daily wind chill using an equation provided by the National Weather Service (see Acknowledgments), where wind chill ($°F$) = $35.74 + 0.6215\,T - (35.75\,V0.16) + 0.4275\,T\,(V0.16)$, where T = temperature ($°F$) and V = velocity (miles h^{-1}), and then converted to Celsius ($°C$). For every woodlot, we first determined the wind chill for the 30 days prior to woodlot repopulation, and then determined the linear regression equation for those wind-chill values. By extending the equation to the day of repopulation, we determined the wind-chill value predicted for that day by the long-term trend. To obtain an observed wind-chill value for each instance of repopulation, we averaged the average wind-chill conditions on the day of detection and the two days preceding detection, when we had not visited. Using Wilcoxon signed-ranks tests, we tested the prediction that if Caroloina Chickadees reoccupy woodlots during periods of relatively benign weather, the

TABLE 1. Component matrix of a principal component analysis (PCA) of woodland vegetation metrics, including component eigenvalues and percentage of variance explained by each component.

	Principal components		
	1	2	3
Eigenvalues	3.387	1.914	1.536
Broken-stick eigenvalues	2.829	1.829	1.329
Percentage of variance explained	37.630	21.261	17.065
Cumulative variance explained	37.630	58.891	75.956
Variables [a]			
Ln_Shrub	0.021	−0.525	0.706
Ln_PI	−0.340	−0.157	0.841
Ln_DBH	0.822	0.318	0.143
Ln_20%	0.806	0.499	0.220
Ln_10%	0.740	0.467	0.172
Logs	−0.543	0.629	0.188
Saplings	0.529	-0.523	0.127
Snags	−0.507	0.585	0.407
Trees	−0.753	0.181	−0.120

[a] Ln_Shrub = ln (average percentage of shrub cover); Ln_PI = ln (density of trees with poison ivy vines); Ln_DBH = ln (average diameter at breast height [DBH]); Ln_10% = ln (average DBH of largest 10% of trees); Ln_20% = ln (average DBH of largest 20% of trees); Logs = average number of fallen trees ha^{-1}; Saplings = average number of saplings ha^{-1}; Snags = average number of dead upright trees ha^{-1}; and Trees = average number of trees ha^{-1}.

observed wind-chill values should be milder than the predicted values (Fig. 2).

Marked birds did not always respond to playback and, thus, may have gone undetected. We performed an analysis of detection to estimate whether lack of detection was attributable to observer error or bird absence. If lack of detections was attributable to observer error, we predicted that either (1) detection ability would not vary predictably with habitat patch and landscape features or (2) observer error would be higher in larger habitat patches because of the greater chance of missing birds. Detection data were analyzed from the first sighting of a reoccupying bird, either to the end of the field season or to the visit before the final sighting of the bird. For each reoccupied woodlot, we arcsine-square-root-transformed the proportion of visits when we detected target birds. The total number of visits differed among woodlots, so we assigned weighting factors ($\sqrt{N}$) for the proportion of visits during which marked birds were detected at each woodlot. For landscape variables in this detection analysis, we considered the total amount of wooded area within 2 km of the focal woodlot (Ln_Area_2K) and the presence–absence of a fencerow connecting the focal woodlot with another woodlot in the vicinity (Fence). Patch variables included patch area (Ln_Area), patch shape (Shape, an area:edge index that controls for raster format of data; FRAGSTATS), and PC1. We log transformed nonlinear variables to better approach linearity requirements for regression analysis.

Results

All 25 woodlots were reoccupied over the course of the winter. None of the 102 birds transported from 25 woodlots returned. Immigrants were detected as paired in 12 of the woodlots, and we were able to assign the sex to lone immigrants in 11 of the 13 remaining woodlots. Seven of the lone immigrants were classified by their vocalizations as male, and four as female.

