

A comparison of bird foraging behavior in three Costa Rican forests

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Abstract: Environmental predictability and structural diversity may explain patterns of bird diversity in forests. We examined the diversity of exploited niches by observing bird foraging behavior in three Costa Rican forests. Contrary to our expectations, diversity of foraging strategies showed no consistent pattern across sites, although our predictions regarding use of specific foraging strategies were generally supported. We conclude that site-specific factors may be more important in determining foraging behavior than broad inter-site differences in season or forest structure.

Key Words: environmental predictability, niche, species diversity

INTRODUCTION

Many hypotheses have been proposed to explain why biodiversity is so much higher in tropical versus temperate regions. Bird diversity may increase with forest structural complexity, which is generally higher in the tropics (Orlans 1969). Niche specialization may increase with environmental predictability because more types of resources are available year-round (Karr 1971).

We tested whether bird foraging strategies, a measure of niche occupancy, are more diverse in environmentally predictable tropical forests, compared to more seasonal sites. We predicted that diversity of foraging strategies would be highest in an aseasonal lowland rainforest, in part because fruits are available throughout the year. We expected that a seasonally dry, deciduous forest would have relatively low diversity of foraging strategies. In this forest type we predicted that many birds would hawk (capture aerial insects in flight) because insects are visible in the open canopy during the dry season, and that gleaning from leaves (picking a stationary food item from the substrate while standing), would be infrequent.

METHODS

We observed bird foraging behavior at three Costa Rican forest sites differing in

extent of seasonality, an indicator of environmental predictability. Our methods followed those of Braman et al. (1998), who conducted a similar study. On 12 January 2003 we conducted observations at Palo Verde National Park in Guanacaste province, a seasonally dry forest with deciduous trees and low structural diversity. On 3 February we observed birds at Corcovado National Park, Puntarenas, a moist lowland forest with moderate seasonality. On 14 February we conducted observations at La Selva Biological Station, Heredia, a lowland rainforest with only mild seasonality. We did not collect data at the Monteverde Biological Reserve because of unfavorable weather conditions.

At each site between 06:00 and 10:00, three pairs of observers walked different routes in both forested areas and open areas, within 1.5 km of each biological station. We observed each bird encountered until it foraged or we lost sight of it. We recorded foraging maneuver type, foraging substrate and height stratum for each bird. We classified foraging maneuvers as glean (bird picks stationary food item from substrate while standing), hawk (bird flies and captures flying prey), hover (bird flies, hovers, and picks stationary prey from substrate), probe (bird probes into or pries up substrate), or snatch (bird flies and picks stationary prey from substrate). Foraging substrates were classified as air, tree bole, branch, flower, ground, or leaf. Vertical stratum was cat-

egorized as ground, understory/shrub, subcanopy, canopy, or air.

We calculated the Shannon-Wiener Diversity Index (H') to assess evenness of the foraging characteristics at each site. Because the number of categories ("richness") is fixed, higher values of H' indicate greater evenness among classes. Using approximations of the variance, we calculated the 95% confidence interval around each H' value. We also used a G-test to determine whether the three sites differed in their proportions of maneuver type, stratum and substrate.

RESULTS

Foraging maneuvers were most even at Palo Verde (Fig. 1; $H' = 0.69$), followed by La Selva ($H' = 0.56$), and Corcovado ($H' = 0.44$). The proportions of maneuver types varied among the three sites (Fig 2; $X^2 = 19.4$, $df = 8$, $P = 0.01$). We observed hawking twice as frequently at Palo Verde as at any other site.

