Foraging Behavior and Coexistence of Two Sunbird Species in a Kenyan Woodland

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ABSTRACT

We investigated the mechanism of coexistence of the rare Amani Sunbird (*Hedydipna pallidigastra*) and the widespread Collared Sunbird (*H. collaris*), within *Brachystegia* woodland in the Arabuko-Sokoke Forest, Kenya. We compared how prey abundance and search strategies affect resource exploitation by the two species. We used foraging theory to direct our measures of feeding activities as influenced by sunbird species, tree species and foraging height. We evaluated invertebrate abundance among tree species at different heights within trees. The Collared Sunbird primarily used the understory, and the Amani Sunbird primarily used the upper-canopy. Overall, the rate of prey attacks per flight of the Amani Sunbird was 2.8 times greater than that of the Collared Sunbird. The Amani Sunbird, however, used increased search and attack rates in the understory compared with the mid- and upper-canopies, but the Collared Sunbird foraged similarly throughout all strata. We hypothesize that the increased foraging rate of the Amani in the understory reflects increased foraging costs due to interference from the Collared Sunbird in that stratum. Furthermore, the Collared Sunbird exploits rich patches by moving frequently from place to place. The Amani Sunbird forages slowly, with reduced travel rates, and with a greater number of prey captures within a patch. Arthropod density did not differ among the vegetative strata, but was higher in *Brachystegia spiciformis* and *Hymenaea verrucosa* than in six other tree species. We hypothesize that the Amani Sunbird appears dependent upon continued tall *B. spiciformis* trees within the canopy of the Arabuko-Sokoke Forest.

Key words: Arabuko-Sokoke forest; *Brachystegia*; competition; foraging rates; *Hedydipna*; *Hymenaea*; invertebrates.

A CENTRAL GOAL IN ECOLOGY IS TO DETERMINE THE FACTORS UNDERLYING THE ABUNDANCE AND DISTRIBUTION OF SPECIES. One approach correlates characteristics of the physical environment with the presence of particular species (MacArthur & MacArthur 1961, MacArthur 1964, Willson 1974, Roth 1976). Although such studies identify biologically meaningful correlations or environmental factors, the processes producing the patterns remain a matter of conjecture (Holmes 1980). Furthermore, the correlated factors may not be the actual environmental properties that influence the species presence and abundance.

A more mechanistic approach to understanding processes that influence species abundance and presence involves quantifying how animals actually use their habitat. Such studies generally examine foraging behavior of individual species (Parrish 1995, Robakiewicz & Daigle 2004) or co-occurring species (Fitzpatrick 1981; Robinson & Holmes 1982, 1984; Sodhi & Paszkowski 1995; Cueto & Lopez de Casenave 2002). Such studies, resulting in detailed descriptions of resource exploitation systems (Robinson & Holmes 1982, 1984), have identified critical habitat elements in a wide variety of taxa in both terrestrial and aquatic environments. For birds, structural complexity of habitats influ-

ences foraging efficiency (Robinson & Holmes 1984) and predation risk (Brown et al. 1997, Whelan et al. 2003). In some cases, fine scale structural differences among different plant species can have strong effects by influencing the birds' encounter rates on invertebrates (Greenberg & Gradwohl 1980, Robinson & Holmes 1982, Parrish 1995), the relative use of different foraging maneuvers (Holmes & Robinson 1981, Whelan 2001), and the forager's own risk of predation (Brown 1988).

Habitat structural complexity affects the costs of foraging, including costs associated with predation, metabolic costs of foraging, and opportunity costs of foregoing alternative activities (missed opportunities: Brown 1988). Here we build upon these previous approaches by using foraging theory as the conceptual framework linking resource exploitation systems with habitat selection and mechanisms of coexistence (Kotler & Brown 1999). Placing resource exploitation systems within an explicit foraging theory context allows them to be understood predicatively rather than simply retrospectively.

Below we develop our conceptual framework, in which we use foraging theory to derive *a priori* predictions regarding how prey abundances and search strategies affect resource exploitation and coexistence. We then apply the conceptual framework to two congeneric sunbird species, the rare Amani Sunbird (*Hedydipna pallidigastra*) and the widely distributed Collared Sunbird (*Hedydipna collaris*). We conclude by showing how the different

resource exploitation system of these two sunbirds reveals their habitat preferences and mechanism of coexistence.

