Habitat Use by Bats on the Upper Coastal Plain of Virginia

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ABSTRACT

We monitored bat activity on the upper Coastal Plain of Virginia using mist nets and acoustic detection (ANABAT) during April-October 2000 and April-August 2001. We classified forty sites into three forest-cover classes (pine forest, mixed pine, and hardwood forest) and three landscape-feature classes (permanent water, riparian corridor, and upland). We captured 406 bats (8 species) in mist nets; red bats (*Lasiurus borealis*; *n* = 281), big brown bats (*Eptesicus fuscus*; *n* = 47), and eastern pipistrelles (*Pipistrellus subflavus*; *n* = 36) were the most commonly captured species. We captured fewer than 30 individuals of five other species. There were no significant differences in captures per 100 net nights for overall captures or for individual species among forest-cover classes. Overall captures per 100 net nights differed significantly among landscape-feature classes; however, *post-hoc* analyses could not tease out significantly different pairs. Captures of *L. borealis* were higher over permanent waters than along riparian corridors or in uplands. Bray-Curtis polar ordination suggested that landscape features such as beaver ponds and impoundments influenced habitat use by bats more than forest-cover type. Discriminant function analysis identified 713 bat calls (≥ 95% confidence) using ANABAT II detectors. *Lasiurus borealis* and *P. subflavus* were more frequently recorded by ANABAT II than northern myotis (*Myotis septentrionalis*) among the three forest-cover classes and among the three landscape-feature classes. Planned, *a priori*, contrast indicated that for 25 nights when mists nets and acoustic detectors were used simultaneously, mean number of bat species detected for the pooled results of both techniques was higher than the average number of species detected by the mean of each of the two techniques separately. Mean number of bat species detected by the ANABAT II system was higher than mean number detected by mist netting.

Keywords: acoustic detection, ANABAT, bats, *Eptesicus fuscus*, habitat use, *Lasiurus borealis*, mist net, *Pipistrellus subflavus*.

INTRODUCTION

Population declines have been documented for many bat species (Rice, 1955; Thomson, 1982; Richter et al., 1993; Dazak et al., 2000; O'Shea et al., 2003) and usually attributed to roost disturbance, habitat loss, inputs of chemical pollution such as insecticides, and introduced pathogens (Clark et al., 1978; Stebbings, 1980; Clark, 1988; Dazak et al., 2000; Frick et al., 2003). Thirteen of the 45 bat species that occur in the United States and Canada are listed as endangered or threatened (U.S. Fish and Wildlife Service, 2017). Recognition of declines and trends towards 'ecosystem management' have increased public and professional interest in bats (Pierson, 1998). Natural resource managers, forest managers, and environmental policy makers traditionally focused their attention on threatened or endangered species or species with limited ranges (Pierson, 1998; Bellows et al., 2001a; Lacki et al, 2007). However, migration patterns and marginal records for many North American bat species suggest large geographic ranges when actual distributions are often disjunct or patchy (Hall, 1981; Pierson, 1998; Ethier and Fahrig, 2011). In addition, bats are difficult to survey accurately because of their secretive, nocturnal, volant, and, in many species, migratory habits (Humphrey and Cope, 1976; Barclay et al., 2003; Gannon et al., 2003). Thus, studies of bats in the field often require specialized monitoring techniques (Kunz and Kurta, 1990; Ministry of Environment, Lands and Parks Resources Inventory Branch, 1998; O'Farrell and Gannon, 1999; O'Shea et al., 2003). As a result, bats are often overlooked in faunal surveys (Jung et al., 1999; Thomas et al., 1999; Tuttle, 2007), and basic knowledge concerning the general ecology of common bat species is lacking (Fenton, 1997; Whitaker and Hamilton, 1998; Tuttle, 2007). An increased understanding of habitat use by bat species in large, relatively undeveloped landscapes (e.g., government installations and regional and national parks) would assist natural resource managers in developing local management strategies that help to maintain large-scale biodiversity.

Compared to the Mountain and Piedmont regions, the Coastal Plain of the mid-Atlantic region offers few natural overwintering locations (e.g., caves). Inventories of and research on bats in this region rely largely on data collected during active seasons, usually March through November for many species. Most recent surveys of bats in Virginia have been conducted in southeastern Virginia in the Great Dismal Swamp and Virginia Beach, along the James River, and in montane regions (e.g., Dalton, 1987; Padgett and Rose, 1991; Hobson, 1998; Rose et al., 2000; Walker, 2000). Our study in Virginia's upper Coastal Plain represents the first examination of chiropterans in a previously unstudied area of the mid-Atlantic region.

Our primary objective was to determine patterns of habitat use by bat species in a previously unstudied area within the upper Coastal Plain. We based habitat use on composition of bat assemblages and species distributions among different forest cover types and different landscape features. Because all local species have distributions far greater than our study area (Hall, 1981; Biggs, 1985; Whitaker and Hamilton, 1998; Wilson and Ruff, 1999), our have management implications at larger spatial scales. A secondary objective was to evaluate and compare the effectiveness and efficacy of two monitoring techniques—mist netting and acoustic detection. Because both techniques have advantages and disadvantages, we hypothesize that these two techniques together will be more effective in explaining habitat-use patterns for a wider suite of species than either technique alone.

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Study Area

We conducted this study on U.S. Army Fort A. P. Hill (APH), Caroline County, Virginia. APH is located on the western side of the Chesapeake Bay and centered at approximately N 77° 15′ and W 38° 05′. It is a military field-training installation with 30,329 ha site mostly in managed forest. With the exception of a few remnant old-growth stands, silvicultural practices on APH have produced a mosaic of successional old fields and forest cover types representative of the region (Mitchell and Roble, 1998; Bellows et al., 2001b).

Mist netting

We monitored bat activity ~ six days/month (70 sampling nights), April-October 2000 and April-August 2001 in 40 sites we selected. We captured bats were using 4-tiered mist nets (50 denier/2ply, 38 mm mesh) that were 3 m in height and ranged in length from 2.6 m to 18.0 m (Avinet, Inc., Dryden, New York, USA). Mist nets were set across openings in interior forests, logging roads, edges of ponds and impoundments, slow-moving woodland creeks with little or no emergent vegetation, small power line openings, over road ruts (puddles), over and under bridges, and other likely corridors of bat movement. Vertical coverage of mist nets ranged from ground or water level to heights of ~ 10 m.

