SHORT-TERM DYNAMICS OF CAVITY-NESTING BIRD COMMUNITIES IN DISJUNCT FLOODPLAIN HABITATS[1]

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Abstract. We studied turnover rates in cavity-nesting bird communities during 1983 and 1984 in 34 cottonwood-willow (*Populus-Salix*) habitat fragments along the North Platte River in southeastern Wyoming. Our principal goal was to determine whether the equilibrium theory of island biogeography was applicable to this system. We tested two hypotheses: (1) equilibrial turnover of cavity-nesting bird species does not occur in disjunct floodplain habitats, and (2) no significant relations exist between absolute turnover rate (ATR) and habitat-fragment features. Paired-*t* tests and a one-sample sign test corroborated equilibrial turnover for the group of fragments collectively, but examination of the hypothesis at the level of individual fragments did not support the equilibrium model. Simple- and partial-regression coefficients indicated ATR was positively associated with fragment size, the reverse of what equilibrium theory predicts; ATR, however, was negatively related to distance to nearest streamside habitat fragment (analogous to degree of isolation), which is consistent with the theory. ATR was significantly related to five fragment features in a validated multiple regression model: amount of edge/hectare, size of fragment, frequencies of snag classes 4 (56 to 70 cm dbh) and 6 (>85 cm dbh), and the presence of palustrine wetland bordering each fragment. Short-term dynamics of cavity-nesting bird communities in the system we studied are not completely predictable from the equilibrium theory. Fragment features appear to be the important deterministic forces affecting species richness and dynamics, but stochastic immigration and extinction may also be operative. Application of equilibrium island-biogeographic theory to conserve the system we analyzed is inappropriate. Instead, recommendations that recognize the deterministic influences we have identified should be used.

Key words: Cavity-nesting birds; disjunct floodplain communities; habitat fragments; island-biogeographic theory; nonequilibrial flux; seasonal communities; turnover; Wyoming.

INTRODUCTION

During the past two decades, the theory of equilibrium island biogeography (MacArthur and Wilson 1963, 1967) has been summoned repeatedly to account for the number of bird species breeding on oceanic islands and in fragments of mainland habitats. Designs for nature preserves apparently consistent with the results and the theory have been recommended (e.g., Diamond 1975, Terborgh 1975, Wilson and Willis 1975, Diamond and May 1976). But there is doubt among many ecologists that such applications are justified (Simberloff and Abele 1976, Game 1980, Higgs and Usher 1980, Higgs 1981, Margules et al. 1982, Simberloff and Abele 1982, Blouin and Connor 1985, and many others). Indeed, in a thorough review of the literature, Gilbert (1980:229) found that "none of the continental [habitat-fragment] situations, and very few of the insular ones, warrant the application of MacArthur and Wilson's model." Gilbert's (1980: 209) principal conclusion was that "the equilibrium theory remains insufficiently validated to permit its widespread application to many problems of biogeography, ecology, and nature conservation."

MacArthur and Wilson proposed their equilibrium model to account for the number of resident species on oceanic islands. With an interest in this model's scope of relevance, we asked whether it applied to breeding communities of cavity-nesting birds in habitat fragments. The system we studied differed substantially from the situation for which the theory was initially developed: our system included both resident and migrant species; the rangeland and agricultural fields surrounding fragments were not completely inhospitable habitats; and the breeding communities assembled anew each year. We do not

test the validity of the equilibrium theory for oceanic islands here. Instead, we determine whether the model is useful outside of the context for which it was first proposed. Attempts to reconcile dynamics of avian breeding populations in habitat fragments with the equilibrium theory have been unsuccessful because important conditions of the model were not adequately addressed (see McCoy 1982), so the general applicability of the theory to such situations remains unclear.

For the theory to be applicable, (1) area and number of species must be positively related, (2) number of species cannot fluctuate widely (i.e., extinctions should be balanced by immigrations), (3) at least part of the species complement must change identity between sampling times, and (4) avifaunal turnover must be stochastic and cannot be attributable to ecological changes within fragments (e.g., plant succession, human alteration) between census periods (Lynch and Johnson 1974, Gilbert 1980). Assessment of whether the equilibrium model applies in a given situation has been plagued by various problems, particularly (1) the difficulty in identifying immigrating species (breeders) and those that have gone extinct (no longer breeding), (2) the inability to demonstrate equilibrial turnover, and (3) the occurrence of large-scale environmental change leading to changes in number of species between observation times (Lynch and Johnson 1974, McCoy 1982).

Our information on habitat-fragment use by cavity-nesting birds enabled us to circumvent two of these problems immediately. First, we used the presence of active nests (not simply a species' presence in a fragment during the breeding season) to distinguish between breeding and nonbreeding species. Further, we searched for breeders in each fragment during two consecutive breeding seasons, and no visible vegetation changes occurred during this interval. Equilibrial turnover was our topic of investigation. Our data set also enabled us to test for relations between turnover rates and fragment characteristics. MacArthur and Wilson (1967) predicted that absolute turnover on oceanic islands should decrease with increasing island area and increasing isolation from a colonizing source. Do these predictions hold for breeding populations of cavity-nesting birds in habitat fragments? Are other fragment features more closely related to short-term turnover rates for cavity nesters?

