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CONDITION VARIES WITH HABITAT CHOICE IN POSTBREEDING FOREST BIRDS

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Abstract.—Many birds that are experiencing population declines require extensive tracts of mature forest habitat for breeding. Recent work suggests that at least some may shift their habitat use to early-successional areas after nesting but before migration. I used constant-effort mist netting in regenerating clearcuts (4–8 years postcut) and dense mature-forest understories to assess (1) whether most bird species of mature forests show habitat shifts after breeding; and (2), on the basis of several measures of condition, whether birds using early-successional habitats garnered any benefits or penalties, compared with those that remained in forests. I captured 3,845 individual birds of 46 species at four pairs of sites in mature Allegheny hardwood forests in northwestern Pennsylvania during the postbreeding periods of 2005–2008. Most, but not all, forest birds were captured at higher rates in cuts than in forests, and that pattern persisted through the postbreeding season. Using an information-theoretic approach, I found strong support for a species–habitat interactive effect on both molt progression and body condition as measured by residuals from species-specific regression of mass on wing chord. Some, but not all, forest birds appeared to be in better condition when captured in cuts than when in forests. I found no support for a habitat effect on presence of fat or ectoparasites. My results reveal that habitat choice in the postbreeding season is correlated with physiological condition for a subset of forest birds, which suggests that the maintenance of such early-successional habitats in mature forest may benefit these species. *Received 15 November 2012, accepted 2 May 2103.*

Key words: body condition, clearcut, early-successional forest, habitat choice, mature-forest birds, postbreeding period.

La condition corporelle varie avec le choix de l'habitat chez les oiseaux forestiers en période de post-reproduction

Résumé.—Plusieurs oiseaux qui subissent des déclins de leurs populations nécessitent de vastes étendues d'habitat de forêt mature pour se reproduire. Des travaux récents suggèrent que certains d'entre eux peuvent changer leur utilisation de l'habitat pour des zones en début de succession entre le moment où ils ont terminé de nicher et la migration. J'ai utilisé la méthode du filet japonais avec effort constant dans des coupes totales en régénération (4–8 ans après la coupe) et des sous-bois de forêt mature afin d'évaluer : (1) si la plupart des espèces d'oiseaux des forêts matures changent d'habitat après la reproduction; et (2) sur la base de plusieurs mesures de la condition, si les oiseaux qui utilisent les habitats en début de succession étaient avantagés ou pénalisés par rapport à ceux qui restaient dans les forêts. J'ai capturé 3 845 oiseaux de 46 espèces à quatre paires de sites dans les peuplements de feuillus matures de la forêt d'Allegheny du nord-ouest de la Pennsylvanie au cours des périodes de post-reproduction de 2005–2008. La majorité des oiseaux forestiers, mais pas tous, ont été capturés à des taux plus élevés dans les coupes totales que dans les forêts et ce patron a persisté tout au long de la saison de post-reproduction. En utilisant une approche basée sur la théorie de l'information, j'ai trouvé des éléments soutenant la théorie d'un effet interactif des espèces-habitat sur la progression de la mue et la condition corporelle, tel que mesuré par les résidus de la régression de la masse sur la longueur de l'aile non aplatie de chaque espèce. Certains oiseaux forestiers, mais pas tous, semblaient être en meilleure condition lorsqu'ils étaient capturés dans les coupes totales plutôt que dans les forêts. Je n'ai trouvé aucun résultat appuyant la théorie de l'effet de l'habitat sur la présence de graisses ou d'ectoparasites. Mes résultats révèlent que le choix de l'habitat en saison de post-reproduction est corrélé avec la condition physiologique pour un sous-ensemble d'oiseaux forestiers, ce qui suggère que le maintien d'habitats en début de succession dans les forêts matures peut être favorable à ces espèces.

Widespread declines in the populations of many songbirds have spawned research to understand and mitigate the factors causing those declines (Askins et al. 1990, Martin and Finch 1995, Greenberg and Marra 2005). Many species that are experiencing declines require extensive tracts of mature forest habitat for breeding. Most research on this group has focused on understanding their habitat requirements during the nesting season; indeed, the designation of birds as mature-forest species has been

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based entirely on nesting ecology. Most forest birds typically complete breeding by midsummer. Migratory species remain on the breeding grounds until late summer or early autumn, thus spending 6–10 weeks in a postbreeding period. During this period, birds abandon territorial defense behaviors, cease singing regularly, and wander extensively, making study difficult. For these reasons, this portion of the annual cycle has been virtually ignored until recently, yet it may be a critical time for both adult birds and their newly fledged young (Anders et al. 1997, Nislow and King 2006).

It has become increasingly clear that events in this period can have significant effects on the demography of songbird populations (Faaborg et al. 2010). After young become independent, most species undergo a partial (juveniles) or complete (adults) molt, a very energy-demanding process (Murphy 1996, Pyle 1997, Pagen et al. 2000). Young develop essential survival skills by gaining experience in foraging and predator avoidance. Mortality of recently independent young can be exceptionally high during this stage of the life cycle because of predation or starvation (Anders et al. 1997, Streby and Andersen 2011) and may represent a major constraint on population growth (Sillett and Holmes 2002, King et al. 2006). Both adults and young of migratory species begin to accumulate fat deposits to store energy for migration. Thus, habitat choice may be especially critical during this period, while at the same time habitat options may be broader than during the breeding season because most species no longer defend territories.

Recent work suggests that at least some birds that are considered mature-forest specialists often frequent early-successional habitats in the postbreeding season. Rappole and Ballard (1987) first reported postbreeding movements of both adult and young forest birds into early-successional habitats and argued that active molt and low fat reserves indicated that such movements did not constitute migration. Several mist-netting studies found that certain mature-forest species comprised a sizable portion of captures in regenerating clearcuts during the postbreeding season (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006, McDermott and Wood 2010, Streby et al. 2011b, Chandler et al. 2012, Major and Desrochers 2012). Juveniles of several mature-forest specialists were among the most abundant birds captured in each study. In addition, radiotagging of fledgling Ovenbirds (*Seiurus aurocapilla*), Wood Thrushes (*Hylocichla mustelina*), and adult Scarlet Tanagers (*Piranga olivacea*) revealed that individuals of these species tend to move from forest interiors into edge and early-successional habitats (Dellinger 2007; Anders et al. 1998; Vega Rivera et al. 1998, 2003; King et al. 2006). These two lines of evidence suggest that, for numerous forest birds, habitats used after breeding can differ substantially from those used for breeding.

Several researchers of postbreeding forest birds have suggested that maintaining some amount of early-successional habitat within forested landscapes might be beneficial to mature-forest species (Anders et al. 1998, Pagen et al. 2000, Vitz and Rodewald 2006, Chandler et al. 2012). However, two critical questions need to be answered before any conclusions should be drawn concerning the value of early-successional habitats for mature-forest birds. First, do most mature-forest birds use early-successional habitats disproportionately? Radiotracking of fledged young suggests this is true for young birds of several species (Anders et al. 1998, Vega Rivera et al. 1998, King et al. 2006). Rather than being indicative of beneficial habitat, however, the high rate of use of clearcuts by juvenile birds may reflect a choice of poorer-quality habitat because they are naive or were excluded from better-quality habitat by older, more dominant birds. It is unclear, however, how such exclusion might occur without active territorial behaviors.