Mist nets were deployed shortly after sunset after diurnal bird activity ended and monitored continuously for ~ 7 hours. One net night (NN) equals one 6x3-m area of mist net/sampling night, regardless of vertical placement. For example, a set consisting of two 9x3 m nets equals 3.0 NN. Bats were lightly marked with a black felt pen on their dorsal pelage to identify recaptures and then released unharmed. Recaptured individuals were not included in analyses.

Acoustic Detection

We used an ANABAT II bat detector (Titley Electronics, Ballina, New South Wales, Australia) to record bat calls using ANABAT software (version 5.7i). This system supplemented our mist netting efforts on 25 sampling nights during 2000 (10 sites) and 2001 (15 sites of which 10 were new). We did not deploy ANABAT II on rainy nights.

ANABAT II enabled remote identification of bats based on diagnostic characteristics (e.g., variations in frequency/time) of echolocation calls (sequence recordings—Corben and O'Farrell, 1999). Sequence recordings were passively collected (i.e., "monitor" mode) by directing the ANABAT II detector over likely corridors of bat movement (e.g., openings under the forest canopy, over riparian corridors, impoundments and beaver ponds, logging roads). Detectors were positioned such that recordings did not include distress calls from bats entangled in mist nets. We assumed that all species were equally susceptible to acoustic detection when calling in range of a detector. ANABAT receiver sensitivity was set the same throughout the study. A sampling unit (night) consisted of the data collected by a single ANABAT II detector, for one night, at one location. Sequence recordings were downloaded directly to a laptop

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computer in the field using a Zero Crossing Analysis Interface Module (Titley Electronics, Ballina, New South Wales, Australia). Sampling night duration was the same as mist netting (~ 7 hours).

Raw sequence recordings were processed using ANALOOK software (version 3.5) to cull non-bat recordings (e.g., insects, human activity) and remove background noise from potentially identifiable recordings. We also culled all remaining recordings with fewer than six echolocation pulses. Methods of analysis and identification of cleaned sequence recordings are discussed in the *Statistical Analyses* section below.

Study Sites

Each of the 40 study sites was classified into one of three general forest-cover classes (FCC), pine forest (PN), mixed pine and hardwood forest (MX), or hardwood forest (HW), based on dominant canopy tree species. Loblolly pine (*Pinus taeda*) and Virginia pine (*P. virginiana*) dominated PN sites and were the only pine species in MX sites. Hardwood species composition of MX and HW sites varied from red maple (*Acer rubrum*) and river birch (*Betula niger*) in bottomland forest to American beech (*Fagus grandifolia*), hickories (*Carya* spp.) and oaks (*Quercus* spp.) in upland forest. Each study site was also classified into one of three landscape-feature classes (LFC): permanent water (e.g., impoundments, beaver ponds) (PW), riparian corridor (RC), or upland (UP). For more comprehensive descriptions of habitat types on APH refer to Mitchell and Roble (1998) and Bellows et al. (2001b).

Statistical Analyses

Replication of both mist netting and acoustic detection for sampling sites was often difficult because of military-training activities and restricted access. We used captures/100 NN for mist netting analyses because effort among sampling sites varied (i.e., variation in the number and sizes of nets set). We used a significance level of $\alpha < 0.05$ for all univariate tests.

Captures/100 NN for individual species for a given FCC or LFC class were calculated using the following equation:

$$C_{ij} = N_{ij} / M_j \qquad \text{(Equation 1.0)}$$

Where C_{ij} = captures/100 NN for the ith species in the jth class (i.e., j^{th} class = Forest Cover or Land Cover class (FCC or LFC), N_{ij} = total number of the ith species captured in the jth FCC or LFC, and M_j = total number of mist-net sampling nights for the jth class. Overall captures/100 NN for individual classes of FCCs and LFCs was calculated using the following equation:

$$C_j = \sum C_{ij} / R_n \qquad \text{(Equation 1.1)}$$

Where C_j = overall captures/100 NN for the jth FCC or LFC, C_{ij} = captures/100 NN for the ith species captured in the jth FCC or LFC (as per Equation 1.0), and R_n = total number of species captured using mist nets.

Single-factor ANOVA was used to test the null hypotheses of no FCC effect on mean overall captures/100 NN among the three FCCs and of no LFC effect on mean overall captures/100 NN among the three LFCs (Equation 1.1; Zar, 1996). We used single-factor ANOVA to test null hypotheses of no differences in mean captures/100 NN among FCCs and no

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differences in mean captures/100 NN among LFCs for each bat species represented by ≥ 30 captures (Equation 1.0) where the assumptions of normal distributions and equality of variances were met. We used Student-Newman-Keuls multiple comparison procedure to isolate significant differences in mean captures/100 NN among FCCs and mean captures/100 NN among LFCs in these ANOVAs (Zar 1996). Were used either Kruskal-Wallis one-way ANOVA on ranks (three treatments; critical statistic = H) or Mann-Whitney rank-sum tests (two treatments; critical statistic = U) to test null hypotheses of similar captures/100 NN for FCCs and of similar captures/100 NN for LFCs for each bat species represented by ≥ 30 captures (Equation 1.0) when the assumptions of normality and equal variance were not met (Zar, 1996).

We used Bray-Curtis polar ordination (a Euclidean distance measure) to identify subtle patterns in bat species use of LFC represented by mist net captures among the 40 study sites (Ludwig and Reynolds, 1988). Bray-Curtis was selected because it is relatively insensitive to the nonlinear relationships common in most ecological data sets (Gauch and Whitaker, 1972) and, as an indirect gradient analysis, results are based solely on species distributions among study sites and not on environmental data (Gauch, 1984). Euclidean distance among sites in relation to each ordination axis correlates with general similarity of species composition among sites—shorter distance represents increased similarity (Ludwig and Reynolds, 1988). We overlaid captures/100 NN for each species (from Equation 1.0) for each study site on the main matrix to correlate explained variance for the first three ordination axes to the distribution of individual species (McCune and Mefford, 1995). We used Pearson's correlation coefficient (r) for species where parametric assumptions were met or Kendall's rank correlation coefficient (τ) for species where assumptions were not met to numerically describe relationships between species distributions and positions of study sites along ordination axes (McCune and Mefford, 1995).

