BAT HABITAT USE IN WHITE MOUNTAIN NATIONAL FOREST

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Abstract: In 1992 and 1993, we surveyed the foraging and feeding activity of bat species with broadband bat detectors at 2 foliage heights in 4 age classes of northern hardwood and spruce/fir forest stands in White Mountain National Forest, New Hampshire and Maine. The association of bat activity with trails and water bodies and the effect of elevation were measured. Mist nets, a harp trap, and ultrasonic detectors were used to establish species presence. Bat activity was concentrated at trail and water body edges and was uniform within a forest stand at the same sampling height. Within the forest, bat activity was highest in overmature (>119 yr, 35% of mean bat activity/night) hardwood stands and in regenerating (0–9 yr) stands of both forest types (26% of mean bat activity/night). The majority of bats trapped (56%) were adult male little brown bat (*Myotis lucifugus*). Our data indicate that a matrix of forest types and age classes including areas of regeneration (clearcuts and group cuts) and overmature hardwood, in combination with trails and water bodies, help fulfill the summer habitat requirements of bats in White Mountain National Forest.

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Determination of habitat associations of species, or groups of species, is fundamental to the maintenance of biodiversity and provides baseline data vital to management and conservation. Knowledge of the habitat requirements of bats in forested areas is rudimentary or nonexistent. Historically, 9 species of bat have been identified in New England (Godin 1977). Of these, the Indiana bat (*Myotis sodalis*) is presumed extirpated and 5 species are considered uncommon to rare, including small-footed bat (*M. leibii*), eastern pipistrelle (*Pipistrellus subflavus*), silver-haired bat (*Lasionycteris noctivagans*), red bat (*Lasiurus borealis*), and hoary bat (*L. cinereus*). The northern long-eared bat (*Myotis septentrionalis*), little brown bat, and big brown bat (*Eptesicus fuscus*) are thought to be common.

To provide a comprehensive view of habitat requirements throughout the life cycle of a species, it is important to consider its use of habitat at the landscape level, among forest stands within a landscape, and within stands (DeGraaf et al. 1992). Huff et al. (1993) examined the associations between bat activity and landscape characteristics and forest stands. They found that the age class of stands was the best indicator of bat activity; landscape features were poor predictors. Stand level surveys of bat communities conducted in Douglas-fir (*Pseudotsuga menziesii*) forests of the Oregon Coast Range (Thomas 1988), the Southwestern Cascade Range (Erickson 1993), and Wallowa Whitman National Forest (J. M. Perkins and J. M. Peterson, unpubl. data) indicated that bat activity was not distributed evenly among structural forest types. Forest structure can be manipulated with timber management techniques that subsequently affect habitat and species diversity. In U.S. national forests, a goal of ecosystem management is to balance timber production with habitat preservation and the protection of threatened and endangered species.

The purpose of this study was to identify bat species in White Mountain National Forest and to determine the species' patterns of habitat use. The distribution of bat flight and feeding activity was surveyed in relation to forest stand type and age, and compared to activity recorded at habitat features (water bodies and trails). Temporal and spatial differences in bat activity within forest stands were noted. Before this study, bat habitat associations had not been identified in forests of the northeastern United States.

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STUDY AREA

The White Mountain National Forest (WMNF), located in north central New Hampshire and southwestern Maine, encompassed 304,050 ha, of which 139,300 ha (46%) were available for habitat manipulation through timber management. Nearly 97% of the WMNF was forested, representative of the surrounding New England states that averaged >80% forest land (DeGraaf et al. 1992). New England forests were dominated by northern hardwood tree species, including maple (*Acer* spp.), beech (*Fagus* spp.), yellow birch (*Betula alleghaniensis*), and red spruce (*Picea rubens*) (Hornbeck and Leak 1992). In this region, the U.S. Forest Service divided forest stands into 4 age categories: regeneration (0–9 yr), sapling/pole (10–59 yr hardwood, 10–39 yr softwood), mature (60–119 yr hardwood, 40–89 yr softwood), and overmature (>119 yr hardwood, >89 yr softwood). Sites representative of these 4 age classes of both hardwood and softwood forest types were described. Softwood stands were predominantly of the spruce/fir forest type (*Picea rubens* and *Abies balsamea*) and hardwood stands were comprised of northern hardwood tree species (*Acer* spp., *Fagus* spp., *Betula alleghaniensis*, and *P. rubens*). In combination, these forest types represented vegetation that covered over 60% of WMNF (U.S. For. Serv. 1986).