We examined the length of time between induced extinction and reoccupation using an AIC analysis of regression models (Table 2), employing AIC_c (corrected for small sample size). The distribution of elapsed time to reoccupation of study woodlots is shown in Figure 3. The "best" model by parsimony was Ln_Area_2k and Fence ($r^2 = 0.355$, Ln_Area_2k $\beta = 17.159$,
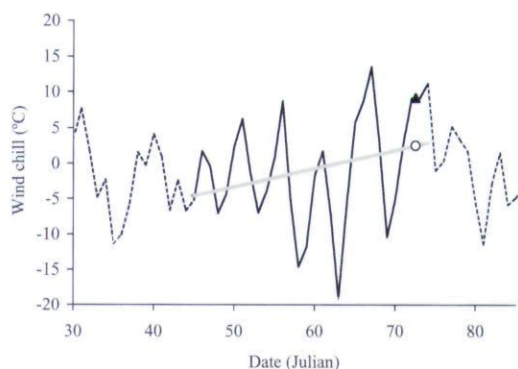

FIG. 2. Technique for calculating predicted and observed wind-chill values related to woodlot reoccupation by Carolina Chickadees. Average daily wind chill (dashed line) is a regional average. Predicted wind chill is from the regression of wind chill on Julian date (gray line) for the 30 days before observed reoccupation (solid black line). Observed (triangle) and predicted (circle) wind chills are the respective averages of the observed and predicted mean daily wind chills on the day of reoccupation and all days since the most recent observer visit when the woodlot was empty.

Fence $\beta = -22.220$, Constant = -27.782, $\Delta AIC_c = 0$, $w_i = 0.459$), which indicates that birds moved sooner into woodlots situated in less-wooded landscapes and connected to other woodlots by fencerows. The variables Ln_Area_2k and Fence were correlated ($r^2 = 0.442$, $P = 0.027$). A *post hoc* analysis indicated that the interaction term between the two variables was not significant ($r^2 = 0.355$, Ln_Area_2k $P = 0.017$, Fence $P = 0.740$, Ln_Area_2k * Fence $P = 0.988$). The only other model that performed similarly ($\Delta AIC_c < 2$) contained the variables Ln_Area_2k, Fence, and PC1 ($r^2 = 0.404$, Ln_Area_2k $\beta = 16.261$, Fence $\beta = -19.927$, PC1 $\beta = 4.621$, Constant = -4.741, $\Delta AIC_c = 1.169$, $w_i = 0.256$).

We examined the date of reoccupation in relation to weather conditions by comparing the predicted and observed wind-chill values for each woodlot. Independent of calendar date, birds were more likely to reoccupy woodlots during periods when observed wind chill was milder than that predicted by a long-term trend ($Z = 2.275$, $P = 0.023$, $n = 25$).

Using the 3-May criterion, we found that Carolina Chickadees bred in 18 of the 25 woodlots. We examined breeding occurrence using

TABLE 2. Ranked AIC_c multiple linear regression models for the length of time woodlots remained empty between removal of resident Carolina Chickadees and reoccupation by immigrant Carolina Chickadees. The best model, by parsimony, is shown in bold. Models are evaluated by comparisons of ΔAIC_c values and number of model parameters (K). See Table 1 for definitions of variables. Akaike weight (ω_i) is the probability that a model is the best model of the set, discounting parsimony. Variable beta values are indicated by plus and minus signs, and P values by letters: (a) $P < 0.01$, (b) $P < 0.05$, (c) $P \leq 0.10$, and (d) $P > 0.10$.

Model	K	r^2	ΔAIC_c	ω_i
Ln_Area_2k[+, a], Fence[−, a]	**4**	**0.355**	**0.000**	**0.459**
Ln_Area_2k[+, a], Fence[−, b], PC1[+, d]	5	0.404	1.169	0.256
Ln_Area_2k[+, a], Fence[−, b], Ln_Patch_Area[−, d]	5	0.366	2.721	0.118
Ln_Area_2k[+, d]	3	0.113	5.092	0.036
PC1[+, d]	3	0.111	5.152	0.035
Fence[−, d]	3	0.085	5.879	0.024
Ln_Patch_Area[+, d]	3	0.034	7.227	0.012
Ln_Patch_Area[+, d], Fence[−, d]	4	0.133	7.396	0.011
Ln_Area_2k[+, d], PC1[+, c], PC2[−, d]	5	0.230	7.576	0.010
Ln_Patch_Area [+, d], PC1[+, d]	4	0.121	7.725	0.010
PC2[+, d]	3	0.003	8.039	0.008
PC3[+, d]	3	0.000	8.101	0.008
Fence [−, d], PC1[+, d], PC2[−, d]	5	0.168	9.507	0.004
Ln_Patch_Area[+, d], PC2[−, d]	4	0.037	10.258	0.003
Ln_Area_2k[+, a], Ln_Patch_Area[−, d], Fence[−, b], PC1[+, d], PC2[+, d], PC3[+, d]	6	0.466	10.022	0.003
PC1[+, d], PC2[+, d], PC3[+, d]	5	0.114	11.093	0.002