Cleaned sequence recordings collected by ANABAT II were compared to bat calls of known origin (vouchers) in the Virginia Department of Game and Inland Fishery's (VDGIF) bat call library using discriminant function analysis (DFA: SPSS version 7.5). We selected within-group covariance matrices and prior probabilities assuming all groups equal (after Walker, 2000). We used only sequence recordings classified to species by DFA with $\geq 95\%$ confidence in acoustic detection analyses.

We made no assumptions regarding the numbers of individuals for each species detected on a single night because of the difficulties associated with estimating population abundance using acoustic detection (Hayes, 1997). As a result, we considered only the use (occurrence) by individual species during a sampling night at a sampling site (i.e., use or nonuse of a FCC and LFC type). We calculated frequency of occurrence for individual species for a given FCC or LFC class using the following equation:

$$F_{ij} = N_{ij} / A_j \qquad \text{(Equation 2.0)}$$

where F_{ij} = frequency of occurrence for the ith species in the jth class (i.e., j^{th} class = FCC or LFC class), N_{ij} = total number of nights the ith species was acoustically detected in the jth FCC or LFC, and A_j = total number of ANABAT II sampling nights for the jth class. Overall frequency of occurrence for individual classes of FCCs and LFCs was calculated using the following equation:

$$F_j = \sum F_{ij} / R_j \qquad \text{(Equation 2.1)}$$

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where F_j = overall frequency of occurrence for the jth FCC or LFC, F_{ij} = frequency of occurrence for the ith species detected in the jth FCC or LFC (as per Equation 2.0), and R_j = total number of species identified using acoustic detection.

We used single-factor ANOVA to test null hypotheses of no FCC effect on overall frequencies of presence among the three FCCs for the six species identified by DFA and of no LFC effect on overall frequencies of presence among LFCs for the six species identified by DFA (Equation 2.1—Zar, 1996). We used single-factor ANOVA to test null hypotheses of similar frequencies of occurrence for FCCs and of similar frequencies of occurrence for LFCs among the six bat species represented in the DFA model (Equation 2.0—Zar, 1996).

We used ANOVA with two planned, *a priori*, contrasts (critical statistic = *t*: Sokal and Rohlf, 1981) to test the following two null hypotheses. The first hypothesis (A) is of no difference in mean nightly species richness obtained by pooling mist netting and ANABAT II (-2) and the average species richness for the two techniques, mist netting (1) and ANABAT II (1), for the 25 nights when both techniques were used simultaneously within the same sampling area—planned contrast A (-2, 1, 1). Pooled results did not include replicate species detected by both techniques; thus, a species captured in mist nets and recorded with ANABAT II on the same night represents occurrence of a single species. The second hypothesis is of no difference in mean species richness obtained by mist netting (-1) and ANABAT II (1)—planned contrast B (0 [both], -1, 1). We did not compare numbers of sequence recordings among sites or compare them to numbers of captures because of the difficultly of accurately determining relative abundance using acoustic detection (Hayes, 1997); multiple calls could be a single bat circling over the detector.

RESULTS

Mist netting

We captured a total of 406 bats in mist nets representing 8 species in 733.5 NN from April-October 2000 and April-August 2001 (Tables 1 and 2). The most commonly captured species were red bats (*Lasiurus borealis*; $n = 281$), big brown bats (*Eptesicus fuscus*; $n = 47$), and eastern pipistrelle (*Pipistrellus subflavus*, $n = 36$). Captures for the remaining five species were all ≤ 13 individuals (Tables 1 and 2).

Bats were captured at all but two of the 40 sites sampled during 70 sampling nights. Number of species captured at each site ranged from zero to five (mean = 2.4 ± 1.4). Overall captures/100 NN averaged 54.6 ± 39 bats. Mean overall captures/100 NN were not significantly different among forest-cover classes (FCCs) ($F = 0.64$, P = 0.535; Table 3), and ranged from 39.2 ± 36.3 for PN to 59.8 ± 53.7 for MX (Table 1). There were significant differences in mean overall captures/100NN ($F = 3.31$, P = 0.048) among landscape-feature classes (LFCs); however, *post-hoc* analyses could not tease out significantly different pairs (Table 3). Mean overall captures/100 NN for LFCs ranged from 71.3 ±44.4 for RC to 36.0 ± 36.7 for UP (Table 2).

Lasiurus borealis, captured at 35 of the 40 study sites, was the sole species at nine of these sites. *Eptesicus fuscus*, *P. subflavus*, and northern myotis (*Myotis septentrionalis*) were

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captured at 19, 16, and 6 sites, respectively. The remaining four species were captured at 1 to 4 sites. There were no significant differences in mean captures/100 NN for *L. borealis* ($F = 0.86$, P $= 0.432$), *P. subflavus* ($H = 1.86$, P $= 0.394$), or *E. fuscus* ($H = 1.54$, P $= 0.463$) among FCCs (Table 3). Comparisons of captures for FCCs and LFCs for the remaining five species, $n \leq 30$ (Tables 1 and 2), were not conducted because of small sample sizes.

Mean captures/100 NN for *L. borealis* was significantly higher ($F = 3.92$, P $= 0.029$) in PW (54.2 ±33.4) than in RC (27.3 ±24.0) and UP (26.6 ±26.5; Tables 2 and 3). There was no significant difference ($U = 180.50$, P $= 0.279$) in captures/100 NN of *P. subflavus* between PW and RC (Table 3); however, none was captured in UP (Table 1). There were no significant differences ($H = 0.07$, P $= 0.966$) in captures/100 NN of *E. fuscus* among the three LFCs (Table 3).

The first three Bray-Curtis polar-ordination axes explained 97.53% of the variation in bat assemblages among study sites. For bats as a group, no clear-cut patterns of LFC use were apparent. PW sites tended to be more diversely distributed than RC and UP, and RC more so than UP. Sites positioned near endpoints of each of the three axes were generally PW and RC (Figures 1 - 3).

Variation in bat species composition among the 40 study sites described by the first three polar-ordination axes was largely explained by one species for each axis. Variation for Axis I (74.96%) was best explained ($r = 0.998$) by the distribution (abundances) of *L. borealis* among study sites (Figure 1); for all other species r or τ was < 0.089. Variation in the second ordination axis (12.64%) was best explained by the abundances of *P. subflavus* among sites ($\tau = 0.554$) (Figure 2); for all other species r or τ was < 0.016. Variation in the third axis (9.92%) was best explained by the abundances of *E. fuscus* among sites ($\tau = 0.943$; Figure 3); r for all other species r or τ was < 0.243.