No one has answered these questions, yet their implications for avifaunal reserves are far-reaching. Knowledge of fragment characteristics associated with minimal turnover of diverse breeding populations would be valuable for obtaining consistently diverse avifaunal production. A system of small habitat fragments may collectively be an important source of dispersing individuals, even though each individual fragment may be too small to support self-sustained populations of resident species (cf. Whitcomb et al. 1981:187; Haila 1986). Does the equilibrium model apply to breeding populations of cavity-nesting birds in such a system? Fragmented habitats are becoming ubiquitous (Burgess and Sharpe 1981). If the equilibrium model was applicable to such situations, avian conservationists who work with short-duration assemblages (e.g., migrant, breeding, or wintering communities) could use it to develop strategies for managing specific habitats or broad-scale land-use patterns. If the theory is irrelevant, applications of it would be futile and possibly disastrous. Further, if a group of fragments represented all of the available breeding habitat in an area, alteration of these fragments could have a more drastic effect on populations than if the group was just a small part of a larger habitat system. Earlier work demonstrated that predictions of MacArthur and Wilson's model for one avian taxon may not be consistent with those for another (Terborgh 1973), so our data afford still another advantage in that we address our questions for cavity nesters alone.

We found significant, positive relations between numbers (mean and total for 1983 and 1984) of nesting species and fragment area (Gutzwiller and Anderson 1987), supporting the species-area trend predicted by equilibrium theory. But such relations by themselves do not confirm the relevance of MacArthur and Wilson's model (Gilbert 1980:214). Thus, it remained for us to determine whether the equilibrium theory applied to populations of cavity-nesting birds breeding in riparian habitat fragments by examining short-term turnover rates and assessing relations between turnover rates and characteristics of habitat fragments. We accomplished this by testing the following general null hypotheses: (1) equilibrial turnover of cavity-nesting bird species does not occur in habitat fragments, and (2) no significant relations exist between absolute turnover rates of cavity-nesting bird species and habitat-fragment features.

METHODS

We studied cavity-nesting birds breeding in 34 cottonwood-willow (*Populus-Salix*) habitat fragments between Guernsey and Fort Laramie along the North Platte River in southeastern Wyoming during 1983 and 1984. Each cottonwood-willow community was searched for active nests once every 2 weeks (four times each nesting season) at a rate of 15 min/ha; we randomized searches to prevent daily and seasonal biases due to bird activity levels. Doubling our search periods did not affect the number of nests found, so we judged our method to be adequate and time-efficient.

Immigration (I) occurred when a species' nest was not found the first season (1983), but was found the second season (1984); extinction (E) occurred when a species' nest was found the first season, but not the next (Lynch and Johnson 1974:371–372; Williamson 1981:107). We calculated absolute turnover rate (ATR) for each fragment by averaging the number of turnovers (immigrations and extinctions) during the two successive breeding seasons ([I + E]/2) (Simberloff 1976, Williamson 1978, McCoy 1982). Ten species were involved in the community dynamics we studied: American Kestrel (*Falco sparverius*), Northern Flicker (*Colaptes auratus*), Redheaded Woodpecker (*Melanerpes erythrocephalus*), Hairy Woodpecker (*Picoides villosus*), Downy Woodpecker (*P. pubescens*), Tree Swallow (*Tachycineta bicolor*), Black-capped Chickadee (*Parus atricapillus*), House Wren (*Troglodytes aedon*), European Starling (*Sturnus vulgaris*), and Common Grackle (*Quiscalus quiscula*).

We used a paired-*t* test (Zar 1984:150–152) to test for (1) a difference in the average number of species nesting in the system of fragments between 1983 and 1984, and (2) a difference in the average number of immigrations and the average number of extinctions. For each fragment, we computed the CV for number of nesting species during the 2 years. Instead of using an arbitrary CV to judge whether appreciable change occurred, we used frequencies of fragments having various CVs. We used a one-tailed one-sample sign test (Ryan et al. 1976:243–247) to assess whether the average ATR for the system of fragments equalled zero; the equilibrium theory predicts it should exceed zero. To test for relations among ATR, fragment features, and species richness, *t* ratios associated with simple and multiple regressions were computed (Neter and Wasserman 1974, Dixon 1985). Residual plots (Neter and Wasserman 1974:97–112) confirmed that the removal of linear effects of extraneous variables on the variables of interest was valid. That is, there were no linear or nonlinear patterns in the residuals after we controlled for linear effects. When there are many potential explanatory variables relative to sample size in a regression analysis, statistically significant relations can arise by chance and models can be overfit (Neter and Wasserman 1974:388). We minimized the possibility of these problems by requiring models that were parsimonious, statistically sound, and biologically reasonable.