METHODS

Species Presence

We determined the presence of bat species using live capture and ultrasonic detection. We captured bats on 20 nights, from 2100 through 0430 hours, using 2 vertically stacked, 12- × 2.4-m mist nets placed perpendicularly across streams or forest trails. On 4 nights during swarming, a period during late summer and early fall when bats make nocturnal flights through hibernacula (Fenton 1969), we placed a 1.5- × 1.2-m Tuttle trap (Tuttle 1974) at a mine entrance located on the northern border of WMNF. No other open mines are present in WMNF. Captured bats were identified to species, sex, and age class (ad/juv). We noted the reproductive condition of females by abdominal palpation and inspection of mammary glands. We remotely identified bat species using a tunable narrow band bat detector (Batbox III, Stag Electronics, Cornwall, England). Frequencies used for species identification were based on previously published call signatures (e.g., Fenton and Bell 1979, 1981; Fenton et al. 1983, MacDonald et al. 1994) and our own recordings. We used a broadband ultrasonic detector (AnaBat, Titley Electronics, Australia) to record echolocation calls from captured and released bats marked with a chemiluminescent tag (Buchler 1976).

Habitat Use

Bat activities in softwood regeneration were surveyed in group cuts. On WMNF, softwood regeneration is encouraged by group cutting, an uneven-aged management system that creates a number of proximate cuts, 0.1—0.8 ha in area, surrounded by mature forest (U.S. For. Serv. 1986). We surveyed bat activity associated with hardwood regeneration in clearcuts (max., 12.1 ha, $\bar{x}$ = 7.3 ha) (U.S. For. Serv. 1986). Clearcutting refers to the harvest of almost all trees in an area of at least 1 ha (Hunter 1990).

A subsample of mature sites of each forest type was used to investigate the effect of elevation on bat activity. In each forest type 2 elevation categories were established, each separated by at least 304 m (1,000 ft). These categories were based on the elevational distribution of tree species in WMNF (Leak and Graber 1974). Low mature hardwood stands (H-3L) were located <259 m in elevation, high mature hardwood stands (H-3H) >564 m in elevation, low mature softwood (S-3L) <533 m in elevation, and high mature softwood (S-3H) >838 m in elevation. Sites were selected from Forest Service inventory maps and confirmed by field inspection. A maximum of 4 sites was surveyed on a single night, each of a different forest type and age class. Sites were located randomly, subject to logistic limitations of deploying all detectors in 1 evening. Sites were selected to include a habitat feature, identified as a trail, moving water, or still water. If no habitat feature was available (7 of 78 sites), contiguous forest was sampled.

We used 12 broadband AnaBat detectors to survey the relative abundance of commuting and feeding bats associated with selected forest types and age classes. Voice-activated microcassette recorders (Panasonic RN-112) were used to store this information on magnetic tape, allowing multiple systems to be operated simultaneously. Each detector was placed in weatherproof housing. Surveys were conducted on nights that we determined to have low wind speeds and little precipitation, conditions that ensured a minimum of background noise on tape.

The detection volume of the AnaBat units was estimated before the survey using an ultrasonic pet flea collar (KLT Investments, Miami, Fla.), with an output frequency of 40 kHz and unknown amplitude. Based on these estimates, the detectors deployed at each site were spaced ≥50 m apart to ensure independent sampling. The vertical detection distance of units was estimated to be 15 m, indicating that detectors placed 1.5 m aboveground would sample bats flying below and within the canopy of most forest stands. The detection distance of all AnaBat units was standardized by placing the flea collar 15 m from the microphone, maintaining a constant volume, and adjusting the sensitivity of each unit until the flea collar pulse was no longer audible.

We surveyed each site from approximately half an hour before sunset until half an hour after sunrise; recording systems remained active throughout the night. We activated detectors at each site concurrently (±10 min), allowing direct comparison of bat activity within a stand and at the habitat feature independent of temporal variations in weather and insect abundance.