Netting studies have documented the presence of adults as well as young of forest species in regenerating clearcuts, but presence does not necessarily indicate active use of that habitat. Although it is unlikely, adults may simply be moving through cuts to move from one area of mature forest to another (Remsen and Good 1996, Vitz and Rodewald 2006, Major and Desrochers 2012). Almost all netting studies that have reported high numbers of forest species in cuts sampled birds only within those early-successional habitats (e.g., Marshall et al. 2003, Vitz and Rodewald 2006, McDermott and Wood 2010, Streby et al. 2011b). Therefore, it is unclear whether the incidence of forest-interior birds in early-successional habitats is (1) actually lower than the concurrent incidence in forest interiors, which would suggest a degree of avoidance of early-successional forest; (2) equivalent to the rate in forest, which would suggest no significant habitat selection (i.e., passive dispersal; Marshall et al. 2003); or (3) greater than the incidence in forest, which would argue strongly for habitat preference. To date, only three studies have sampled birds in both early- and late-successional forest habitats; all have shown that at least a subset of forest birds occur at significantly higher densities in cuts, gaps, and other early-successional habitats than in surrounding mature forest in the postbreeding season (Pagen et al. 2000, Bowen et al. 2007, Chandler et al. 2012).

The second and perhaps more important question that remains to be answered is whether the use of early-successional habitats by individuals of mature-forest species actually confers any fitness benefits compared with others that use alternative habitats such as mature forest interiors (Marshall et al. 2003). To date, the only studies to address this issue, by King et al. (2006) and Vitz and Rodewald (2011), showed that postfledging Ovenbirds and Worm-eating Warblers (*Helmitheros vermivorum*) are selective in their habitat use, and their survival is highest in preferred, dense habitats. Whether this benefit extends to other mature-forest species or adults has yet to be demonstrated. Only if mature-forest species use early-successional habitats disproportionately, and can be shown to accrue benefits related to fitness by using those habitats, can the argument be made that early-successional stands are a valuable and necessary habitat component for mature-forest birds.

I used constant-effort mist netting to simultaneously sample bird communities in regenerating clearcuts and in nearby mature forests with dense understories during the postbreeding period. I compared several estimates of condition (molt progression, a condition index, and presence–absence of ectoparasites and subcutaneous fat), to determine whether birds captured in cuts and forest interiors differ in apparent condition. On the basis of previous studies, I predicted that both adults and young of at least some mature-forest species would occur disproportionately in early-successional forest habitats. I also predicted that such disproportionate habitat use would be reflected in the condition of individuals being better in early-successional habitats.

Methods

Study sites.—I conducted the study at four replicate sites, each comprising two plots, on the Allegheny National Forest and private industrial timberland inholdings in northwestern

Pennsylvania (41°40′N, 78°05′W) from 2005 to 2008. All sites were located on relatively flat plateau tops at elevations of 515–635 m within the Allegheny Plateau physiographic province. Sites were established ≥20 km apart to ensure independence. Each site consisted of a regenerating clearcut with scattered residual trees (hereafter "cut") and an adjacent block of mature, closed-canopy forest with relatively dense understory (hereafter "forest"). Cuts ranged in size from 6 to 46 ha, retained 10–15% of original basal area, averaged 1.5–2.5 m in height (excluding residual trees), and were 3–6 years postharvest at the initiation of the study. Forests supported mature (90–110 years old) second-growth Allegheny hardwoods dominated by Black Cherry (*Prunus serotina*), Red Maple (*Acer rubrum*), Sugar Maple (*A. saccharum*), American Beech (*Fagus grandifolia*), Eastern Hemlock (*Tsuga canadensis*), Sweet Birch (*Betula lenta*), and Yellow Birch (*B. alleghaniensis*). Canopy heights averaged 28.0 m, and basal area averaged 37.2 m^2 ha^{-1}. Forest understories contained Striped Maple (*A. pensylvanicum*), beech root suckers, seedlings and saplings of overstory trees, ferns, and grasses. Regenerating cuts supported seedlings and saplings of the forest trees, plus Pin Cherry (*P. pensylvanica*), Bigtooth Aspen (*Populus grandidentata*), Quaking Aspen (*P. tremuloides*), blackberries (*Rubus* spp.), elderberries (*Sambucus* spp.), Devil's Walkingstick (*Aralia spinosa*), and graminoids and forbs. Landscapes within 10 km of all sites were heavily forested (>90%) and managed primarily for timber production, and <8% of forested lands in the region were <20 years old (U.S. Department of Agriculture 2007).

Avian sampling.—I used constant-effort mist netting (Bibby et al. 2002, Dunn and Ralph 2004) to sample bird communities in forests and cuts. Netting was the most appropriate sampling method because most birds do not vocalize during the postbreeding season, and their visibility and, consequently, detectability was lower in regenerating cuts than in forest. Within each habitat, I placed four 12 m × 2.6 m, 30-mm-mesh mist nets, 50–100 m apart and >25 m from habitat edges. Net lanes were placed in natural or anthropogenic openings in vegetation as systematically as possible within each site so that they encompassed comparable areas, and their locations were kept constant through the study. Capture rates by mist netting can vary considerably because of weather, time of season and day, and location (Karr 1981, Jenni et al. 1996), making comparisons among sites difficult. In the present study, simultaneous netting at paired adjacent habitats controlled for much of this spatial and temporal variability. Netting began the first week in July of each year, based on local breeding phenologies of forest birds (S. H. Stoleson unpubl. data), and continued into early September. At each site, nets were opened 15 min before local dawn and kept open 5–6 h. No netting occurred on rainy days or in high winds. Nets were checked at least every 30 min, and more frequently when conditions were warm or rain threatened. I netted at each site 3 times per season for 5 consecutive days and rotated among sites, for an average of 15 netting days $site^{-1}$ $year^{-1}$.

I banded all new captures (except Ruby-throated Hummingbirds [*Archilochus colubris*]) with a standard federal band. For each bird, I recorded wing chord (unflattened, to nearest 0.5 mm), tail length to nearest millimeter, molt status, and mass to nearest 0.1 g using an electronic balance. Age and sex determinations were based on Pyle (1997). Fat deposits were estimated using a 0–3 scale, following the Powdermill Avian Research Center protocol because of its very high repeatability among observers and the fact that the present study used multiple trained observers (Mulvihill et al. 2004; cf. Krementz and Pendleton 1990). Each bird captured was systematically searched for parasites by blowing gently on body feathers and examining holding bags to reveal hippoboscid flies (Diptera: Hippoboscidae), and by examining flight feathers for feather mites (Acari: Astigmata) (Clayton and Walther 1997). For analyses, I considered parasites to be either present or absent. Each bird was assigned three individual molt scores for remiges, rectrices, and body, ranging from zero for all old, worn feathers to 5 for all fully grown new feathers, following Newton (1966). However, to avoid problems in comparing scores among taxa that had different numbers of feathers per tract, I used a single score per tract to represent the average progression of molt for that tract. Scores for the three tracts were added to produce a composite molt score potentially ranging from zero to 15.