logistic regression models followed by AIC analysis (Table 3), employing $QAIC_c$ because of the modest sample size and overdispersion of data ($\hat{c} = 1.829$). The model with the most support ($\Delta QAIC_c = 0$; parsimony) contained only the variable Ln_Patch_Area (Nagelkerke $r^2 = 0.332$,

Ln_Area $\beta = 2.305$, Constant $= -1.706$, $w_i = 0.367$). The only other model that performed similarly ($\Delta AIC_c < 2$) contained the variables Ln_Patch_Area and PC1 ($r^2 = 0.386$, Ln_Patch_Area $\beta = 2.930$, PC1 $\beta = -0.649$, Constant $= -2.317$, $\Delta AIC_c = 1.802$, $w_i = 0.149$).

We performed a logistic regression analysis to examine changes in the probability of detection of birds responding to vocalization playback. Overall, there was no indication that birds were undetected because of seasonal progression or their habituation to repeated playbacks. On average, we detected previously banded birds 75.5% of the time (SD = 20.5%, range: 30.7–100%). We had 100% detection in four woodlots (three < 15 visits, one = 29 visits). To check the possibility that birds habituated to our playback, we compared the response data with patch-visit number. Twelve woodlots were visited ≥15 times. Eleven of these were individually analyzed (we excluded the woodlot with 29 visits, 100% detection success), with no significant results, even though no adjustment was made for multiple comparisons. Of the 11 nonsignificant analyses, seven beta values were negative and four positive.
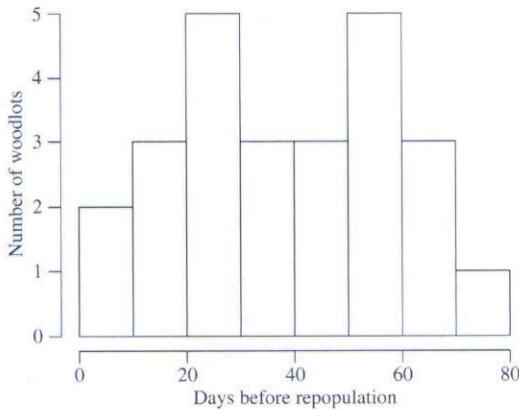

FIG. 3. Histogram of the length of time (days) between induced extinction and reoccupation of study woodlots by Carolina Chickadees, January–March 2002.

TABLE 3. Ranked QAIC$_c$ multiple logistic regression models for the probability of immigrant Carolina Chickadees breeding in study woodlots. The best model, by parsimony, is shown in bold. Models are evaluated by comparisons of ΔQAIC$_c$ values and number of model parameters (*K*). See Table 1 for definitions of variables. Akaike weight (ω$_i$) is the probability that a model is the best model of the set, discounting parsimony. Variable beta values are indicated by plus and minus signs, and *P* values by letters: (a) *P* < 0.01, (b) *P* < 0.05, (c) *P* ≤ 0.10, and (d) *P* > 0.10.