We considered using bivariate path analysis to test hypotheses about relations between ATR and fragment size (AREA), ATR and distance to nearest streamside habitat fragment (DNEARH), mean number of species (MEANSP) and ATR, and total number of species (TOTSP) and ATR. But simple and multiple regression analyses suggested that additional variables influenced each of the variables in these pairs simultaneously and, consequently, that the assumption of causal closure (Nie et al. 1975:385) was probably untenable. A valid multivariate path analysis was unobtainable because unequivocal statements about casual order (Nie et al. 1975:384), or lack thereof, for many pairs of potentially influential variables were impossible to make.

We checked the validity of the regression model relating ATR to five fragment features by calculating an R^2 value for prediction (R^2_{Pred}), which is a measure of the percentage of variation the model would account for if tested with comparable, new observations (Montgomery and Peck 1982:430–433). The optimal model had: the highest R^2 value, the fewest number of variables (with each contributing at least 6% to R^2), a significant ($P = 0.000$) F statistic, all significant ($P < 0.03$) t statistics, variance inflation factors <2 for each explanatory variable, and residual plots and a normal-probability plot consistent with regression assumptions (Neter and Wasserman 1974:97–112; Chatterjee and Price 1977:182–183).

Additional details about the study area, nest searching, habitat measurements, and statistical analyses are in Gutzwiller (1985) and Gutzwiller and Anderson (1987).

RESULTS

NONEQUILIBRIUM TURNOVER

Hypotheses regarding equilibrium turnover were tested using the data in Table 1. For the equilibrium model to apply, the number of nesting species should be constant from year to year and the average number of immigrations should approximately equal the average number of extinctions. For the entire system of fragments, our data support these predictions ($t = -1.11$, df = 33, $P = 0.28$ for comparison of average number of species between years; $t = 1.11$, df = 33, $P = 0.28$ for comparison of average number of immigrations and extinctions). The number of fragments with various CV values for numbers of species during the two breeding seasons were distributed as follows: 0–15% (8), 15–30% (4), 30–45% (1), 45–60% (6), 60–75% (1), 75–90% (2), >90% (5). Seven values were impossible to compute because no species nested in seven of the fragments during the two seasons, although these habitats were evidently acceptable because freshly excavated cavities were obvious in 1982. Even if one were to accept a CV as liberal as 45% as indicative of no appreciable change in number of species, 41.1% of the fragments had more variation; 20.6% of the fragments had CVs that exceeded 75%. These high CVs are inconsistent with the expectation that number of species should change little during the turnover period. Thus, a closer look at changes in number of species on a per fragment basis revealed a nonequilibrium condition in many of the fragments.

The equilibrium model also predicts that ATR should exceed 0.0 for each fragment individually and all fragments collectively. Using this criterion for the two-season period of our study, our results support this hypothesis ($P < 0.001$, sign test) for the system of fragments. But eight of the individual ATRs equalled 0.0; seven of these were associated with fragments where no nests were found during the two seasons. The remaining 26 ATRs ranged from 0.5 to 3.0. Hence, 23.5% of the fragments did not have ATRs >0.0, indicating the equilibrium model does not hold for the system of fragments we studied.

RELATIONS BETWEEN TURNOVER RATES AND FRAGMENT FEATURES

Habitat features used to assess the relation between ATR and fragment characteristics are de-

TABLE 1. Richness and dynamics of 34 cavity-nesting bird communities in southeastern Wyoming during 1983 and 1984.

Habitat fragment no.	No. species 1983	No. species 1984	CV for no. of species (1983 and 1984)	Immigrations (I)	Extinctions (E)	Absolute turnover rate (I + E)/2
1	6	5	0.13	2	3	2.5
2	8	4	0.47	1	5	3.0
3	0	0	—[a]	0	0	0.0
4	0	1	1.41	1	0	0.5
5	5	4	0.16	1	2	1.5
6	3	3	0.0	1	1	1.0
7	1	3	0.71	2	0	1.0
8	1	4	0.85	3	0	1.5
9	5	7	0.24	3	1	2.0
10	0	1	1.41	1	0	0.5
11	2	4	0.47	3	1	2.0
12	0	0	—	0	0	0.0
13	4	4	0.0	1	1	1.0
14	1	2	0.47	1	0	0.5
15	0	1	1.41	1	0	0.5
16	0	0	—	0	0	0.0
17	1	2	0.47	1	0	0.5
18	4	4	0.0	2	2	2.0
19	4	7	0.39	3	0	1.5
20	0	0	—	0	0	0.0
21	3	3	0.0	2	2	2.0
22	0	0	—	0	0	0.0
23	0	0	—	0	0	0.0
24	0	0	—	0	0	0.0
25	2	4	0.47	2	0	1.0
26	0	1	1.41	1	0	0.5
27	2	2	0.0	1	1	1.0
28	6	8	0.20	3	1	2.0
29	1	1	0.0	0	0	0.0
30	6	3	0.47	1	4	2.5
31	4	4	0.0	1	1	1.0
32	4	1	0.85	0	3	1.5
33	5	4	0.16	1	2	1.5
34	0	1	1.41	1	0	0.5

[a] CV impossible to compute because number of nesting species equalled zero both years.

scribed in Table 2. We assumed temporarily that habitat fragments were functionally equivalent to oceanic islands. We thus expected a negative relation between ATR and fragment area (AREA) because of predicted lower turnover rates on larger islands (MacArthur and Wilson 1967), but we observed the reverse ($t = 4.66$, df = 32, $P = 0.000$). To test our hypotheses we also assumed temporarily that distance between a given fragment and the nearest streamside habitat fragment (DNEARH) was analogous to the distance between an oceanic island and its colonizing source. The equilibrium theory predicts a negative relation between absolute turnover and dis-

TABLE 2. Statistics for 26 variables measured during late summer 1983 at 34 habitat fragments in southeastern Wyoming.