We listened to tapes to count number of bat passes, defined as a sequence of ≥2 echolocation calls (Thomas 1988) recorded as a bat flies through the air space sampled by the AnaBat detector. Feeding buzzes, indicated by the high pulse-repetition rates associated with attacks on prey (Griffin et al. 1960), also were recorded. Data are presented as measurements of activity, calculated as the number of passes/detector/night or number of feeding buzzes/detector/night.

On each sampling site a transect was established that extended perpendicularly from the habitat feature into the forest. Detector stations were positioned at the habitat feature and at ≥50-m intervals along the transect. Stands of each forest type and age class were selected at 8 different locations that ranged in elevation from 130 to 1,129 m. The effect of elevation on bat activity in mature stands of each forest type was investigated on ≥6 sites.

In regenerating hardwood clearcuts 1 detector was placed at a habitat feature, 1 at the interface of cut and mature stands, and the rest within the clearcut itself. On sites of regenerating softwood (group cuts) we located 1 detector at the habitat feature, 1 at the edge of the first group cut, and the rest centrally within other cuts. We maintained all detectors at ≥50-m spacing.

In 1992, we surveyed bats on 18 sites representing 3 age classes (regeneration, mature, and overmature) of both forest types. Using the AnaBat system, we placed 6 detectors about 1.5 m from the ground along a 250-m transect. In 1993, 60 new transects were established to sample all 4 age classes of both forest type and each elevation category. Based on results from 1992, transect length was reduced to 100 m; 2 detectors were placed within the forest and 1 where the transect originated. Each transect was surveyed 3 times in 1992 and twice in 1993.

We used an AnaBat detector to make recordings at a single location (44°05′N, 71°21′W, 198 m in elevation) on 54 of 84 survey nights. Data from this permanent detector was used as a composite indicator of temporal differences in activity due to changes in weather, insect abundance, etc., and to allow among stand comparisons of bat activity independent of these factors.

To survey the vertical distribution of bat activity within forest stands, a detector was placed in the upper canopy at 4 transects of each forest type and age class during the 1993 field season. These canopy-level surveys supplemented the general survey that used detectors positioned 1.5 m above ground. The canopy-level detectors were located in small natural openings (<0.05 ha) created by the presence of a snag. Using a bow and arrow to fire line over an upper tree branch, we hoisted detectors to an average height of 11.1 m (SD 6.1 m).

Temporal variations of within stand activity were assessed by attaching a digital watch to each AnaBat microphone. Watches had an ultrasonic component to their hourly chime, allowing us to time-mark tapes and compare hourly levels of bat activity.

The General Linear Model (GLM module of SYSTAT for Windows Version 5, Wilkinson et

Table 1. Age and sex of bat species captured using a mist net and harp trap over 24 nights in WMNF, 1992–93.

	M		F	
Species	Ad	Juv	Ad	Juv
Little brown bat	47	5	7	4
Northern long-eared	1	5	2	2
Small-footed bat	0	0	1	0
Indiana bat	1	0	0	0
Big brown bat	5	1	2	0
Hoary bat	0	0	1	0

al. 1992) was used for ANOVA, tests of mean separation (Tukey's test), and simple linear correlations. Counts of bat echolocation passes and feeding buzzes were square root transformed before analysis to correct for non-homogeneous variance (Zar 1984). Back-transformed least squares means are reported and used to plot all figures. We used ANOVA to test for differences in bat activity among forest type, age class, foliage height, and position along transects.

RESULTS

Species Presence

We captured 84 bats representing 3 genera and 6 species in WMNF (Table 1). The eastern pipistrelle, silver-haired, and red bat were identified in the town of Bartlett (location (44°05′N, 71°17′W, 143 m in elevation) using a narrow band bat detector. Adult, male little brown bats represented 56% of the bats trapped. Only 5 of 19 adult females showed evidence of reproductive activity. In 1992, only adult male bats were captured before 25 July; juveniles were captured after 16 August. In 1993, these dates were 22 July and 4 August. After these dates, the ratio of adult:juvenile bats captured was about equal.