Model	K	Nagelkerke r^2	ΔQAIC$_c$	ω$_i$
Ln_Patch_Area[+, b]	**3**	**0.332**	**0.000**	**0.367**
Ln_Patch_Area[+, b], PC1[-, d]	4	0.386	1.802	0.149
Ln_Patch_Area[+, b], Fence[+, d]	4	0.342	2.586	0.101
Ln_Patch_Area[+, b], Shape[+, d]	4	0.238	2.654	0.097
Ln_Patch_Area[+, c], Ln_Area_2k[+, d]	4	0.332	2.849	0.088
Ln_Patch_Area[+, b], Shape[+, d], PC1[-, d]	5	0.397	4.730	0.034
Ln_Patch_Area[+, b], PC1[-, d], PC2[-, d]	5	0.396	4.757	0.034
PC3[+, d]	3	0.023	5.160	0.028
PC2[-, d]	3	0.011	5.350	0.025
PC1[-, d]	3	0.000	5.498	0.023
Ln_Patch_Area[+, b], Ln_Area_2k[-, d], Fence[+, d]	5	0.347	5.731	0.021
Ln_Area_2k[+, d], Fence[+, d]	4	0.108	6.717	0.013
Ln_Patch_Area[+, b], Shape[+, d], PC1[-, d], PC2[-, d]	6	0.404	8.105	0.006
Ln_Patch_Area[+, c], Ln_Area_2k[-, d], PC1[-, d], PC2[+, d]	6	0.397	8.238	0.006
Ln_Patch_Area[+, b], Fence[+, d], PC1[-, d], PC2[-, d]	6	0.396	8.256	0.006
PC1[-, d], PC2[-, d], PC3[+, d]	5	0.034	11.010	0.001
Ln_Patch_Area[+, b], Ln_Area_2k[-, d], Fence[+, d], Shape[+, d], PC1[-, d], PC2[-, d], PC3[-, d]	7	0.407	21.367	0.000

When we performed a linear regression of the arc-sine-transformed proportion of our visits during which Carolina Chickadees were present at a woodlot and examined models using AIC (Table 4), we found that the model with the most support was Shape and Ln_Patch_Area (r^2 = 0.332, Shape β = –0.500, Ln_Area β = 0.352, Constant = 1.340, w_i = 0.522). All other models achieved ΔAIC$_c$ > 2 and, thus, were not considered further. In a *post hoc* analysis, when we included the interaction term between Shape and Ln_ Area, the r^2 value improved to 0.539 (Ln_ Patch_Area *P* = 0.03, Shape *P* = 0.102, Ln_ Area * Shape *P* = 0.011).

DISCUSSION

If interpatch movements by other species are similar to those of the Carolina Chickadees in the present study, habitat corridors may not be necessary for ensuring recolonization in fragmented landscapes. Regardless of their characteristics and their degree of isolation, all 25 woodlots were reoccupied. Although all woodlots were reoccupied in a matter of weeks or months, woodlots were reoccupied sooner if they were connected to other habitat patches by fencerows and were located in more heavily wooded landscapes. This result appears to be at odds with that of Lens and Dhondt (1994), who found evidence that natal Crested Tit dispersers immigrated into less-fragmented habitat before appearing in fragmented habitat patches, and Turcotte and Desrochers (2005), who found that Black-capped Chickadees may effectively be gap-locked in isolated fragments by harsh winter weather. Winter weather conditions were more extreme in Turcotte and Desrochers's (2005) study than in the present study. It is possible that our result would have been similar to theirs had our winter been substantially colder.

The correlation between the amount of woodland within 2 km of a focal woodlot and the presence of a fencerow is likely a result of fragmentation history. We can expect the distance between woodland fragments to increase as fragments are reduced in size or eliminated with the conversion of woodland into farmland. Fencerow connection between woodlots

Table 4. Ranked AIC_c multiple linear regression models for the probability of detection of marked immigrant Carolina Chickadees during woodlot visits. Models are evaluated by comparisons of ΔAIC_c values and number of model parameters (K). See Table 1 for definitions of variables. Akaike weight (ω_i) is the probability that a model is the best model of the set, discounting parsimony. Variable beta values are indicated by plus and minus signs, and P values by letters: (a) $P < 0.01$, (b) $P < 0.05$, (c) $P \leq 0.10$, and (d) $P > 0.10$.