The Amani Sunbird is globally and regionally vulnerable, inhabiting just two sites in Tanzania and one site in Kenya (Collar et al. 1994, Bennun & Njoroge 1999). An Amani Sunbird feeds singly, in a pair or in family parties with other sunbirds or as part of a mixed species flock (Fry et al. 2000). When feeding, they move continuously, searching leaves for arthropods and visiting flowers. The Collared Sunbird is common and widespread in sub-Saharan Africa across a variety of forest and woodland habitats (Zimmerman et al. 1996). They usually occur in pairs while gleaning insects from foliage, but larger numbers may gather at flowering trees. For both sunbird species, males possess distinctive and different plumage. During this study (June to October 2003), the two species fed almost exclusively by gleaning arthropods from foliage. We rarely observed individuals capturing insects from flowers, and we never observed any individuals feeding on nectar. The two sunbirds foraged preferentially in Brachystegia spiciformis and Hymenaea verrucosa (both Fabaceae, Caesalpinioideae), which were in bloom during the study period. In Arabuko-Sokoke, B. spiciformis grows up to 25 m (Chudnoff 1984). Little is known about its regeneration requirements, annual seed production, or seed consumers within the Arabuko-Sokoke Forest (Oyugi et al. 2007). However, its phenology, flowering and fruiting, seed germination and regeneration, growth and mortality are known for the Miombo Woodland of Zambia and Zimbabwe (Chidumayo & Frost 1996). H. verrucosa is primarily evergreen and may grow to a height of 25 m emerging above the forest.

CONCEPTUAL FRAMEWORK.—The interpretation of feeding observations, time budgets, and foraging rates through the lens of foraging theory can be used to elucidate habitat requirements, species interactions, and potential mechanisms of coexistence. Resource exploitation systems are thus derived from specific morphological and behavioral traits of foragers that determine patterns of movement through the available habitats. The interaction between foraging behavior and habitat complexity determines the set of resources consumed from some subset of available habitats (Robinson & Holmes 1982).

We consider the foraging behavior of birds seeking insects in a highly heterogeneous, forested environment. In such environments, different tree species, with their contrasting foliage structures may constitute distinguishable resource patches (Airola & Barrett 1985, Whelan 2001, Oyugi 2005). At a finer scale, arthropods may also be patchily distributed within a given tree. For instance, larval Lepidoptera were highly clumped within the lower and upper canopies of each of the dominant tree species within a northern hardwood forest in New Hampshire, U.S.A. (Holmes & Schultz 1988).

We develop predictions relating foraging rates to prey density and sunbird search strategies (Table 1). Bird foraging reflects food availability for birds between seasons (Lovette & Holmes 1995) and between habitats (Lyons 2005). Foraging also provides insight into coexistence mechanisms (Latta & Wunderle 1996). We focus on foraging movements within and between patches.

TABLE 1. *Predicting how foraging rates in sunbirds change with prey availability and predator search strategy. Foraging rates are established on the basis of the number of foraging motions performed/time.*

Variables	Predictions for search and attack rates			
	Attack rate	Hop rate	Flight rate	Attacks/flights (food items per patch)
(a) Prey abundance				
Low prey abundance	Low	High	High	Low
High prey abundance	High	Low	Low	High
(b) Search strategy				
Thorough foragers	—	Low	Low	High
Cursory foragers	—	High	High	Low

We categorize different foraging activities using standard descriptions of avian foraging behavior (Remsen & Robinson 1990). We assume that foraging activities taking place within an individual tree constitute a foraging bout (Bell et al. 1990). Within each foraging bout, two types of search movements occur: (1) hops, in which a bird rapidly moves within branches and twigs when searching for prey; and (2) flights, in which a bird uses flight to move between branches or twigs. We assume that hops reflect movements within a food patch (within patch) and flights reflect movements between food patches (between patch). Search movements often result in prey attack. Attack behaviors include gleaning, in which a hopping bird picks a food item from a nearby substrate, and hang gleaning, in which a bird flies to a leaf and hangs from it while plucking prey. The variations in these activities may result from resource heterogeneity or patchiness (Kotler & Brown 1988), which exists at a variety of spatial scales within forests.

Specifically, we expect that when foraging costs are the same, a forager should attempt to leave all patches, rich or poor, at the same quitting harvest rate—the harvest rate at which gains equal costs (Brown 1988). Hence, when other foraging costs, such as predation or exploitative and interference competition, are negligible, a forager will devote more search effort in richer than poor patches (Charnov 1976). Mean attacks rates should reflect patch richness, or how often suitable prey are encountered (Robinson & Holmes 1984): a sunbird in an area of high prey density should decrease hop and flight rates and increase prey attack rate, resulting in high attack/hop (food items per search movement) and attack/flight ratios (food items per patch). Similarly, if prey density varies among microhabitats, such as the understory or canopy of a forest, we expect higher foraging rates where prey density is greatest. We expect continued high foraging rates as long as prey density is sufficient to offset costs.