Variable	$\bar{x}$	SD	Range
Fragment area, ha	7.17	8.50	0.12–32.27
Distance to nearest streamside habitat fragment, m	121.62	106.59	35–492
Amount of edge/ha, m/ha	794.76	421.00	391.60–2,127.50
Size of nearest streamside habitat fragment, ha	14.19	9.98	0.20–32.27
Mean number of snag-diameter classes represented per 60-m^2 sampling plot	0.26	0.10	0.05–0.49
Mean number of plant strata represented per 60-m^2 sampling plot	2.01	0.69	0.65–3.05
Frequency of snags 10.2–25 cm dbh	0.12	0.08	0.0–0.34
Frequency of snags 26–40 cm dbh	0.09	0.07	0.0–0.27
Frequency of snags 41–55 cm dbh	0.03	0.03	0.0–0.13
Frequency of snags 56–70 cm dbh	0.01	0.01	0.0–0.06
Frequency of snags 71–85 cm dbh	0.01	0.03	0.0–0.19
Frequency of snags >85 cm dbh	0.01	0.02	0.0–0.09
Frequency of healthy plants ≤0.5 m in height	0.59	0.27	0.0–1.0
Frequency of healthy plants >0.5 m and ≤2.5 m in height	0.62	0.26	0.0–1.0
Frequency of healthy plants >2.5 m in height and ≤15.2 cm dbh	0.26	0.20	0.0–0.71
Frequency of healthy plants >2.5 m in height and 15.3–40 cm dbh	0.32	0.18	0.0–0.74
Frequency of healthy plants >2.5 m in height and 41–70 cm dbh	0.16	0.11	0.0–0.44
Frequency of healthy plants >2.5 m in height and >70 cm dbh	0.05	0.06	0.0–0.25
Number of snag-diameter classes represented per fragment	3.18	1.29	1–6
Number of healthy plant strata represented per fragment	5.41	0.66	4–6
Presence or absence of adjacent palustrine wetland[a]	0.29	0.46	0–1
Presence or absence of adjacent riverine wetland[a]	0.56	0.50	0–1
Presence or absence of adjacent mixed rangeland[a]	0.21	0.41	0–1
Presence or absence of adjacent irrigated cropland[a]	0.35	0.49	0–1
Presence or absence of adjacent roads (dirt, paved, or rail)[a]	0.47	0.51	0–1
Number of adjoining land-use types[b]	1.88	1.25	0–5

[a] Indicator variables; presence coded as 1, absence coded as 0. Means can be interpreted as the proportion of the 34 fragments bordered by the associated land-use type.
[b] Some fragments were bordered solely by herbaceous rangeland (i.e., none of the other five land-use types adjoined these fragments); the presence or absence of herbaceous rangeland was not, however, considered a variable because it bordered all fragments to some extent.

tance to a colonizing source (MacArthur and Wilson 1967). The negative relation ($t = -3.51$, $df = 32$, $P = 0.001$) between ATR and DNEARH suggests this prediction of the model holds in our system. On our scale of analysis, the colonizing source presumably involved the large streamside fragments in our system in which all nesting territories had been taken and there was a spillover of breeders into smaller, isolated habitat fragments at the floodplain peripheries. DNEARH was our best measure of the degree of isolation for a fragment, but it had local not regional or continental significance. Multiple regression supported these results. The relation between ATR and AREA, after accounting for DNEARH, was still significantly positive ($t = 3.51$, $df = 31$, $P = 0.001$), and the relation between ATR and DNEARH, with AREA in the model, was still significantly negative ($t = -2.16$, $df = 31$, $P = 0.038$). We found a significant correlation between AREA and DNEARH ($r = -0.432$, $df = 32$, $P = 0.01$).

Multiple linear regression indicated ATR was significantly related to five fragment variables: ATR = 1.529 − 0.001(EPHA) + 0.042(AREA) −14.914(SNAG4) + 19.466(SNAG6) + 0.536-(PALUS). EPHA is amount of edge/ha, SNAG4 and SNAG6 are frequencies of snags in classes 4 (56 to 70 cm dbh) and 6 (>85 cm dbh), respectively, and PALUS indicated the presence or absence of palustrine wetland bordering each fragment. These five variables accounted for 73.7% (R = 85.9%, standard error of the estimate = 0.479) of the variation in ATR ($F_{5,28} = 15.706$, $P = 0.000$), and $R^2_{Pred} = 58.4\%$, indicating the model would account for almost 60% of the variation in ATR if tested with new, comparable data. All of these variables except SNAG4 were the same variables that explained most of the variation in MEANSP and TOTSP (Gutzwiller and Anderson 1987). But in those models the size of the nearest streamside habitat fragment (SIZEH), instead of SNAG4, was negatively related to MEANSP and TOTSP.