Evenness of foraging substrate use

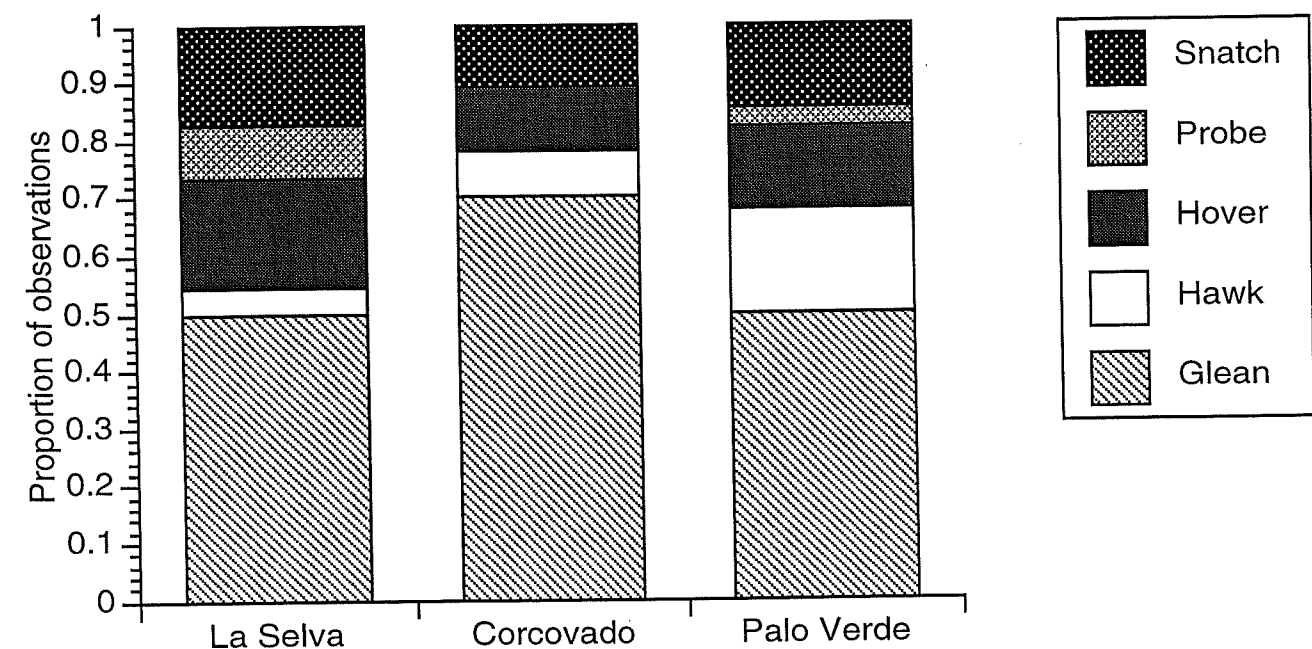


FIG. 1. Comparison of evenness of bird foraging maneuvers, substrates and stratum use in three Costa Rican forests. Error bars indicate 1 SD. Letters indicate values of H' that are different within each foraging class (95% confidence intervals that do not overlap).

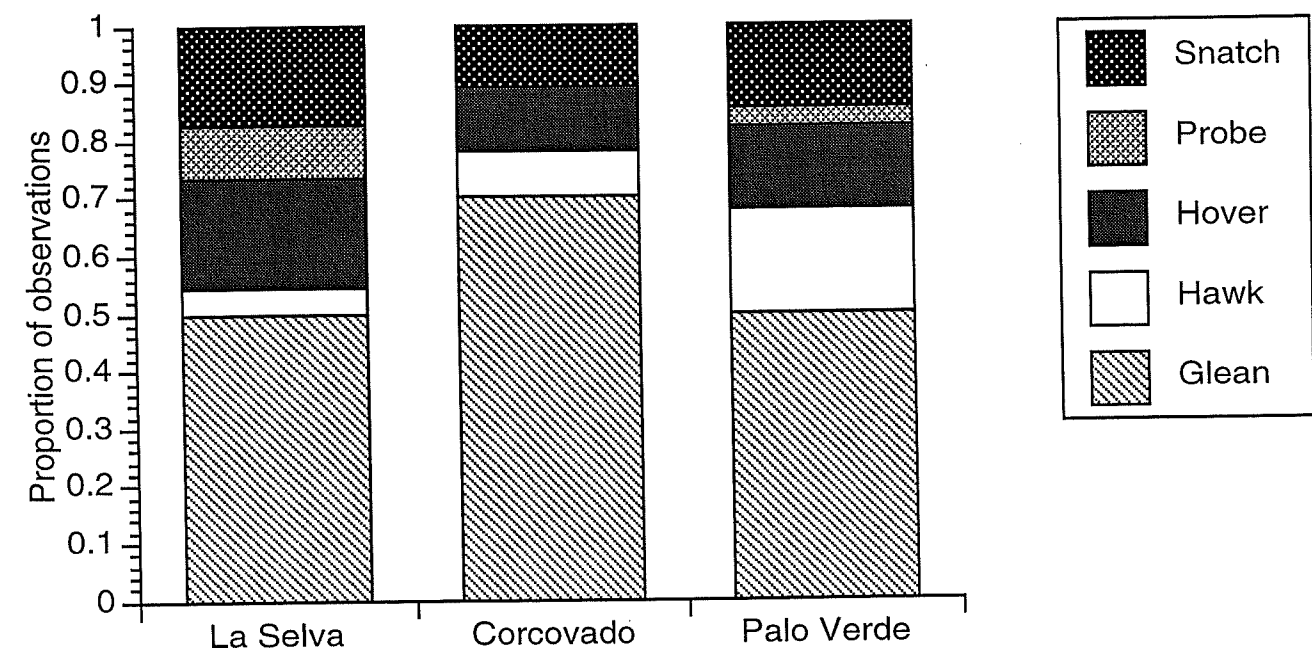


FIG. 2. The distribution of bird foraging maneuvers observed across three Costa Rican forests ($X^2 = 19.4$, $df = 9$, $P = 0.01$). See text for definitions of foraging maneuvers.