Acoustic Detection

We collected 2,187 raw sequence recordings during 25 sampling nights, 342 of which were non-bat calls and 698 had fewer than six pulses, thus, leaving 1,147 sequence recordings to be identified. Of these, DFA was able to identify 713 (~ 62%) to species with $\geq 95\%$ confidence. Our DFA model included voucher calls of six species from the VDGIF's bat call library: *E. fuscus* (23 voucher calls), *L. borealis* (15), hoary bats (*Lasiurus cinereus*: 15), little brown bats (*Myotis lucifugus*: 29), *M. septentrionalis* (11) and, *P. subflavus* (13). Calls of two species we captured, evening bats (*Nycticeius humeralis*) and silver-haired bats (*Lasionycteris noctivagans*), were not in the VDGIF's bat call library at the time of our analysis; thus, these species were not considered in our current DFA model.

All six species identified by the DFA model were detected in all three FCCs (Table 1). There was no significant effect among the three FCCs on overall mean frequencies of presence for the six species identified (by DFA; $F = 1.03$, P $= 0.358$; Table 3), with mean frequency of presence ranging from 0.42 ± 0.20 for PN to 0.65 ± 0.33 for MX (Table 1). Significant differences in mean frequencies of occurrence were detected among the six species (DFA) for FCCs ($F = 4.15$, P $= 0.020$); *L. borealis* (0.77 ± 0.23) and *P. subflavus* (0.81 ± 0.16) were recorded more frequently than *M. septentrionalis* (0.19 ± 0.10) (P < 0.05; Tables 1 and 3).

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Four of the six species identified by the DFA model were detected in all three LFCs. *Lasiurus cinereus* and *M. septentrionalis* were not recorded in UP, but were recorded in PW and RC (Table 2). There was no significant effect among the three LFCs on overall frequencies of presence for the six species identified by DFA ($F = 2.08$, P = 0.380; Table 3), with mean overall frequencies of presence/sampling night among the three LFCs ranging from 0.35 ± 0.20 for RC to 0.57 ± 0.29 for PW (Table 2). Significant differences in mean frequencies of presence were seen among the six species (DFA) for LFCs ($F = 4.91$, P = 0.011); as for FCCs, *L. borealis* and *P. subflavus* were recorded more frequently in than *M. septentrionalis* (P < 0.05; Tables 2 and 3).

Significant differences in species richness/sampling night were obtained among the three protocols: both mist netting and ANABAT II, mist netting alone, and ANABAT II alone ($F = 11.64$, P = 0.000042) (Table 4). Mean combined, or "pooled," species richness/sampling night for the pooled mist netting and ANABAT II treatment was significantly higher than the average species richness/sampling night achieved for either technique (Contrast A; $t = 3.65$, P = 0.0005), and species richness for ANABAT II was significantly higher than for mist netting (Contrast B; $t = 3.16$, P = 0.0023, Table 4).

DISCUSSION

Four species (*L. cinereus*, *M. lucifugus*, *M. septentrionalis*, *N. humeralis*) were not captured in pine forest (PN), and *L. cinereus* was not captured in mixed hardwood and pine forest (MX). None of these five species was well represented in mist net captures; however, calls for these species, except *N. humeralis* (not in DFA model), were recorded in all forest-cover classes (FCCs). In fact, all of the six species in our DFA model were recorded in all FCCs (Table 1). By comparison, captures/100 NN for the three most abundant species (*L. borealis*, *E. fuscus*, *P. subflavus*) were similar among FCCs (Ho_3), and their influence, in part, caused the lack of a significant difference in overall captures/100 NN among FCCs (Ho_1). ANABAT results for FCCs were similar to capture results for FCCs in two respects: 1) similar to overall captures/100 NN, overall frequencies of presence were similar and not significantly different among FCCs (Ho_5), and 2) species with high captures/100NN generally had higher frequencies of occurrence than those species with lower captures/100 NN (Ho_7; Table 3). Although the importance of forest-cover type for bats has been well documented (Pierson, 1998; Jung et al., 1999; Elmore et al., 2005; Lacki et al., 2007), no abundant bat species was significantly associated with any particular FCC in our study.

Unlike FCCs, species composition based on mist net captures/100 NN varied among the three landscape-feature classes (LFCs; Table 3; Ho_2). *Myotis septentrionalis* was captured in mist nets in upland forest (UP), but never recorded there. Three of the eight species were not captured in all LFCs. *Pipistrellus subflavus* was not captured in UP, but it was usually acoustically detected there (Table 2). This is interesting because the number of mist-net captures for this species (36) should have been sufficient to determine patterns of forest-cover use at our relatively coarse-grained classification scheme. *Lasiurus noctivagans* was not captured near permanent water (PW) and *L. cinereus* was not captured or acoustically detected in UP. *Lasionycteris noctivagans* regularly feed adjacent to bodies of water (Kunz, 1982) and *L. cinereus* occur in wet and dry habitats (Shump and Shump, 1982). We suggest that the absence

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of *L. noctivagans* in PW and the absence of *L. cinereus* UP are indirect results of seasonal migration habits that largely limited the presence of these species within the region to spring and fall and that *L. cinereus* regularly frequently travels higher than mist nets can be effectively set (Ministry of Environment, Lands and Parks Resources Inventory Branch, 1998; MacCarthy et al., 2006). Solitary habits and sporadic abundance during migrations further reduced our ability to capture these two species (Kunz, 1982; Shump and Shump, 1982). However, we believe that with further effort in spring and fall, *L. noctivagans* would be captured over or near water and *L. cinereus* would be captured or recorded in UP.

Justification for our use of polar ordination was twofold. First was the inability of *post-hoc* analysis to isolate significantly different overall captures/100 NN between pairs of LFCs following ANOVA (P = 0.048, Table 3; Ho_2). Polar ordination illustrated subtle patterns of LFC use by bats as a group; PW and riparian corridors (RC) were used more frequently than UP (Figures 1–3). Second, use of LFCs by bats was largely influenced by the most abundant species. A single abundant species largely explained the variation in species composition for each of the first three polar ordination axes, with most of the more dissimilar (extreme) sites along all three axes being PW or RC (Figures 1–3). Collectively, these findings indicate a tendency for these abundant species, *L. borealis* and *E. fuscus,* and to a lesser degree, *P. subflavus*, to use mesic to hydric habitats.