TABLE 3. t ratios associated with relations between mean number of cavity-nesting bird species (MEANSP) and habitat-fragment features when absolute turnover rate (ATR) is or is not accounted for.

	t ratios	
Fragment features	ATR unaccounted for	ATR accounted for[a]
EPHA[b]	−4.26[c]	−1.65
AREA	8.92[c]	6.83[c]
SIZEH	−2.69[d]	−1.77
SNAG6	3.56[c]	1.49
PALUS	2.95[c]	1.50

[a] t ratio for ATR = 4.16, df = 27, P = 0.000.
[b] EPHA = amount of edge/ha; AREA = fragment area; SIZEH = size of nearest streamside habitat fragment; SNAG6 = frequency of snags in class 6 (>85 cm dbh); PALUS = presence or absence of palustrine wetland.
[c] P < 0.01; df = 28 (ATR unaccounted for) or 27 (ATR accounted for).
[d] P < 0.05; df = 28.

MEANSP may depend on ATR because the number of immigrations and extinctions would have determined the mean number of species during the two sampling periods. It is therefore not surprising that four out of the five fragment variables in the MEANSP model should turn up again in the ATR model. It is also reasonable to observe decreases in the significance levels of t ratios for relations between MEANSP and EPHA, AREA, SIZEH, SNAG6, and PALUS after ATR is accounted for (Table 3), if ATR affects MEANSP. As expected, this pattern of change was similar for relations involving TOTSP (Table 4). After the effects of MEANSP and TOTSP were taken into consideration, however, the significance of the t ratios for relations between ATR and fragment characteristics also decreased (Tables 5 and 6). ATR and MEANSP and ATR and TOTSP were positively related (t = 10.56, df = 32, P = 0.000; t = 15.38, df = 32, P = 0.000,

TABLE 5. t ratios associated with relations between absolute turnover rate (ATR) and habitat-fragment features when mean number of cavity-nesting bird species (MEANSP) is or is not accounted for.

	t ratios	
Fragment features	MEANSP unaccounted for	MEANSP accounted for[a]
EPHA[b]	−4.90[c]	−2.02
AREA	3.69[c]	−1.12
SNAG4	−2.44[d]	−1.75
SNAG6	3.82[c]	1.69
PALUS	2.90[c]	1.26

[a] t ratio for MEANSP = 4.35, df = 27, P = 0.000.
[b] SNAG4 = frequency of snags in class 4 (56 to 70 cm dbh); other mnemonics are defined under Table 3.
[c] P < 0.01; df = 28.
[d] P < 0.05; df = 28.

respectively). These relations did not change after the effects of 25 habitat variables were controlled for (t = 5.15, df = 7, P = 0.001 [for ATR and MEANSP]; t = 8.90; df = 7, P = 0.000 [for ATR and TOTSP]). The presence of palustrine wetland and the number of land-use types (Table 2) did not have to be individually controlled for (for the ATR-MEANSP and ATR-TOTSP models, respectively) because these variables were linear functions of other variables controlled for; they were automatically removed by the software so covariance matrix inversion could proceed (Dixon 1985:275).

DISCUSSION

NONEQUILIBRIUM TURNOVER

Despite strong species-area relations and considerable agreement between observed and predicted dynamics, the system of fragments we studied does not adhere completely to the ex-

TABLE 4. t ratios associated with relations between total number of different cavity-nesting bird species (TOTSP) and habitat-fragment features when absolute turnover rate (ATR) is or is not accounted for.

	t ratios	
Fragment features	ATR unaccounted for	ATR accounted for[a]
EPHA[b]	−4.64[c]	−1.65
AREA	7.66[c]	6.83[c]
SIZEH	−2.64[d]	−1.77
SNAG6	3.88[c]	1.49
PALUS	3.10[c]	1.50

[a] t ratio for ATR = 8.17, df = 27, P = 0.000.
[b] Mnemonics are defined under Table 3.
[c] P < 0.01; df = 28 (ATR unaccounted for) or 27 (ATR accounted for).
[d] P < 0.05; df = 28.

TABLE 6. t ratios associated with relations between absolute turnover rate (ATR) and habitat-fragment features when total number of cavity-nesting bird species (TOTSP) is or is not accounted for.

	t ratios	
Fragment features	TOTSP unaccounted for	TOTSP accounted for[a]
EPHA[b]	−4.90[c]	−0.90
AREA	3.69[c]	−2.58[d]
SNAG4	−2.44[d]	−1.20
SNAG6	3.82[c]	0.74
PALUS	2.90[c]	0.48

[a] t ratio for TOTSP = 8.01, df = 27, P = 0.000.
[b] Mnemonics are defined under Tables 3 and 5.
[c] P < 0.01; df = 28.
[d] P < 0.05; df = 28 (TOTSP unaccounted for) or 27 (TOTSP accounted for).