I used physiological characters to classify birds as active breeders, postbreeding, or migrants, following Vitz and Rodewald (2006). Specifically, individuals were classified as active breeders if they exhibited full cloacal protuberance or a vascularized brood patch; and as postbreeding if they were (1) hatch-year birds or (2) after-hatch-year birds with wrinkled or refeathering brood patch, flight feather molt, or extensive body molt (>25% of body; Pyle 1997). Individuals classified as migrants (1) were those species that do not breed locally or (2) showed complete or nearly complete molt.

Vegetation sampling.—In August and September of 2008, I sampled vegetation around each mist net used. At each net, I established two 5.0-m-radius circular plots, 8 m from either net end and perpendicular to the direction of the net in a randomly chosen direction. Within each plot, I measured tree canopy cover using a spherical densiometer and visually estimated percent cover of shrubs (all woody vegetation <2 m in height), *Rubus* canes, and herbaceous cover (grasses, forbs, and ferns). I used the mean of the two plots per net as the value for that net. Although vegetation heights increased somewhat through the course of the study, I did not include vegetation height in analyses, and no significant changes in species composition would be expected over a 4-year period (Keller et al. 2003); therefore, I assumed that 1 year of sampling was adequate to describe gross patterns of vegetation.

Data analyses.—For some analyses, I classified birds into three nesting-habitat guilds: (1) mature-forest specialists ("forest-interior" species), (2) forest-edge birds, and (3) early-successional specialists. I based classifications primarily on previous published work on postbreeding habitat use in order to facilitate comparisons with those studies (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006, Bowen et al. 2007, Streby et al. 2011b, Chandler et al. 2012). Because guild assignments often were inconsistent among those studies, I classified ambiguous species on the basis of local habitats and habits (guilds and scientific names in Table 1). When birds were captured multiple times within a season, I used only the first capture of each individual in analyses to avoid confounding abundance with activity levels within a site. Netting results were standardized as the number of new captures per 100 net-hours.

I used standard mist nets that extended 2.6 m above the ground. This height covered most of the vertical structure of the habitat in regenerating clearcuts, but only the lowest stratum of forest interiors. Forest birds that forage above the understory are poorly sampled by ground-based mist nets, biasing any comparisons of capture rates between habitat types (Karr 1981, Remsen

TABLE 1. Birds with >10 total mist-net captures[a] determined to be in postbreeding condition in forest interiors or regenerating clearcuts (cuts), in northern Pennsylvania, 2005–2008, arranged by nesting habitat guild and foraging strata. Mist nets were 2.6 m high, because the study was focused on understory and ground-foraging species.

			Cut		Forest		
Species	Nesting guild[b]	Foraging stratum[c]	AHY[d]	HY	AHY	HY	Total
Alder Flycatcher (*Empidonax alnorum*)	ES	U	11	4	0	0	15
Gray Catbird (*Dumetella carolinensis*)	ES	U	38	67	1	0	106
Yellow Warbler (*Setophaga petechia*)	ES	U	5	6	0	0	11
Chestnut-sided Warbler (*S. pensylvanica*)	ES	U	126	78	1	0	205
Mourning Warbler (*Geothlypis philadelphia*)	ES	U	4	17	0	2	23
Common Yellowthroat (*G. trichas*)	ES	U	61	128	2	5	196
Eastern Towhee (*Pipilo erythrophthalmus*)	ES	G	7	32	1	1	41
Field Sparrow (*Spizella pusilla*)	ES	G	31	24	0	0	55
Song Sparrow (*Melospiza melodia*)	ES	G	69	95	0	2	166
Indigo Bunting (*Passerina cyanea*)	ES	U	51	26	0	0	77
Least Flycatcher (*Empidonax minimus*)	FE	C	3	24	0	0	27
Eastern Phoebe (*Sayornis phoebe*)	FE	U	1	9	1	0	11
Black-capped Chickadee (*Poecile atricapillus*)	FE	M	78	61	3	5	147
Cedar Waxwing (*Bombycilla cedrorum*)	FE	M	22	22	1	0	45
Chipping Sparrow (*Spizella passerina*)	FE	G	15	8	1	0	24
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	FE	M	9	9	0	0	18
Baltimore Oriole (*Icterus galbula*)	FE	C	12	3	0	0	15
Purple Finch (*Carpodacus purpureus*)	FE	M	16	7	0	0	23
Blue-headed Vireo (*Vireo solitarius*)	MF	M	18	8	4	0	30
Red-eyed Vireo (*V. olivaceus*)	MF	M	46	19	0	5	70
Veery (*Catharus fuscescens*)	MF	G	8	7	3	3	21
Swainson's Thrush (*C. ustulatus*)	MF	G	11	1	11	2	25
Hermit Thrush (*C. guttatus*)	MF	G	9	23	3	27	62
Wood Thrush (*Hylocichla mustelina*)	MF	G	5	10	4	0	19
Ovenbird (*Seiurus aurocapilla*)	MF	G	38	20	19	16	93
Hooded Warbler (*Setophaga citrina*)	MF	U	14	11	9	5	39
American Redstart (*S. ruticilla*)	MF	M	53	15	1	0	69
Magnolia Warbler (*S. magnolia*)	MF	M	67	30	5	1	103
Black-throated Blue Warbler (*S. caerulescens*)	MF	U	11	44	6	4	65
Black-throated Green Warbler (*S. virens*)	MF	M	24	15	2	0	41
Canada Warbler (*Cardellina canadensis*)	MF	U	5	6	0	0	11
Scarlet Tanager (*Piranga olivacea*)	MF	C	16	15	0	1	32
Dark-eyed Junco (*Junco hyemalis*)	MF	G	17	41	7	19	84

[a] Species captured infrequently (<10 total) in cuts, forests included Yellow-bellied Sapsucker (*Sphyrapicus varius*; 2, 0), Downy Woodpecker (*Picoides pubescens*; 4, 4), Hairy Woodpecker (*Picoides villosus*; 2, 4), Northern Flicker (*Colaptes auratus*; 7, 0), Blue Jay (*Cyanocitta cristata*; 5, 0), Tufted Titmouse (*Baeolophus bicolor*; 2, 0), White-breasted Nuthatch (*Sitta carolinensis*; 2, 2), Brown Creeper (*Certhia americana*; 1, 1), House Wren (*Troglodytes aedon*; 2, 0), Golden-crowned Kinglet (*Regulus satrapa*; 1, 0), Blue-winged Warbler (*Vermivora cyanoptera*; 2, 0), Blackburnian Warbler (*Setophaga fusca*; 2, 0), and American Goldfinch (*Spinus tristis*; 8, 0).

[b] Nesting guilds: ES = early-successional, FE = forest-edge, and MF = mature-forest specialist.

[c] Foraging stratum: G = ground, U = understory, C = canopy, and M = multiple strata.