Mist nets sample an extremely small area (volume) relative to that used by bats (O'Farrell and Gannon, 1999; Flaquer et al., 2007). Within this small area, proper net placement is critical to capture success (Kunz and Kurta, 1990; Jones et al., 1996), and effective mist net placement is limited to situations where bat movement is restricted, e.g., under overhanging branches over roadways and creeks (Barbour and Davis, 1969; Kunz, 1973; Jones et al., 1996). In contrast, ANABAT II samples a larger proportion of area than mist nets (O'Farrell and Gannon, 1999) and is not as limited to situations where bat flight is restricted. In addition, it is more effective to capture bats in mist nets set along travel corridors than in foraging areas (e.g., over ponds or old fields) because sensory perception in the latter areas is usually more acute (Black, 1974; Kunz and Kurta, 1990; Kunz and Fenton, 2005). We occasionally set nets over foraging areas, but the most successful nets were those across travel corridors as they opened into foraging sites.

Standard mist-netting techniques are also limited by the maximum heights to which nets can be deployed (Kunz and Kurta, 1990; Munn, 1991; Jones et al., 1996). Many species routinely fly above the highest mist nets (O'Farrell and Gannon, 1999). There is also variation among and within species in their ability to avoid even well-placed nets (Cockrum and Cross, 1964; Kunz and Kurta, 1990; MacCarthy et al., 2006). Because ANABAT II data were collected remotely, with no physical impediment, and this technique is capable of functioning over a relatively broad area, our findings are based on the assumptions of no detectability and that all species are equally susceptible to data collection when passing within range of a detector.

Our findings indirectly supported these assumptions; only two of the 11 'species absences' among FCCs and LFCs were with ANABAT II methods, compared to nine of the absences using mist nets (Tables 1 and 2). In addition, we were able to significantly increase the number of species detected/sampling night an average of one species when using both methods simultaneously (Table 4). This increase is likely a function of differences in the spatial nature in

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which these two methods collect data and variation in the detectability of mist nets by each species. We suggest that these results are affected by the potential biases and shortcomings of mist netting described above. However, unlike mist netting, ANABAT II is generally not used to determine relative abundance of species because it does not provide a one-to-one correlation between recorded calls and the number of individuals present (Thomas and LaVal, 1990; Rudran et al., 1996). ANABAT II is also unable to determine sex ratios. Thus, we concur with O'Farrell and Gannon (1999) and Weller (2007) that no single technique provides a complete inventory.

Records from Hall (1981), Whitaker and Hamilton (1998), and others suggest that with the exception of a few extralimital records (described below), our efforts on APH have recorded most of the bat species that should occur in the region. Our captures of two *L. cinereus* in July (adult male) and August (juvenile female) of 2000 are the first records for this species on Virginia's Coastal Plain during the summer (Bellows and Mitchell, 2002), indicating the likelihood of breeding here. Despite our use of two methods of survey, we cannot be certain that no other species of bats occur on APH. There are extralimital records for other bat species that potentially include the study region (Rageot, 1955; Cranford and Fortune, 1994; Webster, 2002). In brief, we believe our surveys revealed all the common resident and migratory species for the region.

Our findings suggest that landscape features such as bottomland and upland areas have a greater influence on patterns of habitat use by bats in fragmented landscapes than the composition of tree species within these areas. We attribute these patterns to the propensity of many bat species to forage over or near a wide variety of mesic and hydric habitats (Barbour and Davis, 1969; Pierson, 1998; Erickson and West, 2002). We present these suggestions with caution because we are aware that habitat fragmentation of our study area has likely affected our results. Day roosts are often located many km away from foraging sites. As bats move from day roosts to foraging areas, the number of habitat types they pass through will increase as fragmentation and fractal dimensions of FCC and LFCs patches increase. Thus, increased fragmentation would increase the likelihood of individuals being captured or recorded as they pass through a habitat for which they have no or only marginal affinity. Because each of the 40 sample sites was assigned to a FCC class and a LFC class, the collective effectiveness of acoustic detectors to provide accurate results is exactly the same for FCCs as it is for LFCs— logic says the same must be true for mist nets. Therefore, it might be expected that differences among FCCs and among LFCs in acoustic detection results should be mirrored in mist-netting results, but this was not true. Our acoustic detection findings of similar, non-significant overall frequencies of occurrence among FCCs (Ho_5) and among LFCs (Ho_6) were contradicted with significant differences in overall captures/100 NN among LFCs (Ho_2), but no differences in overall captures/100 NN among FCCs (Ho_1). Spatially related differences in the abilities of acoustic detectors and mist nets to collect data (e.g., effective heights and ranges, detectability) provide different findings for each technique. Thus, if the activities, e.g., foraging (relatively high sensory perception) vs. traveling to and from roosts (relatively low sensory perception), within the various FCCs were not the same as within LFCs, then the above contradiction suggest that habitat utilization by bats is different with regard to LFC attributes than for FCC attributes. We realize such conclusions cannot be drawn from our current sampling design; however, this does provide sufficient justification for additional hypotheses. Further study on roosting habits

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and daily movements (i.e., radio tracking and simultaneous monitoring stations) is needed to achieve a fine-grained resolution of spatial habitat and landscape use by bats.

Studies of chiropterans on this and other government installations should be an ongoing focus of natural resource managers because such relatively undeveloped landscapes are quickly disappearing. Trends in the ecological conditions in these "refuge-like islands" should be used to quantify regional effects of landscape-level anthropogenic changes such as deforestation and urban sprawl on chiropterans and other environmentally sensitive taxa. Although our results describe local habitat use patterns, the species we studied have regional to continental distributions. As a result, management at a local scale may provide critical links of protection for vulnerable species with relatively large population ranges. Our results can be used to encourage management efforts that target protection and conservation of the current regional diversity of chiropterans. Conservation efforts should include provisions for common and widely distributed species, as well as endangered and threatened species, because they are all key components of regional biodiversity.