TABLE 7. Number of nests found during 1983 and 1984 in various-sized habitat fragments along the North Platte River, Wyoming.

Fragment number	Fragment area (ha)	Number of nests found[a]									
		AMKE[b]	REDW	DOWO	HAWO	NOFL	TRSW	CHIC	HOWR	EUST	COGR
1	15.05	1,0	1,1	0,1	0,0	1,0	2,0	0,1	4,8	13,8	0,0
2	10.05	1,0	1,0	1,1	0,0	2,0	0,0	1,0	1,3	9,9	1,0
3	0.32	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,0
4	0.12	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0
5	13.10	1,1	1,0	1,0	0,0	1,1	0,0	0,0	0,5	13,10	0,0
6	1.34	0,0	0,0	0,0	1,0	1,1	0,0	0,0	0,0	1,2	0,1
7	2.90	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,1	2,4	0,0
8	6.82	0,0	0,0	0,0	0,0	0,1	0,0	0,1	0,1	4,9	0,0
9	13.10	1,0	1,2	0,2	0,1	2,1	0,0	0,1	1,2	11,8	0,0
10	0.84	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0
11	1.99	0,1	0,1	0,0	0,0	1,0	0,0	0,0	0,1	2,2	0,0
12	0.34	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
13	12.81	2,0	0,0	1,2	0,0	0,1	0,0	0,0	1,3	2,3	0,0
14	0.80	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	1,1	0,0
15	0.54	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0
16	0.14	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
17	3.58	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0	3,1	0,0
18	7.83	0,1	0,0	2,1	0,0	1,0	0,0	0,1	2,0	3,1	0,0
19	32.27	3,3	0,1	0,2	0,1	4,2	0,0	0,0	7,4	19,21	0,0
20	0.14	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
21	17.14	0,0	0,0	1,0	0,0	2,0	1,0	0,0	0,2	7,5	0,0
22	0.22	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
23	0.20	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
24	0.20	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
25	6.86	0,1	0,0	0,1	0,0	0,0	0,0	0,0	1,3	7,5	0,0
26	0.52	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0
27	7.66	0,0	0,0	0,0	0,0	1,0	0,0	0,0	0,2	3,3	0,0
28	27.60	1,1	1,1	1,2	0,1	1,0	0,0	0,1	3,3	17,10	0,2
29	0.63	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	1,1	0,0
30	12.77	1,0	0,1	1,2	0,0	2,0	0,0	0,0	1,0	8,9	1,0
31	19.07	0,1	1,3	1,0	0,0	0,0	0,0	0,0	3,1	10,8	0,0
32	3.89	0,0	0,0	1,0	0,0	1,1	0,0	0,0	1,0	1,1	0,0
33	20.29	0,0	2,2	1,1	0,0	1,0	0,0	0,0	4,0	4,8	0,2
34	2.79	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0

[a] For each species, the first and second integers are the numbers of nests found during 1983 and 1984, respectively.
[b] AMKE = American Kestrel, REDW = Red-headed Woodpecker, DOWO = Downy Woodpecker, HAWO = Hairy Woodpecker, NOFL = Northern Flicker, TRSW = Tree Swallow, CHIC = Black-capped Chickadee, HOWR = House Wren, EUST = European Starling, COGR = Common Grackle.

pectations of MacArthur and Wilson's equilibrium model. Predictions for the entire group of fragments were corroborated, but when we examined hypotheses at the level of individual fragments, the equilibrium model was not supported. We attribute the disparity between our results and the predictions to deterministic factors such as habitat-fragment features and interspecific interactions (Gutzwiller and Anderson, unpubl.), neither of which are emphasized by equilibrium island-biogeographic theory. Further, the equilibrium model was proposed primarily for large habitat areas and sizeable, self-sustained populations. The present study, however, involved very small (0 to 21 breeding pairs) and ephemeral populations in rather small habitats (Table 7). In a system with limited species richness and very small populations, slight changes in the number of species or individuals constitute a greater relative change in community structure than similar changes in a system with higher richness and larger populations. Short-duration assemblages with restricted richness and abundances may, therefore, be less likely to experience dynamic equilibrium (sensu MacArthur and Wilson 1967). Another factor important in our system is that some species' minimum-area requirements were not always satisfied by a single fragment; these species probably used other fragments to meet their needs (Gutzwiller and Anderson 1987). This latter form of habitat use is, of course, very unlikely in the oceanic systems MacArthur and

Wilson addressed, and it is therefore not considered in their model. We conclude that the short-term dynamics of breeding populations of cavity-nesting birds in our study area cannot be adequately modeled by the equilibrium theory (cf. Lynch and Johnson 1974:380–381; McCoy 1982:224).