Model	K	r^2	ΔAIC_c	ω_i
Shape[-, c], Ln_Patch_Area[+, a]	4	0.332	0.000	0.522
Ln_Patch_Area[+, b]	3	0.180	2.274	0.168
Shape[-, c], Ln_Patch_Area[+, b], PC1[-, d]	5	0.335	3.052	0.114
Ln_Patch_Area[+, c], PC1[-, d]	4	0.200	4.512	0.055
PC1[-, d]	3	0.040	6.214	0.023
Ln_Patch_Area[+, b], Ln_Area_2k[-, d], Fence[+, d]	5	0.243	6.299	0.022
Shape[-, c], Ln_Patch_Area[+, b], PC1[-, d], PC2[-, d]	6	0.340	6.367	0.022
PC3[-, d]	3	0.004	7.135	0.015
PC2[-, d]	3	0.002	7.196	0.014
Ln_Area_2k[+, d]	3	0.000	7.228	0.014
Fence[+, d]	3	0.000	7.234	0.014
Ln_Patch_Area[+, c], PC1[-, d], PC2[+, d]	5	0.200	7.669	0.011
Ln_Area_2k[+, d], PC2[-, d]	4	0.002	10.050	0.003
PC1[-, d], PC2[-, d], PC3[-, d]	5	0.046	12.079	0.001
Ln_Area_2k[+, d], PC1[-, d], PC2[-, d]	5	43.000	12.157	0.001
Shape[-, d], Ln_Patch_Area[+, b], Ln_Area_2k[-, d], Fence[+, d], PC1[-, d], PC2[-, d], PC3[-, d]	9	43.100	15.982	0.000

likely decreases as the conversion progresses. Given this, the positive relationship between the amount of woodland within 2 km of a woodlot and the length of time a woodlot remained empty is difficult to explain. More nearby habitat patches or larger habitat patches (or both) should support a higher density of Carolina Chickadees, providing more potential immigrants to reach the study woodlot. Perhaps the less wooded area in a landscape, the higher the disperser visitation rate per woodlot. This effect may be intensified if the target woodlots are relatively large in highly fragmented areas and relatively small in more heavily wooded areas of the landscape, because dispersers may perceive and preferentially move toward the largest local woodlots (Lima and Zollner 1996).

To examine these possibilities, we performed a *post hoc* analysis to determine how focal woodlot size varied in relation to the size of patches in the immediate surrounding landscape. We failed to detect a relationship following the removal of two outliers ($r^2 = 0.080$, $\beta = 1.05$, $P = 0.162$, $n = 23$). The natural log of the amount of woodland within 2 km of a focal woodlot was not related to the number of woodlots larger than the focal woodlot ($r^2 = 0.077$, $\beta = 1.316$, $P = 0.180$, $n = 25$).

Thus, there was no relationship between patch area and landscape woodland cover or between landscape woodland cover and the number of patches larger than the focal woodlot.

An alternative explanation for the positive relationship between the amount of woodland within 2 km of a woodlot and the length of time a woodlot remained empty is that more bird feeders were available in more urbanized, less forested areas. The presence of nearby feeders could have increased the residence times of transient Carolina Chickadees in local woodlots. To investigate this possibility, we re-examined the Landsat imagery to determine the combined amount of low- and high-density residential development within 2 km of each point and normalized data by performing a natural-log transformation of the residential area values (Ln_Development_2k). However, we found no correlation between the amount of woodland area and residential area within 2 km (Pearson's correlation of Ln_Area_2k and Ln_Development_2k = –0.384, $P = 0.175$). There was no evidence that the presence of development near woodlots influenced reoccupation dates when we compared woodlots with development within 2 km ($n = 14$) to those without ($n =$

11) (T = 0.940, df = 18, P = 0.36). For woodlots with development within 2 km (development area range: 0.1–13.1 ha), we additionally found no relationship between the length of time woodlots remained empty and the amount of residential development within 2 km (linear regression, r^2 = 0.03, Ln_Development_2k β = 3.183, Constant β = 30.493, P = 0.551, n = 14).

Carolina Chickadees did not breed in all available woodlots, and breeding was more likely to occur in the larger patches. This result may indicate that large woodlots were more likely to contain resources necessary for reproduction. Three of the seven woodlots in which no breeding occurred contained singleton male Carolina Chickadees, which, by the end of the study season, were observed singing continually. All three of the solo males had had putative mates at the beginning of April. This observation of late-winter habitat-patch abandonment by females is similar to that made by Grubb and Bronson (2001) in their study of Carolina Chickadees, Black-capped Chickadees, and Carolina × Black-capped Chickadee hybrids.