ACKNOWLEDGMENTS

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Table 1. Mist net (MN) and ANABAT II (AB) effort and results (2000 and 2001) for 8 bat species (and the total number captured for each) for FCCs. ANABAT II values represent the frequency of presence (Equation 2.0) for each FCC where each species in the DFA model. Mist net values represent captures/100 NN (Equation 1.0). Forest-cover classes (FCCs) = pine forest (PN), mixed hardwood and pine forest (MX), and hardwood forest (HW).

Species (Number captured)	Device	PN (71.5, 4) mean[a] median[b]	SD[c] min, max[d]	Freq	MX (274.5, 8) mean[a] median[b]	SD[c] min, max[d]	Freq	HW (387.5, 13) mean[a] median[b]	SD[c] min, max[d]	Freq
E. fuscus	AB			0.25			0.88			0.54
(47)	MN	0.0[b]	0.0, 38.1[d]		0.0[b]	0.0, 26.3[d]		4.4[b]	0.0, 52.4[d]	
L. noctivagans[e]	MN	0.0[b]	0.0, 17.4[d]		0.0[b]	0.0, 3.8[d]		0.0[b]	0.0, 17.4[d]	
(9)										
L. borealis	AB			0.50			0.88			0.92
(281)	MN	25.5[a]	19.9[c]		44.7[a]	40.5[c]		39.4[a]	27.5[c]	
L. cinereus	AB			0.25			0.63			0.15
(3)	MN	NC[f]			NC[f]			0.0[b]	0.0, 3.1[d]	
M. lucifugus	AB			0.50			0.25			0.31
(12)	MN	NC[f]			0.0[b]	0.0, 7.1[d]		0.0[b]	0.0, 7.1[d]	
M. septentrionalis	AB			0.25			0.25			0.08
(13)	MN	NC[f]			0.0[b]	0.0, 13.3[d]		0.0[b]	0.0, 13.3[d]	
N. humeralis[e]	MN	NC[f]			NC[f]			0.0[b]	0.0, 5.9[d]	
(5)										

FCC (Total Net Nights and ANABAT II nights)

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P. subflavus	AB		0.75		1.00		0.69
(36)	MN	0.0[b]	0.0, 19.1[d]	0.0[b]	0.0, 80.0[d]	2.5[b]	0.0, 17.4[d]
Means	AB		0.42		0.65		0.45
	MN	39.2[a]	36.3[c]	59.8[a]	53.7[c]	56.5[a]	30.7[c]

[a]mean captures/100 NN (species where basic parametric assumptions were met)

[b]median captures/100 NN (species where basic parametric assumptions were not met)

[c]standard devation for mean captures/100 NN (species where basic parametric assumptions were met)

[d]minimum, maximum captures/100 NN (species where basic parametric assumptions were not met)

[e]indicates species not in the VDGIF's library of ANABAT calls at the time of analysis

[f]not captured

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Table 2. Mist net (MN) and ANABAT II (AB) effort and results (2000 and 2001) for 8 bat species (and the total number captured for each) for LFCs. ANABAT II values represent the frequency of presence (Equation 2.0) for each LFC where each species in the DFA model. Mist net values represent captures/100 NN (Equation 1.0). Landscape features (LFCs) = permanent water (PW), riparian corridor (RC), upland (UP).

		LFC (Total Net Nights and ANABAT II nights)								
		PW (370.5, 12)			RC (236.0, 10)			UP (127.0, 3)		
Species		mean[a]	SD[c] min,		mean[a]	SD[c] min,		mean[a]	SD[c] min,	
(Number captured)	Device	median[b]	max[d]	Freq	median[b]	max[d]	Freq	median[b]	max[d]	Freq
E. fuscus	AB			0.70			0.50			0.33
(47)	MN	0.6[b]	0.0, 38.1[d]		0.0[b]	0.0, 52.4[d]		0.0[b]	0.0, 14.3[d]	
L. noctivagans[e]	MN	NC[f]			0.0[b]	0.0, 17.4[d]		0.0[b]	0.0, 14.3[d]	
(9)										
L. borealis	AB			0.90			0.58			0.67
(281)	MN	52.9[a]	33.4[c]		27.3[a]	24.0[c]		26.6[a]	26.5[c]	
L. cinereus	AB			0.50			0.17			0.00
(3)	MN	0.0[b]	0.0, 10.0[d]		0.0[b]	0.0, 3.9[d]		NC[f]		
M. lucifugus	AB			0.40			0.17			0.67
(12)	MN	0.0[b]	0.0, 7.1[d]		0.0[b]	0.0, 3.6[d]		0.0[b]	0.0, 16.1[d]	
M. septentrionalis	AB			0.10			0.17			0.00
(13)	MN	0.0[b]	0.0, 7.7[d]		0.0[b]	0.0, 13.3[d]		0.0[b]	0.0, 9.2[d]	
N. humeralis[e]	MN	0.0[b]	0.0, 5.8[d]		0.0[b]	0.0, 7.7[d]		0.0[b]	0.0, 4.6[d]	
(5)										
P. subflavus	AB			0.80			0.50			0.67

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(36)	MN	5.4[b]	0.0, 80.0[d]		0.0[b]	0.0, 8.2[d]	NC[f]	
Means	AB			0.57			0.35			0.39
	MN	71.3[a]	44.7[c]		44.2[a]	27.1[c]	36.0[a]	36.7[c]

[a]mean captures/100 NN (species where basic parametric assumptions were met)

[b]median captures/100 NN (species where basic parametric assumptions were not met)

[c]standard devation for mean captures/100 NN (species where basic parametric assumptions were met)

[d]minimum, maximum captures/100 NN (species where basic parametric assumptions were not met)

[e]indicates species not in the VDGIF's library of ANABAT calls

[f]not captured

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Table 3. Results of mist netting and ANABAT II univariate analyses (i.e., ANOVA [*F*], Kruskal-Wallis ANOVA on ranks [*H*], and Mann-Whitney rank sum test [*U*]). Numbers in the Ho: column refer to the numbered null hypotheses below. "ALL" species include all 8 species captured. Individual species include: *L. borealis* (*LB*), *P. subflavus* (*PS*), and *E. fuscus* (*EF*). "DFA" includes the six species modeled in our DFA analysis.