If equilibrium turnover was really occurring, we should have been able to detect it with our analysis. Our two-season test minimized or precluded the confounding factors of (1) vegetation change, (2) compounded, yearly stochastic effects, and (3) underestimated turnover rates, the effects of all of which would have been magnified by an interval exceeding two seasons (Jones and Diamond 1976, Diamond and May 1977). But perhaps a better test would be to examine cavity-nester dynamics for a series of two-season intervals spanning 5 to 10 years. Equilibrium hypotheses could be tested for each two-season period, and a decision could be reached about the applicability of the model for the 5- or 10-year period as a whole (cf. Jones and Diamond 1976). Yet, even this approach entails the difficulty of finding environments that would remain unchanged during the study. Vegetation and weather changes could, of course, be measured and compared to changes in cavity-nester communities to determine whether environmental changes may have had an effect, so this problem is surmountable.

Because our system of communities was quite close to an equilibrial state, it may have been rapidly approaching or recently retreating from equilibrium during the period we studied it (Abbott and Grant 1976). We do not, however, have the long-term turnover data necessary to test whether either of these movements was occurring. With respect to habitat dynamics, little change in the areal coverage or structure of fragments occurred during the 8 years prior to and including this study, based on an examination of 1976 large-scale aerial photographs, conversations with landowners, and stand maturity. If our system has never been in equilibrium, there may be several deterministic and/or stochastic forces responsible. Possible deterministic factors include: the set of fragment features we found significantly related to ATR; area-dependent habitat differences (Gutzwiller and Anderson 1987); interspecific interaction; differential predation; food availability; changing decay states of nesting or feeding substrates; year-to-year nest-site fi-

delity; and the degree of proximity ($\approx$5 to 20 km) and connectedness of our system with others (Abbott and Grant 1976, Ambuel and Temple 1983). Interspecific interaction and differential predation appeared to influence species' abundances only slightly, if at all (Gutzwiller and Anderson, unpubl.). The actual influences of the other forces listed have not, to our knowledge, been adequately quantified for cavity-nesting bird communities; hence, inferences about their effects must await additional data.

Stochastic factors may also be effecting nonequilibrial flux in number of nesting species (Rice et al. 1983). Yearly changes in weather, for example, may influence food availability, and consequently, the abundance of nesting individuals. Weather may act directly on adults or young of the year during migration and on the wintering grounds. For residents, severe winter conditions might limit the number of breeders the following spring. Disease and density-independent forces may also be acting indirectly or along with weather changes. Substantial differences between 1983 and 1984 in the regional breeding populations of a species due to a weather anomaly or other stochastic factor would probably have been manifested as a significant difference in yearly nest abundances across all fragments for that species. But such effects are not strongly evident from our data; only one (Northern Flicker) of the 10 species differed slightly (average difference = 0.38 nests, two-tailed one-sample sign test, P = 0.022, with more nests in 1983) in average number of nests among the fragments between 1983 and 1984, despite an abundance of suitable but unused trees and cavities each year. The equilibrium theory does not rely heavily on deterministic forces to explain the assemblage of insular faunas, yet such forces seem dominant in the periodic communities we studied.

RELATIONS BETWEEN TURNOVER RATES AND FRAGMENT FEATURES

ATR was significantly correlated with EPHA, AREA, SNAG4, SNAG6, and PALUS in a validated multiple regression model. All of these fragment variables are the same (including sign) as those in multiple regression models for MEANSP and TOTSP, except SNAG4 replaced SIZEH. These results, the logical time sequence of turnover events and resulting patterns of mean and total number of species, and the t ratios above all suggest that (1) turnover rates (measured by

ATR) are significantly related to fragment features, and (2) turnover events in turn determine MEANSP and TOTSP. The relations described between MEANSP, TOTSP and the five fragment characteristics still make sense in the way we described them initially (Gutzwiller and Anderson 1987), but from our present analysis, turnover events appear to be the actual link between these overall measures of richness and fragment attributes. This connection is consistent with MacArthur and Wilson's (1967) idea that the number of species on an "island" should result from the opposing forces of immigration (nesting) and extinction (no longer nesting), although equilibrial turnover is not supported by our work.

An equally plausible interpretation of our results is that species richness determined ATR. Specifically, MEANSP and TOTSP may have influenced I and E (hence ATR) via diffuse competition or commensalism involving nest trees or cavities. But habitat features were the primary factors influencing fragment occupancy; after controlling (statistically) for the effects of habitat features on species' abundance, the evidence for competition and commensalism was weak. Our assessment of the strength of these latter forces is supported by the paucity of observed interspecific interactions (Gutzwiller and Anderson 1986) and statistical power analyses indicating strong interactions would have been easily detected (Gutzwiller and Anderson, unpubl.). Nevertheless, considering all of our analyses, reciprocal effects between ATR and species richness seem possible.

An alternative hypothesis about relations among habitat features, turnover events, and species richness is that species richness is simply the result of independent species-specific habitat responses and that turnover events are inconsequential. Our earlier analyses demonstrated significant relations between fragment features and abundances of individual species (Gutzwiller and Anderson 1987). But this alternative ignores the actual time sequence of turnover events and consequent species-richness patterns, and it fails to account for the yearly changes in richness (ATR) that occurred while habitat features were essentially constant.