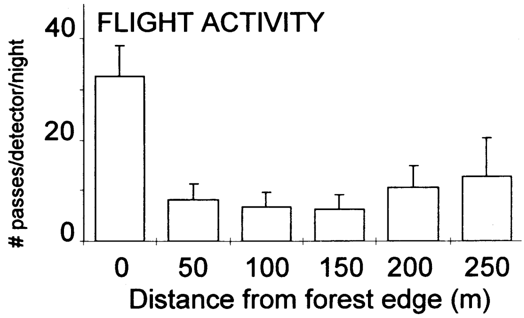

Fig. 2. Horizontal distribution of bat flight activity ($\bar{x}$ + 1 SE) within a forest stand, WMNF 1992–93. Bat activity was recorded at detectors placed at increasing distances from a habitat feature at the forest edge.

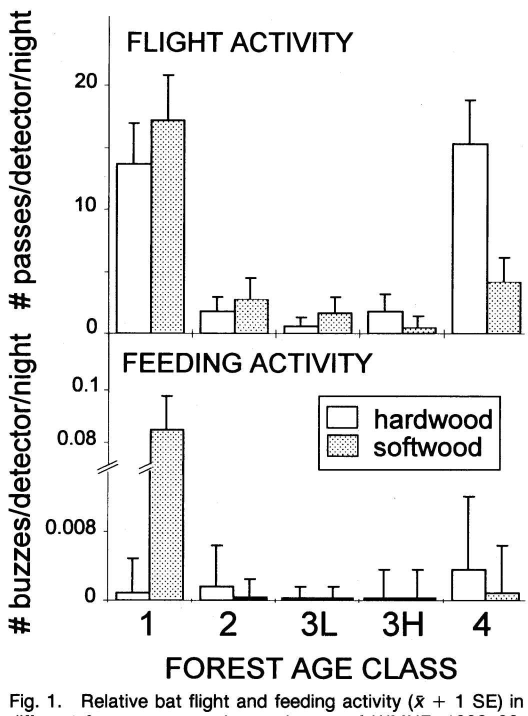

Fig. 1. Relative bat flight and feeding activity ($\bar{x}$ + 1 SE) in different forest types and age classes of WMNF, 1992–93. Forest age classes; 1 regeneration, 2 sapling/pole, 3L mature at low elevation, 3H mature at high elevation, 4 overmature.

Habitat Use

Forest types and age classes.—All interstand comparisons of flight and feeding activity were made using data from the forest interior only (i.e., excluding data from the habitat feature). About 2% of tapes were filled before the end of the sample period because of frequent bat activity, or extraneous sources of ultrasound (e.g., insect stridulation). Forest age class ($F = 19.95$, 4, 297 df, $P < 0.0001$) rather than forest type ($F = 0.84$, 1, 297 df, $P = 0.36$) was the primary determinant of activity (Fig. 1), although within the overmature age class there was a significant difference between forest type ($P = 0.02$, 1, 297 df). Tukey pairwise comparisons of least mean difference ($P \leq 0.05$, 1, 297 df) showed that bat flight activity was significantly greater in regenerating stands of both forest types and in overmature hardwood stands (Table 2, Fig. 1). Flight activity in all other forest types and age classes averaged only 1.3 passes/detector/night (Table 2). Feeding activity was low throughout the forest ($\bar{x}$ = 0.01 feeding buzzes/night), but was concentrated in areas of softwood regeneration (92.6% of total feeding activity, Fig. 1).

There was no consistent trend in the effect of elevation on bat flight activity in mature stands

Table 2. Tukey pairwise comparison probabilities of significantly different mean bat flight activity in different forest types and age classes recorded in WMNF 1992–93 (* $P = 0.05$, ** $P = 0.01$). Key: H hardwood, S softwood, 1 regeneration, 2 sapling/pole, 3L mature at low elevation, 3H mature at high elevation, 4 overmature.

Forest type and age class	$\bar{x}$	H-1	H-2	H-3L	H-3H	H-4	S-1	S-2	S-3L	S-3H	S-4
H-1	13.6										
H-2	1.74	**									
H-3L	0.53	**									
H-3H	1.77	**									
H-4	15.2		**	**	**						
S-1	17.2		**	**	**						
S-2	2.76	*				**	**				
S-3L	1.66	**				**	**				
S-3H	0.49	*				**	**				
S-4	4.16					*	**				

of both forest types. Flight activity in mature hardwood was 3 times greater at sites at least 304 m (1,000 ft) higher in elevation. Conversely, activity was reduced by more than half in comparable softwood sites (Fig. 1).