<div align="center">Critical Statistic</div>

Ho:	Species	*df*	*F*	*H*	*U*	P	Significant Pairs
1	ALL	2	0.64			0.535	-
2	ALL	2	3.31			0.048[†]	none
3	*LB*	2	0.86			0.432	-
3	*PS*	2		1.86		0.394	-
3	*EF*	2		1.54		0.463	-
4	*LB*	2	3.92			0.029[†]	PW > RC, UP
4	*PS*	2			180.5	0.279	n/a
4	*EF*	2		0.07		0.966	-
5	DFA	2	1.10			0.358	-
6	DFA	2	1.03			0.380	-
7	DFA	5	4.14			0.020[†]	*LB, PS > MS*
8	DFA	5	4.91			0.011[†]	*LB, PS > MS*

† term significant at α = 0.05

1) no FCC effect on mean overall mist net captures/100 NN

2) no LFCs effect on mean overall mist net captures/100 NN

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3) similar mean captures/100 NN among FCCs for an individual species

4) similar mean captures/100 NN among LFCs for an individual species

5) no FCC effect on overall frequencies of presence for the six species identified (by DFA)

6) no LFC effect on overall frequencies of presence for the six species identified (by DFA)

7) similar frequencies of presence among FCCs among species represented in DFA

8) similar frequencies of presence among LFCs among species represented in DFA

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Table 4. Analysis of Variance with planned contrasts testing the null hypotheses: A) no difference in mean nightly species richness obtained by pooling mist netting and ANABAT II (-2) and the average species richness for the two techniques, mist netting (1) and ANABAT II (1)—*a priori* contrast A (-2, 1, 1); B) no difference between mean species richness obtained by mist netting (-1) and ANABAT II (1)—*a priori* contrast B (0 [both], -1, 1).

Source	*df*	SS	MS	*F*	P
Treatments	2	26.8	13.4	11.64	0.000042*
Error	72	83.2	1.2		
Total (Adjusted)	74	110.0			

Planned contrast A: *df* = 72, *t* = 3.65, P = 0.0005*

Group	Comparison Coefficient	Count	Mean
Both	-2	25	3.44
ANABAT II	1	25	2.96
Mist netting	1	25	2.00

Planned contrast B: *df* = 72, *t* = 3.16   P = 0.0023*

Group	Comparison Coefficient	Count	Mean
Both	0	25	3.44
ANABAT II	-1	25	2.96
Mist netting	1	25	2.00

* Term significant at alpha < 0.05

FIGURE LEGENDS

Figure 1. Graphic overlay of *Lasiurus borealis* on Bray-Curtis polar ordination plot. Size of the circles indicates proportion of captures/100 net nights for *L. borealis* for that site among the 40 study sites. Scatterplots depict the relationship between *L. borealis* and the explained variance for each axis represented. Pearson's correlation coefficients (*r*) are provided. PW = permanent water body; RC = riparian corridor.

Figure 2. Graphic overlay of *Pipistrellus subflavus* on Bray-Curtis polar ordination plot. Size of the circles indicates proportion of captures/100 net nights for *P. subflavus* for that site among the 40 study sites. Scatterplots depict the relationship between *P. subflavus* and the explained variance for each axis represented. Kendall's correlation coefficients (τ) are provided. PW = permanent water body.