[d] Age classes: AHY = after-hatch-year (adults) and HY = hatch-year (young of the year).

and Good 1996, Rappole et al. 1998, Mallory et al. 2004). However, because ground-based mist nets adequately sample forest species that typically limit their foraging to the ground or understory layer (Remsen and Good 1996), and McDermott and Wood (2010) demonstrated that capture rates of understory species did not vary with residual canopy density in Appalachian forests, I assumed that comparisons of capture rates between habitats for these specific guilds are legitimate. I report capture rates in both habitat types of all species for informational purposes, acknowledging that rates for forest captures of canopy birds and multiple-stratum birds likely will be biased and do not necessarily represent relative abundances.

Condition index.—From field measurements, I calculated a residual index (RI) for each of the 10 forest species with sufficient captures (≥5) in each habitat type to allow analysis (Schulte-Hostedde et al. 2005; Table 1). The RI was derived from the residuals from an ordinary least-squares (OLS) regression of mass against wing chord for each of the 10 species.

I analyzed condition metrics using an information-theoretic approach (Burnham and Anderson 2002). I used this approach because the study was strictly observational, and my aim in assessing condition was to assess the weight of evidence for how habitat and other potential explanatory variables influenced the physiological condition of birds sampled, rather than test an unrealistic null hypothesis of zero difference between habitats (Burnham and Anderson 2002). Because there was no reason *a priori* to assume that capture probabilities varied with condition, I included birds of all foraging guilds in analyses of condition.

I used logistic regression (PROC LOGISTIC in SAS, version 9.2; SAS Institute, Cary, North Carolina) to determine the factors that influenced the likelihood of parasitism and fat deposition. I considered both variables as dichotomous yes–no variables because (1) quantifying ectoparasite load was difficult, in part because hippoboscid flies tended to fly off of hosts when birds were removed from nets; and (2) very few birds classified as postbreeding had fat scores >1. I constructed a set of *a priori* models to predict parasitism and fat as a function of species, ordinal date, year, age class (hatch-year vs. after-hatch-year), habitat (cut vs. forest), and the interaction of species and habitat.

I developed generalized linear mixed models using PROC GLIMMIX (Bolker et al. 2009) to model the effects of species, age class (hatch-year vs. after-hatch-year), sex, habitat (forest vs. cut), ordinal date, and year on molt scores and the RI. Condition indices have been criticized for failing to account for differences in body size associated with age and sex independently of condition (Peig and Green 2010); I addressed these issues by including these covariates in models. Models considered year and date as random effects, and species, habitat, sex, and age class as fixed effects. I modeled molt scores using a gamma distribution and log link function, and RI using a Gaussian distribution with an identity link. GLIMMIX models used the restricted maximum-likelihood (REML) method and the Kenward-Roger procedure to adjust denominator degrees of freedom.

For each condition metric, I evaluated support for candidate models by comparing Akaike's information criterion (AIC) values. Because the number of observations ($n \geq 681$) was >100 times the number of estimated parameters in all global models ($K = 6$, including intercept), I did not use the correction for small sample size (AIC_c). Factors likely to have occurred in the present study, such as territoriality, spatial autocorrelation, family groups, or mixed-species flocks, can create a lack of independence among individuals, thereby causing overdispersion of data (Burnham and Anderson 2002). However, because the variance inflation factors, $\hat{c}$, estimated from the global models' goodness-of-fit tests (Hosmer and Lemeshow 2000) were consistently >0.49 and <1.16, correction for data overdispersion was unnecessary.

For each condition variable, I ranked models by their ΔAIC values and considered all models within 2 AIC units of the "best" model as competing models potentially having substantial explanatory power, based on my data. Because a model that differs from the "best" model by a single parameter can result in a ΔAIC <2 without substantially improving the deviance explained, in such cases I considered the added parameter uninformative (Anderson and Burnham 2002, Arnold 2010). I assessed model uncertainty using Akaike weights (w_i; Burnham and Anderson 2002) and determined the relative support for specific explanatory variables by summing Akaike weights (w_S) across all candidate models containing that variable (Burnham and Anderson 2002). For those variables for which coefficients could be calculated, I used model averaging of all competing models to generate coefficients and unconditional confidence intervals (Burnham and Anderson 2002).

I used PROC GLM to compare average vegetation cover variables (canopy, shrub, *Rubus*, and herbaceous) between habitat types, and chi-square contingency tests (PROC FREQ) to compare captures overall, by age class, by species, and by nesting guild.

RESULTS

Vegetation structure and composition.—Vegetation in the two habitat types differed primarily in the amount of canopy cover and composition of the woody understory. Not surprisingly, canopy cover in forests was significantly greater than that provided by residual trees in cuts ($P < 0.001$), but percent cover of shrubs did not differ ($P = 0.47$; Fig. 1). Composition of that shrub layer did, however: *Rubus* canes and cherry (*Prunus* spp.) seedlings dominated most cuts, whereas forest understories were dominated by American Beech and Red Maple seedlings and generally lacked *Rubus*. Percent cover of grass and forbs did not differ between forests and cuts, separately or combined as herbaceous cover (all $P > 0.13$; Fig. 1).

Avian captures.—I sampled birds for a total of 10,616 net-hours over 217 days in 4 years (2005–2008). A total of 3,845 individuals were netted and banded, for an average capture rate of 36.2 birds per 100 net-hours. Of these new captures, 2,021 individuals representing 46 species were clearly in the postbreeding stage, based on physiological criteria. Of these, 672 individuals (33%) were mature-forest specialists, 444 (22%) forest-edge species, and the remaining 905 (45%) were early-successional specialists (Table 1). All 46 species were captured in cuts, but only 29 species were captured within forest. Five of 10 bird species captured most frequently in cuts were early-successional species (Chestnut-sided Warbler, Common Yellowthroat, Song Sparrow, Gray Catbird, and Indigo Bunting). Forest birds made up the other half: Black-capped Chickadee, Magnolia Warbler, American Redstart, Red-eyed Vireo, and Ovenbird. By contrast, 7 of the 10 birds captured most frequently in forests were mature-forest specialists; only one was an early-successional species (Common Yellowthroat). Half of the early-successional species were never captured in forest nets, yet all forest species captured were captured in cuts. Several

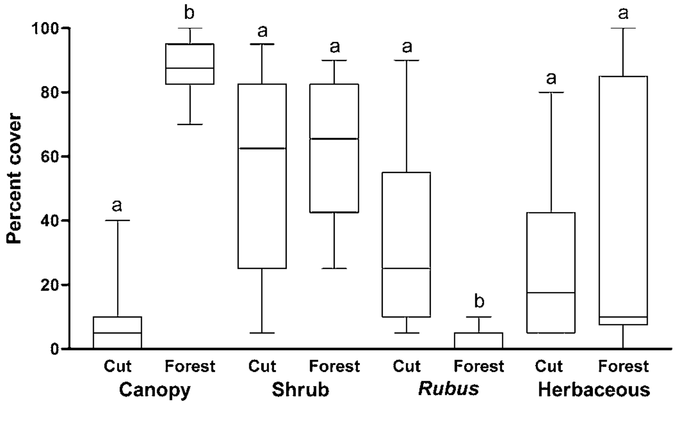

FIG. 1. Percent vegetation cover on regenerating clearcut and mature forest sites, northwestern Pennsylvania, 2008. Overstory cover and *Rubus* cover differed significantly, whereas total shrub cover (including *Rubus*) and herbaceous cover did not. Pairs of columns topped by different letters differed significantly at $P < 0.05$; boxes indicate upper and lower quartiles, bars maximum and minimum values, and midlines the medians.

forest species were never captured within the forest in postbreeding condition; these were primarily canopy-foraging species (see Table 1). Almost all the bird species that breed regularly in surrounding mature Allegheny hardwood forests were captured in cuts, the primary exceptions being Pileated Woodpecker (*Dryocopus pileatus*), Eastern Wood-Pewee (*Contopus virens*), American Robin (*Turdus migratorius*), and raptors.