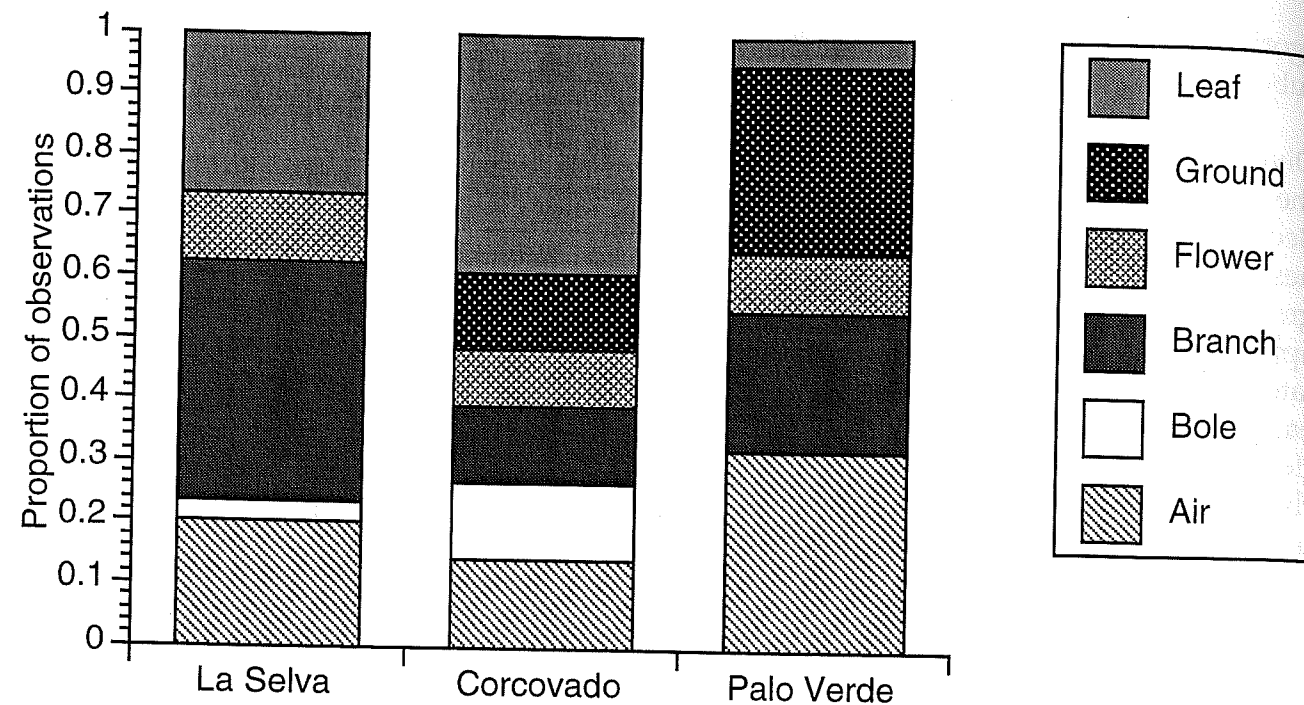


FIG 3. Proportions of foraging substrates used by birds in three Costa Rican forests ($X^2 = 19.4$, $df = 8$, $P < 0.001$).

DISCUSSION

was highest at Corcovado (Fig. 1; $H' = 0.83$), followed by Palo Verde ($H' = 0.75$), and finally La Selva ($H' = 0.61$). The distribution of substrate use varied among sites (Fig 3; $X^2 = 72.5$, $df = 8$, $P < 0.001$). Foraging on leaves was much less frequent at Palo Verde than at the other sites (5%), and ground foraging was especially frequent (31%). Considering only gleaning maneuvers, substrate use also differed among sites ($X^2 = 76.2$, $df = 6$, $P < 0.001$). Gleaning from leaves was very rare at Palo Verde (3% of observations). Branches and leaves combined were the most common gleaning substrates at Corcovado (64%) and La Selva (100%).