Figure 3. Graphic overlay of *Eptesicus fuscus* on Bray-Curtis polar ordination plot. Size of the circles indicates proportion of captures/100 net nights for *E. fuscus* for that site among the 40 study sites. Scatterplots depict the relationship between *E. fuscus* and the explained variance for each axis represented. Kendall's correlation coefficients (τ) are provided. PW = permanent water body; RC = riparian corridor.
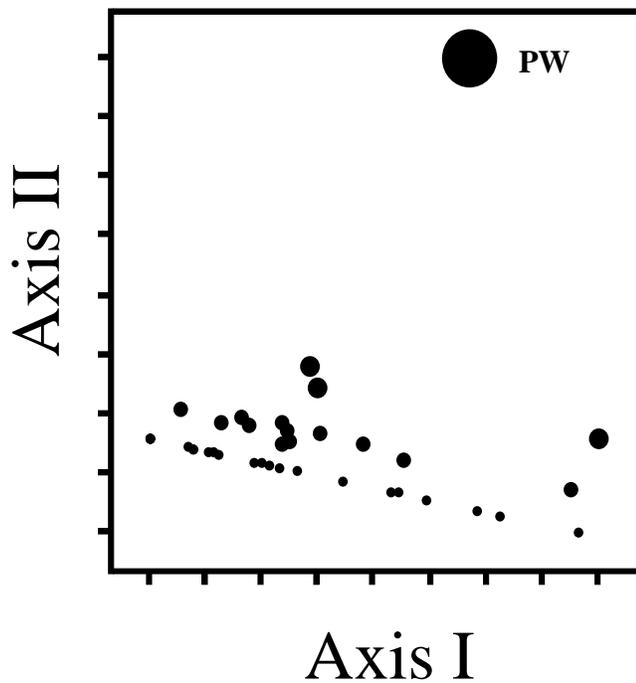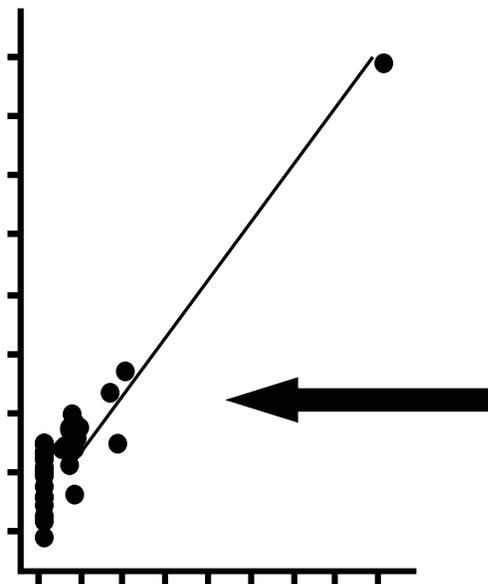
24
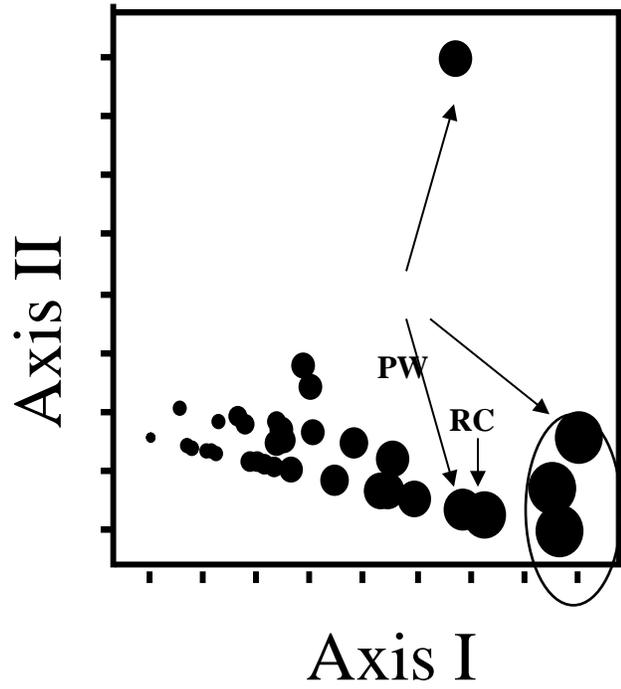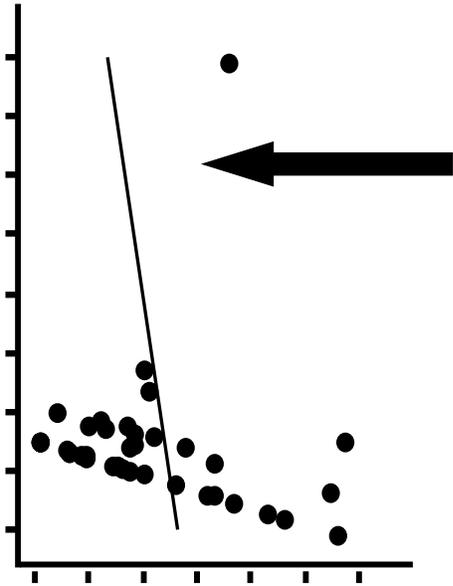
L. borealis
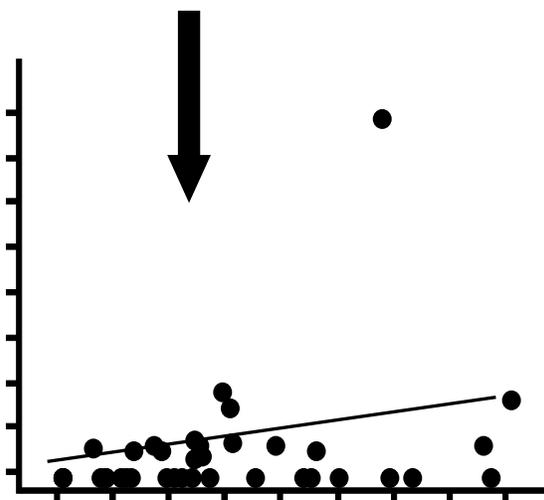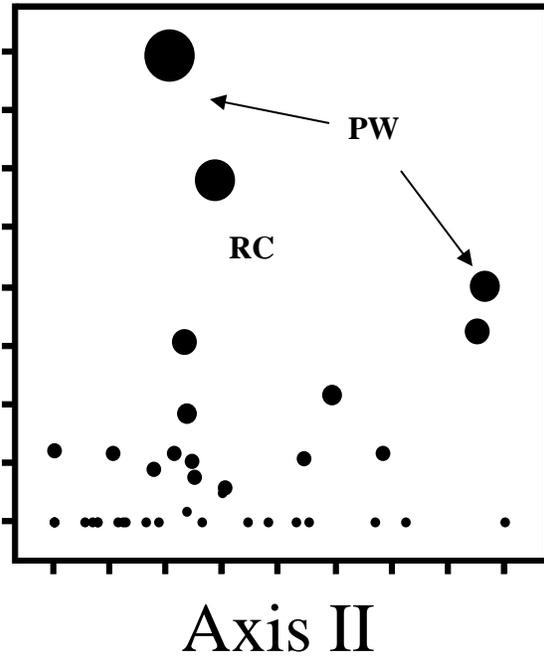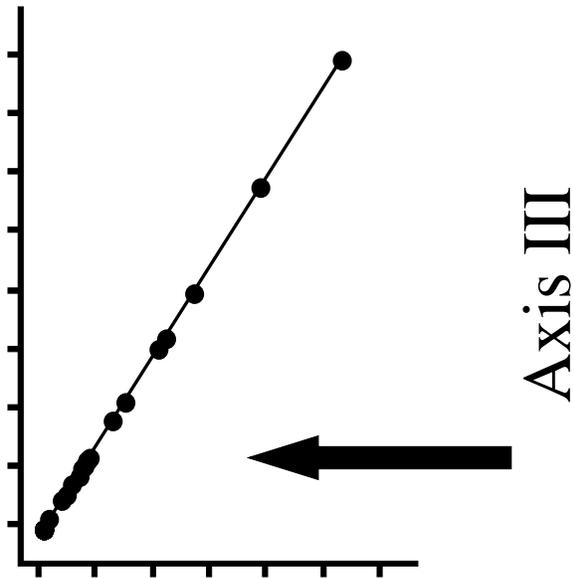
Axis I: $r = 0.998$
Axis II: $r = 0.346$
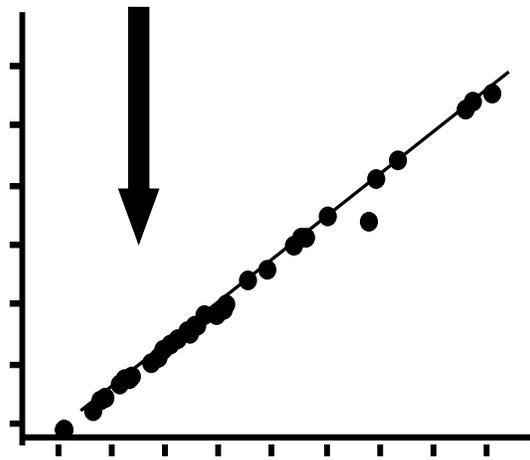
P. subflavus

Axis I: $\tau = 0.251$
Axis II: $\tau = 0.554$

E. fuscus

Axis II: $\tau = 0.187$
Axis III: $\tau = 0.943$

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