Overall, many more birds were captured in clearcuts (*n* = 1,826) than in the forest interior (*n* = 195) in the postbreeding period. Forest birds made up 51.3% of all captures in clearcuts, with similar numbers of forest-edge (420) and mature-forest species (516) captured. Capture rates for all three nesting-habitat guilds were higher in cuts than in forests (Fig. 2). Considering only those species of the ground- and understory-foraging guilds, significantly higher numbers of forest birds were captured in the cuts than in forests overall ($\chi^2 = 71.4$, df = 2, $P < 0.001$; Fig. 3). However, patterns differed among species. Capture rates of two ground-foraging thrushes, Hermit and Swainson's, did not differ significantly between habitat types (both $\chi^2 \geq 0.76$, df = 2, $P > 0.14$; Fig. 3). Understory-foraging Hooded Warblers were captured more frequently in cuts, but not significantly so. Capture rates for all other ground- and understory-foraging species were significantly higher in cuts than in forests (all $P < 0.05$; Table 1). This pattern of higher capture rates in cuts than in forests remained consistent throughout the postbreeding season for all three nesting guilds (Fig. 4).

Age classes.—Hatch-year birds comprised 45% of all captures, and that proportion did not differ between cuts and forests (all species combined; Fig. 2). Hatch-year birds comprised a significantly higher proportion of cut captures for mature-forest specialists (55.3%) than for either forest-edge (47.7%) or early-successional (45.8%) species ($\chi^2 = 6.16$, df = 3, $P = 0.04$). For those species with sufficient captures in both habitats for analysis, the proportion of young birds differed considerably. For example, a significantly higher proportion of hatch-year Hermit Thrushes were captured in forests than in cuts, whereas Black-throated Blue Warblers had higher proportions of young in cuts than in forests (both $P < 0.03$). Other species showed no differences in age ratios between habitats (e.g., Swainson's Thrush and Dark-eyed Junco).

Recaptures.—Only 58 of the 1,116 (5.1%) forest birds captured and banded were subsequently recaptured within the same year. Of these, the majority remained in the same habitat in which they were initially captured: 74% of individuals originally captured in cuts (*n* = 42) were later captured in cuts, and 75% of those captured in forests (*n* = 16) were recaptured in forests. Of the 15 individuals that switched habitats between captures, most were either Black-capped Chickadees (*n* = 8) or Hermit Thrushes (*n* = 3). The median time between within-year captures was 22 days (range: 2–84 days).

Fat.—Of the 2,021 birds captured in postbreeding condition, 282 (14.0%) carried non-zero fat loads. Overall, a significantly higher percentage of birds captured in cuts had non-zero fat loads (14.4%) than those captured in forests (9.7%; $\chi^2 = 7.2$, df = 1, $P = 0.007$); the presence of fat did not differ significantly with age class (14.4% vs. 13.5%; $\chi^2 < 0.01$, df = 1, $P = 0.98$). The global logistic regression model fit the data adequately ($\chi^2 = 4.99$, df = 8, $P = 0.76$). The best model indicated that species, date, and year influenced the likelihood of a bird having fat in the postbreeding season (Table 2). The likelihood of having non-zero fat increased through the season (odds ratio = 1.02, 95% confidence interval [CI]: 1.02 to 1.04). A model that included habitat was within 2 ΔAIC units, although the model without habitat was 2.72× more likely to be the best model, based on the evidence ratio. The sum of Akaike weights for habitat across all candidate models was only 0.34, which is modest evidence for an association between habitat and fat. Similarly, although the odds ratio suggested that birds captured in cuts were 1.69× more likely to carry non-zero fat loads, the 95% CI spanned 1.0 (0.83–3.17), indicating no support for a habitat effect given my data. I found almost no support for an age

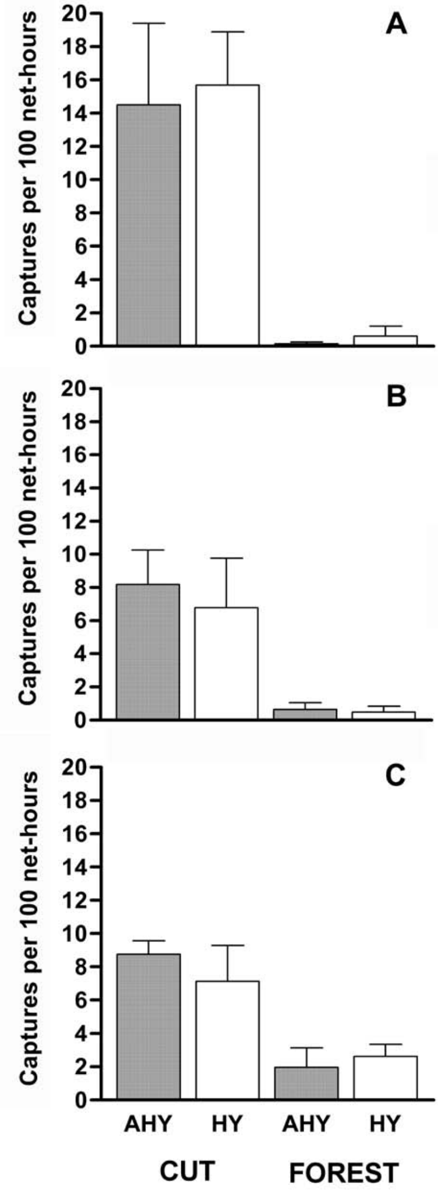

Fig. 2. Mean capture rates of (A) early-successional, (B) forest-edge, and (C) mature-forest nesting birds in the postbreeding period (July to mid-September, 2005–2008) in northwestern Pennsylvania. All three guilds were captured at significantly higher rates in cuts than in mature forest for both after-hatch-year (AHY) and hatch-year (HY) birds. Error bars represent sample SDs.