Habitat Features.—Bat flight and feeding activity were highly concentrated along trail and water bodies at the forest edge compared to the forest interior ($F = 4.75$, 5, 455 df, $P = 0.0003$; Fig. 2). In edge areas, flight activity was not distributed evenly among habitat features ($F = 3.78$, 3, 131 df, $P = 0.01$; Fig. 3) and was minimal where forest stands interfaced directly. Bat feeding activity (Fig. 3) was concentrated over still water ($\bar{x} = 0.11$ buzzes/detector/night, 65% of total activity) compared to other habitat features ($\bar{x} = 0.02$ buzzes/detector/night).

Within Forest Stand Activity.—The configuration of detectors used in 1992 indicated that frequent flight and feeding activity at the forest edge was localized ($F = 4.75$, 5, 455 df, $P = 0.0003$), and that there was no difference in bat activities among detectors extending 50–250 m into the forest ($F = 0.36$, 4, 297 df, $P = 0.84$; Fig. 2). This observation of the horizontal distribution of bat activity within a stand was consistently supported by walking transects with a hand-held AnaBat detector and counting the number of passes/5 minute at 5-m intervals. Infrequent flight activity was recorded at distances ≥ 10 m from the habitat feature.

Within the forest, greater flight activity was recorded at detectors in the mid-upper canopy than in the subcanopy ($F = 4.63$, 2, 297 df, $P = 0.01$; Fig. 4), while feeding activity was distributed more evenly among stations ($F = 1.18$, 2, 297 df, $P = 0.31$).

The permanent detector indicated a great variability in nightly flight activity (0–251 passes/detector/night); feeding activity showed a 5-fold variation between nights. We found no relation between temporal variability in bat activities at the stationary detector and those recorded along forest transects on the same night ($r = 0.03$, $n = 325$, $P = 0.56$).

DISCUSSION

Our data confirm the historical list of bat species found in New England. Resident breed-

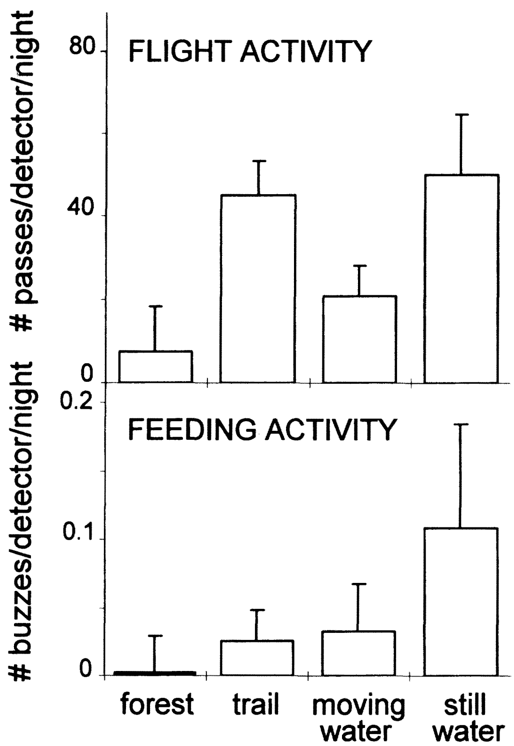

Fig. 3. Relative bat flight and feeding activity ($\bar{x}$ + 1 SE) at habitat features in WMNF, 1992–93.

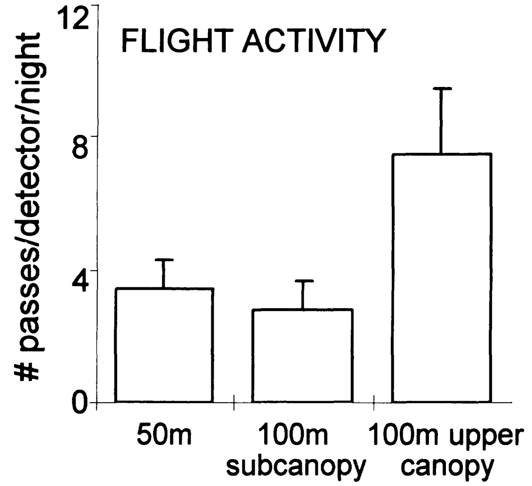

Fig. 4. Vertical distribution of bat flight activity ($\bar{x}$ + 1 SE) within a forest stand, WMNF 1992–93. Bat activity was recorded at detectors placed at increasing distances from a habitat feature at the forest edge.

ing populations of each species, however, were not validated. The female small-footed bat, captured during swarming at a hibernaculum, may only winter in the study area, and the Indiana bat, red bat, and silver-haired bat either were not captured or were represented only by males. The capture of a single male Indiana bat (43°59′N, 71°18′W) extends the northeastern range of this species by about 30 miles as mapped by Barbour and Davis (1969) and Harvey (1992).