Abiotic factors, such as weather, may mediate the likelihood of interpatch dispersal. We found that throughout our winter study, birds were more likely to arrive at a habitat patch during periods of relatively mild wind chill. It is conceivable that the severity of weather during the winter will constrain, to varying degrees, the likelihood of interpatch movements by Carolina Chickadees. The effect of forest fragmentation on these birds may be a temporal as well as a spatial phenomenon.

We did not elicit response to playback on all post-reoccupation visits. Birds may have either been elsewhere when playbacks occurred, or in the woodlot but unresponsive to playbacks. We have two lines of evidence suggesting that birds were absent from the woodlots, and not simply ignoring our playbacks. The first is that there did not appear to be a pattern to the order of Carolina Chickadee absences. In no woodlot did Carolina Chickadees respond less frequently with increasing numbers of woodlot visits. Therefore, it does not appear likely that bird response declined with habituation, experience, or the approach of the breeding season.

The second line of evidence relates to our being less likely to elicit a response to playback in smaller woodlots. This trend was contrary to what would be expected had our playbacks

been more limited in attracting birds than we assumed they were. The observed pattern is also readily interpretable biologically. Those individuals in small patches may have had the most to gain by venturing to investigate other local patches. Birds defending large woodlots would gain less by searching for better territories. Andreassen and Ims (2001) found that root voles (*Microtus oeconomus*) were more likely to emigrate from relatively smaller, more sparsely populated patches. Individuals using small patches of habitat may also meet resource requirements through habitat supplementation (Dunning et al. 1992). Smaller habitat patches should be inhabited by such individuals less often than larger patches. From a management perspective, it would be useful to know whether the likelihood of birds foraging from small habitat patches is as great in landscapes where habitat fragmentation has resulted in even higher degrees of patch isolation (Blake and Karr 1987).

Our results suggest that the assumptions, from studies of unmarked birds, that winter presence indicates breeding presence (Opdam et al. 1985) and that disappearance of winter residents from a habitat patch necessarily indicates a death or emigration event (Doherty and Grubb 2000) are potentially unwarranted. We found that marked individuals were sometimes not detected in a woodlot, but would be present during a subsequent visit. For habitat patches that support exceedingly small populations, a single finding of species absence does not necessarily indicate that a patch remains unused or is necessarily unimportant to local resident individuals.

Much of the variance in bird absence was explained when patch size and shape and their interaction were taken into account. Bird presence was positively associated with patch area and negatively associated with the edge:area index. Severe wind chill can reduce the amount of woodlot area a bird can forage in during cold periods (Dolby and Grubb 1999). Therefore, during winter months, Carolina Chickadees in highly fragmented areas preferring woodlots with low edge:area ratios may maximize the proportion of a woodlot available for foraging. Another edge-related threat to chickadees is the House Wren (*Troglodytes aedon*), an intense competitor for nest sites. Carolina Chickadees preferentially nest toward the center of a woodlot

(Doherty and Grubb 2002), whereas House Wrens tend to nest close to a woodlot edge. Therefore, the closer to the edge of a woodlot a Carolina Chickadee is forced to nest, perhaps the less its fitness gain.

Conservation plans for even highly vagile species, like birds, may do well to include corridors and to protect small habitat patches. Carolina Chickadees accomplish interpatch movements in a fragmented landscape, yet our study indicates that their movements are constrained. It appears that corridors facilitated movement, possibly offering refuge from predators such as accipitrine hawks. Once they become "residents" of a habitat patch, the degree to which Carolina Chickadees exhibit site fidelity and the likelihood of breeding within the patch appear to be determined by patch features. Smaller habitat patches may not be as likely to support breeding pairs of birds, but they may serve other functions, such as habitat supplementation. Small patches, therefore, may not necessarily function only as sink habitat, but may confer fitness benefits to dispersing organisms.

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Associate Editor: K. A. Hobson