Evenness of stratum use was greatest at Palo Verde (Fig. 1; $H' = 0.75$), moderate at La Selva ($H' = 0.63$), and lowest at Corcovado ($H' = 0.54$). The distribution of stratum use was significantly different among the sites (Fig. 4; $X^2 = 32.6$, $df = 8$, $P < 0.001$). Ground was the most common stratum used at Palo Verde (34% of observations).

Diversity in foraging strategies across sites did not match our expectations. La Selva was the least seasonal site and had the highest structural diversity (Broughton et al. 1994), but was not the most diverse site in any category of foraging strategy, i.e. maneuver type, substrate, or stratum. Although Palo Verde is highly seasonal, we observed the most diversity in maneuvers and stratum use there. Leaf drop by deciduous plants at Palo Verde may actually increase the evenness of substrates available, because when leaves are present, they make up such a high surface area as to make other substrates relatively uncommon.

Our most specific predictions about foraging strategies were generally supported. Gleaning from branches and leaves was most common at La Selva and least common at Palo Verde. Because these maneuvers are used by frugivores, we would expect them to be highest at aseasonal sites. As predicted, hawking was

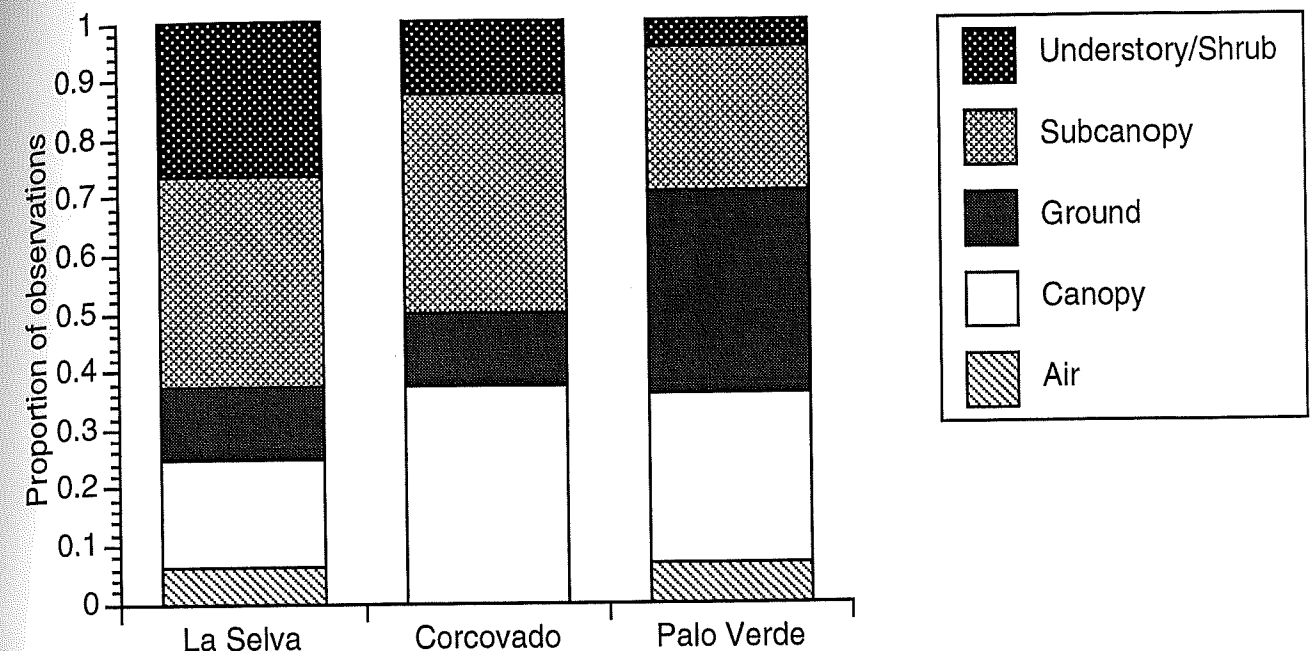


FIG 4. Proportion of forest strata used by birds foraging in Costa Rican forest sites ($X^2 = 32.6$, $df = 8$, $P < 0.001$).

LITERATURE CITED

most frequently observed at Palo Verde, where it may have been facilitated by the open forest structure.

Overall, we did not find a clear influence of environmental predictability on the diversity or distribution of foraging strategies among Costa Rican forests. Our results do not support the hypothesis that less seasonal habitats and more structurally diverse forests support greater diversity. We conclude that site-specific factors may be more important in determining foraging behavior than broad, inter-site differences in seasonality or forest structure. Future studies that combine data sets from multiple years to examine combinations of maneuver, substrate and stratum, would improve our understanding of the diversity of foraging niches used across Costa Rican forests.

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