Still another hypothesis is that species-rich communities may experience higher turnover than species-poor communities solely because there are more species involved and hence greater chance for change (cf. MacArthur and Wilson

1967:22). One would thus expect the positive relation between MEANSP or TOTSP and ATR that we found, but no habitat influences on ATR should be evident. Nor should there be a change in the relations between habitat features and MEANSP or TOTSP after one accounts for ATR (or vice versa). The chronology of events is valuable for inferring possible causal order here. Species richness at any point in time appears to be the product of preceeding turnover events, even if species richness in turn influences turnover; a chance hypothesis does not account for this sequence or the statistical support for it presented above.

In our system of fragments, habitat variables that had the potential to influence whether a species nested should have been significantly related to ATR. The negative relation between ATR and EPHA indicates that small, narrow, or irregularly shaped fragments have little chance of consistently attracting cavity-nesting birds. Such fragments had no or very few nesting species (European Starling, House Wren) each year, leading to little potential for change. Larger areas had more territories and more diverse resources, thus there was a greater potential in larger areas for more species to immigrate or go extinct (cf. Rice et al. 1983:1454). Hence the positive (not negative, as predicted by the equilibrium model) relation between ATR and AREA. AREA, DNEARH, and ATR were all correlated. Why then did AREA, not DNEARH, appear in the five-variable multiple regression model? Essentially because AREA was more closely related to ATR than DNEARH. DNEARH could not add significantly to the model once AREA was in because of the significant correlation between AREA and DNEARH. Apparently, AREA not only accounted for the positive area effects on ATR, but also the negative effects of DNEARH on ATR, via the negative DNEARH-AREA correlation. Thus, AREA was the best, single variable to account for the positive ATR-AREA relation and the negative ATR-DNEARH relation.

Only a small proportion (9.9%) of the nests in snags were in class-4 snags (56 to 70 cm dbh). The negative relation between ATR and SNAG4 suggests that higher frequencies of this seldom-used class would decrease the number of potential immigrants, and ultimately, the number of species that could go extinct. We found a positive relation between ATR and SNAG6; class-6 snags (>85 cm dbh) were used by several uncommon species simultaneously (Gutzwiller and Anderson

1986). With increasing frequencies of class-6 snags, the chance that several infrequent nesters would nest would be higher. Therefore, the potential for immigration (hence turnover) was greater. PALUS was positively correlated with ATR and the frequency of class-2 snags (26 to 40 cm dbh), which were used by most (eight of 10) of the species. Fragments bordered by palustrine wetland had somewhat higher frequencies of class-2 snags ($r = 0.377$, df = 32, $P < 0.05$) (Gutzwiller and Anderson 1987), and hence greater potential for both immigration and extinction.

Can the relations between ATR and fragment features be more parsimoniously explained? Perhaps a model in which species settle in fragments solely as a consequence of habitat size (i.e., a sampling effect) or the potential of fragments to accommodate species' minimum-area requirements for breeding is sufficient. Our results indicate this alternative is inadequate; fragment characteristics describing degree of isolation, shape, amount of edge, and the availability of nest trees appear influential, even after fragment area is accounted for (cf. Boecklen 1986). Certainly, AREA is important in determining the number and size of territories that may be established (Gutzwiller and Anderson 1987), and there may even be a chance sampling effect involved. The results indicate, however, that other fragment features are important as well. The relative strengths of association between EPHA, AREA, SNAG6, PALUS, SNAG4, and ATR are reflected in the absolute values of the standardized regression coefficients (0.599, 0.412, 0.408, 0.288, 0.245, respectively). The turnover of secondary cavity nesters was undoubtedly due, in part, to the availability of cavities; some were excavated by woodpeckers while many others originated from damage by wind, lightning, and/or disease (Gutzwiller and Anderson 1987). Our analyses (Gutzwiller and Anderson 1986, 1987, unpubl.) and the presence of SNAG4, SNAG6, and PALUS in the ATR model are in accord with this idea; but EPHA and AREA appear important too, presumably because of minimum-area requirements (Gutzwiller and Anderson 1987).

RELEVANCE OF EQUILIBRIUM THEORY

Application of the equilibrium theory to maximize species richness and abundance in our system would be inappropriate and perhaps self-defeating. For instance, from the theory one might recommend minimizing turnover by maximizing DNEARH. But this approach would reduce species richness and abundance within fragments because of the negative relation between AREA and DNEARH and positive species-area relations. A more effective strategy would be to capitalize on pertinent deterministic factors that are manipulatable. Based on species-area relations and area-dependent habitat conditions, for example, fragment size should be maximized to accommodate a variety of species' minimum-area requirements and to support higher abundances of each species (see Gutzwiller and Anderson [1987] for detailed analyses and data). Such fragments could also be maintained in close proximity so that species with very large territory requirements could satisfy them by using more than one fragment. The equilibrium theory indicates turnover should be minimal in larger areas, but our results indicate this prediction is not relevant to breeding cavity-nester communities in the size range of habitat fragments we studied. Minimizing fragment area in our system would minimize turnover, but it would also minimize species richness and abundance.

ACKNOWLEDGMENTS

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