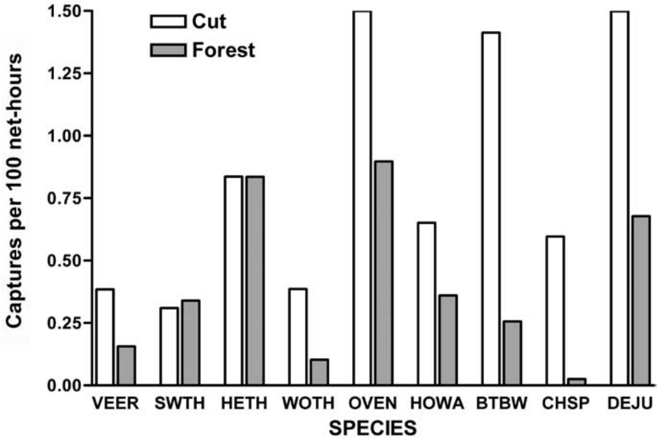

FIG. 3. Mean capture rates of the nine most common forest birds of the ground and understory foraging guilds in cuts (hollow bars) and forests (solid bars) were significantly ($P < 0.05$) greater in cuts for all but Hermit Thush (HETH), Swainson's Thrush (SWTH), and Hooded Warbler (HOWA). VEER = Veery, WOTH = Wood Thrush, OVEN = Ovenbird, BTBW = Black-throated Blue Warbler, CHSP = Chipping Sparrow, and DEJU = Dark-eyed Junco. Data are from northwestern Pennsylvania, 2005–2008.

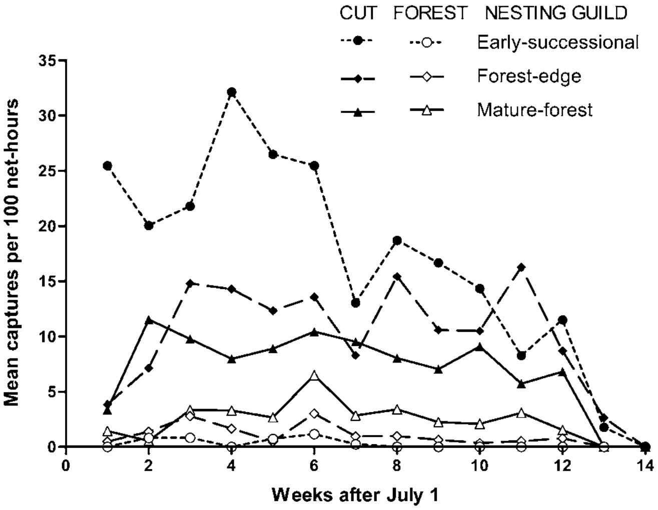

FIG. 4. Mean weekly mist-net capture rates in cuts (solid symbols, top three lines) remained consistently higher than capture rates in forests (hollow symbols, bottom three lines) throughout the postbreeding season for all three avian habitat guilds. Date from four pairs of sites in northwestern Pennsylvania, 2005–2008.

effect on fat ($w_S = 0.03$). By contrast, species, date, and year all had summed model weights (w_S) >0.99.

Ectoparasites.—Ectoparasites were encountered on 210 individuals (10.4% of all captures). Hippoboscid flies were the most frequently detected parasite; feather mites and ticks occurred on far fewer birds. The incidence of parasites varied among species and nesting-habitat guilds and between habitats. For example, only a single Black-capped Chickadee of the 147 captured had parasites, compared to 25% of 84 Dark-eyed Juncos. Generally, parasites were more often found on young birds than on adults (15.4% compared to 9.1%); on early-successional species than on either forest guild (15%, vs. 9.1% for forest-edge birds and 9.9% for mature-forest birds); and on birds captured in forest nets than on those captured in cuts (13.8% vs. 10.0%).

Generally, logistic regression models of parasite loads on forest birds confirmed these trends. The global model fit the data adequately ($\chi^2 = 3.92$, df = 8, $P = 0.86$). The model that received the most support given the data included age, species, year, and date as significant factors influencing parasite presence (Table 2). The only other model within 2 ΔAIC units of the best-supported model included habitat. Models based on the full data set had difficulty converging on a solution, in part because of excessive zeros for many bird species. I reran analyses using just the nine species of forest bird in which >10% of individuals had ectoparasites (n = 681). The best-supported model from this data set included age, date, and year. A second model that included habitat was the only competing model within 2 ΔAIC units, had an Akaike weight of 0.30, and was 2.4% less likely on the basis of evidence ratios (Table 2). Model averaging these two candidate models indicated that the likelihood of parasitism generally was lower for after-hatch-year birds ($\beta_{age} = -0.52$, 95% CI: −0.76 to −0.28) and decreased with ordinal date ($\beta_{date} = -0.02$, 95% CI: −0.03 to −0.01), but did not vary significantly with either year ($\beta_{year} = -9.03$, 95% CI: −223.5 to 205.4) or capture habitat ($\beta_{habitat} = -0.02$, 95% CI: −0.08 to 0.12).

Molt scores.—Most individuals captured in postbreeding condition were undergoing molt. Composite molt scores ranged from 0 to 15 (mean = 6.3, 95% CI: 6.07 to 6.52). Generally, birds captured in cuts tended to be slightly more advanced in their molt than those captured in forests, although variance was high (cut: mean = 6.34, 95% CI: 6.02 to 6.67; forest: mean = 5.92, 95% CI: 5.13 to 6.70). The best-supported model indicated that molt progression in postbreeding forest birds was associated with age,

TABLE 2. Top and competing logistic regression models explaining likelihood of fat deposition and likelihood of ectoparasitism in forest birds during the postbreeding seasons of 2005–2008 in northern Pennsylvania. Age was classified as hatch-year versus after-hatch-year, date as ordinal date, and capture habitat as forest versus cut. Species are listed in Table 1. k = number of estimable parameters, and w_i = Akaike weight.

Variable	Model	K	Log-likelihood	AIC	ΔAIC	w_i
Fat	Species + year + date	38	697.916	773.916	0.000	0.66
	Habitat + species + year + date	39	697.915	775.915	1.999	0.25
Ectoparasitism	Age + date + year	6	353.353	365.353	0.000	0.59
	Age + date + year + habitat	7	353.094	367.094	1.741	0.25

Table 3. Top general linear mixed models of factors affecting measures of physiological condition in forest birds during the postbreeding seasons of 2005–2008 in northern Pennsylvania; no other models qualified as competing models (within 2 ΔAIC units). Residual index (RI) was calculated as the residuals from species-specific regressions of mass on wing chord for the subset of the 10 forest species with ≥5 captures in each habitat type [a]; molt score used all forest bird species. Age was classified as hatch-year versus after-hatch-year, and capture habitat as forest versus cut. Scientific names and sample sizes are listed in Table 1.

Variable	centre	k	Log-likelihood	AIC	ΔAIC	w_i
Molt score	Age + sex + habitat × species + date + year	6	6,351.25	6,363.25	0.00	0.99
Condition residuals (RI)	Age + date + habitat * species	3	1,998.13	2,004.13	0.00	0.91

[a] Species were Red-eyed Vireo, Black-capped Chickadee, Veery, Swainson's Thrush, Hermit Thrush, Ovenbird, Hooded Warbler, Magnolia Warbler, Black-throated Blue Warbler, and Dark-eyed Junco.