All inferences of bat habitat use in this study are biased to reflect the preferences of adult, male little brown bats (56% of individuals trapped). The echolocation calls of northern long-eared bats have a low amplitude, making this species less detectable with the AnaBat system. However, this species represented only 0.07% of individuals trapped.

In contrast to studies in the western United States (Thomas 1988, Carey 1989, Erickson 1993, J. M. Perkins and J. M. Peterson, unpubl. data), we found a decrease in bat activities with increasing forest age in softwood areas. In our study area, the age of overmature softwood stands (>89 yr) is comparable to the age of mature stands (approx. 100 yr) in the Douglas-fir forests of the western United States, where bat activity has consistently been found to be low (Thomas 1988, Carey 1989, Erickson 1993; J. M. Perkins and J. M. Peterson, unpubl. data). If old growth stands of softwood were commonly available in New England, bat habitat use might reflect the same pattern as found in the West. However, the lack of bat activity on 2 survey sites located in virgin stands of spruce/fir forest (U. S. For. Serv. 1986) suggests that hardwood forests are preferred by bats.

Flight activity was recorded most frequently in overmature hardwoods, but feeding activity was not high. Perhaps such areas are used primarily as roost sites by foliage and tree-roosting bat species. Flight activity and feeding activity were minimal in mature areas of both forest types. Because of their relatively young age compared to western forests, these stands contain few natural openings for feeding, and few snags large enough to be used as roost trees. A combination of areas of regeneration of both forest types (clearcuts and group cuts) and overmature hardwoods, probably provides feeding and roosting resources for forest bat communities during summer.

Concentration of activity at the forest edge indicates the importance of linear landscape elements to foraging bats for commuting and navigation across the landscape (Limpens et al. 1989). However, if repeated detections of individual bats passing the detector microphone are more common in the well-defined corridors created by trails and streams, the importance of these habitat features may be accentuated. Comparison of flight and feeding activity indicates that, although bats feed along trails and moving water bodies, these habitat features were used disproportionately as travel corridors. However, still water is an important resource within the forest that attracts bats from a wide area, providing drinking and feeding opportunities. Recordings of bat activity in edge areas are of value, but may obscure localized activity relevant to the interior of each forest stand. The dearth of reproductive females of our most commonly captured species (little brown bats) indicates that the forest types and age classes identified as centers of bat activity in this study may not correspond to quality maternity habitat.

MANAGEMENT IMPLICATIONS

A matrix of different forested and nonforested habitat is used by bats in WMNF. The importance of nonforest habitats, such as aquatic habitats, are integral to the activities of bats during summer. These habitat features at the edge of a stand are affected minimally by timber management techniques. In combination with areas of regeneration (clearcuts and group cuts) and overmature hardwood forest, our data indicate that these habitat features help fulfill the major habitat requirements of bats present in WMNF.

The probable use of overmature stands for roosting, and openings for feeding, indicates that the habitat requirements of bats are associated with those found in pristine forests. Bats presumably used large dead and dying trees as roost sites, and openings from natural disturbances as feeding sites. Timber harvesting could simulate natural disturbances, such as fire or wind, that create large openings and may also replicate smaller openings caused by natural tree fall in pristine forests. Because natural openings are rare in WMNF, it seems important to maintain cutting practices that create group cuts and small clearcuts. Harvest of large trees, however, may destroy potential roost sites of bats (J. M. Perkins and J. M. Peterson, unpubl. data), so it is also important to maintain areas of older forest. Older forest stands usually contain trees with larger diameter stems and a greater abundance of snags than other forest age classes. Survival in a matrix of forest types is potentially feasible for bats because their volant nature allows them to use widely dispersed resources.

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