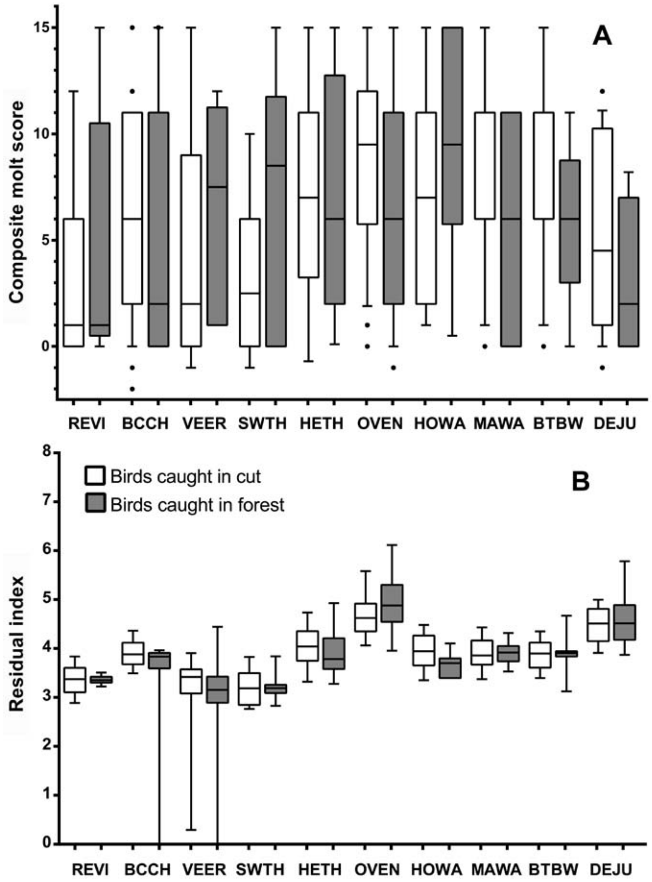

FIG. 5. (A) Composite molt score and (B) condition residual index both differed significantly between birds captured in forests and those captured in cuts during the postbreeding seasons of 2005–2008, for the 10 most frequently captured species of forest birds in northwestern Pennsylvania, based on generalized linear mixed models. Midlines = medians, boxes = second and third quartiles, whiskers = 10% and 90%, and dots = 5% and 95% (present only when sample sizes allow for calculation); white boxes = cuts, gray boxes = forests. BCCH = Black-capped Chickadee, BTBW = Black-throated Blue Warbler, DEJU = Dark-eyed Junco, HETH = Hermit Thrush, HOWA = Hooded Warbler, MAWA = Magnolia Warbler, OVEN = Ovenbird, REVI = Red-eyed Vireo, SWTH = Swainson's Thrush, and VEER = Veery.

sex, date, year, and the interaction of habitat and species (Table 3). The next best-supported model lacked sex as a variable, differed by >18 ΔAIC units, and was >1,700 times less likely on the basis of evidence ratios. The interaction of species and habitat was strongly supported as influencing molt score, having a w_S value >0.999. Molt tended to be more advanced in birds in cuts than in those in forests (Fig. 5A), in hatch-year birds than in adults (β_{age} = –1.63, 95% CI: –2.28 to –0.98), and in females than in males (β_{sex} = –1.23, 95% CI: –2.20 to –0.26), and increased through the season (β_{date} = 0.03, 95% CI: 0.02 to 0.04).

Residual index.—The RI was calculated for just the subset of 10 species with sufficient captures from both habitats to calculate an OLS regression model. Values for RI ranged from –9.3 to 5.5, and no difference was found between habitat types (cut: mean = –0.007, 95% CI: –0.073 to 0.058; forest: mean = 0.035, 95% CI: –0.18 to 0.25). The model incorporating age, date, and the habitat * species interaction received the most support; the next closest model was 5.5 ΔAIC units greater, and >16.9 times less likely than the best model on the basis of evidence ratios (Table 3). The RI increased slightly with date (β_{date} = 0.0094, 95% CI: 0.0057 to 0.0131) and was higher for hatch-year birds than for after-hatch-year birds (β_{age} = 0.34, 95% CI: 0.18 to 0.51). Habitat-based differences in RI varied with species (Fig. 5B). Most species showed no significant difference, some (e.g., Ovenbird) averaged better condition in forests, and others (e.g., Red-eyed Vireo) had a significantly higher RI in regenerating cuts.

Discussion

Most forest bird species in my study occurred disproportionately in early-successional habitats in the postbreeding season, which corroborates results from previous studies (Pagen et al. 2000, Chandler et al. 2012). Capture rates for understory- and ground-foraging birds were significantly higher in cuts for almost all species, consistent with the predictions for habitat preference. Although I had few recaptures, a majority of those remained in their original habitat (≤84 days), which suggests consistency in habitat use by individuals. This pattern was true for both forest-edge species and mature-forest specialists and was sustained through the entire postbreeding season (Fig. 4). Two species, Hermit and Swainson's thrushes, showed no apparent preference for postbreeding habitat, consistent with the pattern of utilizing any dense habitat. Recapture data showed that the Hermit Thrush was one of two species that regularly changed habitats within a season, again suggesting no preference between the two habitats sampled. Recapture data suggest that Black-capped Chickadees also may have had no preference between habitat types.

The preferential use of early-successional habitats by mature-forest birds in the postbreeding period in my study appears to be a widespread phenomenon, having been reported from southern bottomland hardwoods (e.g., Bowen et al. 2007), oak–hickory forests (Vitz and Rodewald 2006), northern hardwoods (Chandler et al. 2012, present study), and boreal forests (Major and Desrochers 2012). Some individual species appear to show regional differences, however. For example, Ovenbirds showed clear preferences for early-successional habitats in Missouri and Pennsylvania but preferred mature forests in New Hampshire (Pagen et al. 2000, Chandler et al. 2012, present study). Such differences may be related to regional differences in food resources available or in habitat structure, and this merits further research.

Although age ratios varied considerably among species, adults comprised a substantial portion of birds captured in cuts for most species. Consequently, it seems highly unlikely that avian use of early-successional habitats can be attributed to naiveté of young birds or to the exclusion of young birds from forests by adults.

Condition consequences.—My data provide strong evidence for a habitat * species interaction on the extent of molt progression and condition residuals in postbreeding forest birds. Generally, forest birds captured in cuts were more advanced in molt and in better condition (as indicated by RI) than those captured in forests when controlling for species. These patterns would be consistent with birds spending the initial part of the postbreeding period in forests, then moving into cuts as molt progresses and their condition improves over time; this scenario is unlikely, however, given that my analyses controlled for date, and recapture data suggested that very little movement occurred from forests to cuts. The consequences of reduced condition in the postbreeding period can include delayed molt, later migration, and the potential for carry-over effects into wintering grounds (Stutchbury et al. 2011).

Although my data reveal a correlation between condition and postbreeding habitat in forest birds, they cannot discriminate between habitat choice as the cause or a consequence of condition. If habitat choice influences condition, one might expect all birds (at least of some species) to select early-successional habitat in the postbreeding season to maximize their condition, but they clearly do not. Why some individuals might opt for the forest-interior habitat if it results in poorer condition is unclear. Because large clearcuts are not a natural disturbance of northern hardwood forests (Lorimer and White 2003), they may not provide the cues birds have evolved with to recognize high-quality habitat (i.e., they may function as perceptual traps; Gilroy and Sutherland 2007, Patten and Kelly 2010). If the prevalence of these perceptual errors varies among individuals in a population, then some individuals might avoid cuts while others frequent them, as observed in the present study.

Conversely, condition might influence habitat choice; those birds in good condition may preferentially select early-successional habitats, while those in poor condition select late-successional or, perhaps, make no selection at all. Pruitt et al. (2011) demonstrated experimentally that spiders in poor condition were less choosy about web-placement habitat than spiders in good condition. A similar mechanism may function in forest birds. Another possibility is that individuals in poor condition may opt for the risk-prone strategy of remaining in relatively open mature forest rather than the presumed safety of dense early-successional thickets, if food were more available in forests (Lima and Dill 1990, Moore and Aborn 2000). However, most evidence suggests that food availability is equivalent or greater in early-successional habitats (Keller et al. 2003, Vitz and Rodewald 2007). Alternatively, there may be value for males of some forest species in remaining on or near their territory to defend it from prospecting individuals (J. Rappole pers. comm.). Further research is needed to clarify this issue.

There has been much debate about why many forest birds shift to early-successional habitats after breeding, with some identifying predation as the primary factor (e.g., Vitz and Rodewald 2007, McDermott and Wood 2010, Chandler et al. 2012) whereas others suggest food abundance (e.g., Streby et al. 2011a). My observations that most birds captured in clearcuts were in better condition support the food abundance hypothesis. Many early-successional plants produce large crops of fruit in late summer (e.g., Major and Desrochers 2012). In the present study, cuts supported high densities of fruit-producing *Rubus* as well as Pin Cherry and *Aralia*, which were almost absent from forests. In addition, despite the low stature of these habitats, the amount of leaf volume (and, hence, foraging substrate for insectivores) can be similar to that of mature forests (Keller et al. 2003), creating a highly concentrated supply of phytophagous invertebrates available to foraging birds.

Mature-forest birds may choose structurally complex early-successional habitats in the postbreeding season to reduce the risk of predation. Molting adults and recently independent young that are inexperienced with predators may be especially vulnerable and, hence, seek out dense habitats not available in mature forests (Chandler et al. 2012). Similarly, Cimprich et al. (2005) reported that migrant passerines sought denser habitats when there were increased numbers of predators. King et al. (2006) demonstrated that recently fledged Ovenbirds experienced higher survival in denser habitats. In the present study, shrub density did not differ between forests and cuts, at least as measured by percent cover (Fig. 1). Cuts had higher proportions of spiny *Rubus* and *Aralia* that may provide better protection from predators than spineless tree seedlings; otherwise my data provide little support for the idea that habitat choice is based on predator avoidance.

I found little support for a habitat * species effect on the presence of ectoparasites and fat deposition. Ectoparasite load can affect a bird's condition, feather quality and dimensions, breeding behavior, movements, and survival (Loye and Zuk 1991, Senar et al. 1994, Brown et al. 1995, Harper 1999). My analysis of parasite effects was based solely on presence–absence rather than any quantification of actual parasite loads. Avian condition declines with increasing parasite load (Harper 1999), which suggests that the condition of individuals with low loads may not be detectably different from those with no parasites but substantially different from those with high loads.

Similarly, I found little support for a habitat effect on fat deposition, again on the basis of dichotomous presence–absence data. Any real signal from the data may have been lost because of the categorical rather than the numerical response variable. Birds begin to accrue fat for migration only late in the postbreeding season (as suggested by the significant date effect in the best model), in part because major fat deposition may be too energetically demanding while they are undergoing molt (Murphy 1996). Pooling captures from throughout the postbreeding period for analysis almost certainly included many birds that were not yet physiologically capable of substantial fat deposition because they were undergoing molt, potentially biasing the results. Further, because I classified postbreeding birds on the basis of active molt, I probably excluded those birds that had completed their molt but had not yet begun to migrate (i.e., the very individuals most likely to have non-zero fat loads). This lack of a significant habitat effect on fat contrasts with the significant effect on condition residuals, which were based on size-specific mass. Therefore, differences in condition likely represent differences in mass of protein, carbohydrate, or both.

Conservation implications.—My results and those of previous studies on postbreeding habitat use indicate that many mature-forest birds use two different habitat types on their summering grounds, one for breeding and another for postbreeding. This dichotomy creates an "interesting conservation dilemma" (Vitz and Rodewald 2006), in that clearcutting may reduce the area or quality of mature-forest breeding habitat, yet may provide critical habitat and resources for adult and young birds after breeding. Some have suggested that within extensively forested landscapes, the presence of regenerating clearcuts may increase the suitability of habitat for some forest interior birds; declines in such species may be due in part to the increasing maturity and homogenization of forests (e.g., Ahlering and Faaborg 2006). Indeed, the area of eastern deciduous forest in an early-successional seral stage has declined to its lowest levels since the U.S. Forest Service's Forest Inventory and Analysis program began in the 1950s (Trani et al. 2001, Brooks 2003). In this region, most forests now support homogeneous, mature second growth with impoverished understories (Brawn et al. 2001, Rooney et al. 2004, Schulte et al. 2007). Declines in early-successional habitats have resulted from shifts away from clearcutting to uneven-aged forest management or forest preservation, anthropogenic alterations of disturbance regimes (e.g., fire prevention and flood control), and declines in farmland abandonment (Lorimer and White 2003, Nowacki and Abrams 2008).

Although regenerating clearcuts constitute a novel habitat type not present before settlement, they currently provide the primary form of early-successional habitat in extensively forested areas of eastern North America (Trani et al. 2001). My results and those of prior studies provide strong evidence that these anthropogenically created early-successional habitats are used heavily by many forest birds after breeding. Birds may use these relatively novel habitats readily because they probably differ little in plant species composition and structure from early-successional habitats created by natural disturbances such as windstorms, ice storms, and fire. In addition, the alternative postbreeding habitat of dense forest understory (e.g., Vitz and Rodewald 2010) has become sparse in many areas, primarily because of overbrowsing by deer (McShea and Rappole 1997, Rooney et al. 2004, Holt et al. 2011).

The fact that many forest birds shift their habitat use to early-successional habitats in the postbreeding period and apparently benefit from that use now seems well established, but numerous questions remain. We need to determine whether spatial variation in condition, as observed in the present study, actually manifests as differences in fitness (Johnson 2007) or carries over into migration. Further research is needed to understand the relative value to postbreeding birds of regenerating clearcuts, forested wetlands, riparian areas, and dense understories within mature forest. How far individuals will travel to reach a particular habitat patch and how long they remain there are unknown. Answers to these latter questions would help to inform land managers as to how much early-successional habitat should be created or retained in a forested landscape, and how arranged, to ensure that sufficient postbreeding habitat remains available for mature-forest birds.

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