Furthermore, foragers competing exploitatively for a common resource that is patchily distributed may coexist if there is a trade-off between foraging efficiency and the cost of travel between patches (Brown 1989, Richards et al. 2000). Thus two strategies might be envisaged: one which trades off a low forag-

ing efficiency with frequent movements among many patches (high hop and flight rates) and which we refer to as 'cursory foraging'; and a second that exploits food patches more efficiently and remains in patches longer (low hop and flight rates, more food items per search movement and more food items per patch), a strategy we refer to as 'thorough foraging'. Cursory foragers select high-quality patches, but consume few food items per search movement and per patch, and have higher quitting harvest rates (Brown et al. 1997), though gain priority access to rich patches via interference competition (Persson 1985). Thorough foragers, on the other hand, are more effective exploitative competitors (Persson 1985).

We use foraging activities as indicators of the relative ease or difficulty of obtaining adequate food. We consider how foraging rate changes with prey abundance and search strategy. Foraging rates are established on the basis of the number of foraging motions performed per unit time by individual birds (Robinson & Holmes 1982, Robinson & Holmes 1984, Lyons 2005). We use rates of search movements and rates of attack as measures of foraging behavior and habitat relationships.

METHODS

STUDY SITE AND FOREST STRUCTURE.—The Arabuko-Sokoke Forest lies between 39°50' E and 39°40' E and 3°10' S and 3°30' S along the eastern Kenyan coast with flat topography at 60 m asl. It is the largest extant fragment of a forest that once covered much of the east African coast (Bennun & Njoroge 1999). Annual rainfall occurs as long rains from April to June and short rains from November to December. A dry season extends from December to March. The mean annual rainfall ranges from 600 mm in the northwest part to 1100 mm at the Gedi station in the northeast (Muchiri et al. 2001). Arabuko-Sokoke Forest is ranked by Birdlife International as the second most important forest for bird conservation in mainland Africa (Collar & Stuart 1988). Six globally threatened bird species, including the Amani Sunbird occur in Arabuko-Sokoke Forest. In addition, six taxa of butterflies endemic to the East African coast are present, as well as three rare species of mammals (Collar & Stuart 1988).

We conducted this study during the short rains, June to October 2003, within the Brachystegia woodland (7636 ha), which runs in a strip at the center of the Arabuko-Sokoke Forest, Kenya. This is relatively open habitat dominated by B. spiciformis. The Arabuko-Sokoke Forest has two other distinct habitat types: Mixed forest (6865 ha) which is relatively dense, tall and undifferentiated, with a diversity of tree species, and Cynometra forest and thicket (26,785 ha) dominated by Cynometrawebberi, Manilkara sulcata and Oldfieldia somalensis. Amani Sunbird occurs only in the Brachystegia woodland within the Arabuko-Sokoke Forest (Collar & Stuart 1988).

During this study, 22 tree species were identified, but 88.6 percent of foraging activity occurred in just B. spiciformis and H. verrucosa. Only these two species provided a sufficiently large sample size of foraging activities for the subsequent analyses of foraging behavior.

BIRD MORPHOLOGY.—Differences in morphology among birds are often associated with the profitability of different foraging behaviors (Grant et al. 1976). Bill structure influences resource use (Grant et al. 1976), body mass may relate to energetic profitability, species dominance and interference competition (Pimm & Pimm 1982), and tarsal length may be associated with different feeding techniques (Patridge 1976, Alatalo & Moreno 1987, Parrish 1995). We obtained data on body mass (recorded and scribed on specimen tags when fresh by the collectors), bill length and tarsal measurements from specimens at the American Museum of Natural History, Durban Natural Science Museum, National Museums of Kenya, and the Smithsonian Institution. Relative tarsal lengths were obtained by dividing absolute tarsal length with the cube root of body mass (tarsal length/body mass$^{1/3}$).

BIRD FORAGING MANEUVERS, SEARCH AND PREY ATTACK PATTERNS.— We collected foraging observation from June through October 2003, between 0600 and 1100 h, when birds were most active (pers. obs.). We systematically walked within the Brachystegia woodland and located birds by sound or visually. Once actively foraging birds were encountered, we observed them for as long as they remained within the same individual tree. We ignored additional trees used by the same bird as subsequent use of other trees may not be independent of the initial tree used by the bird under observation (Bell et al. 1990). When birds were encountered in pairs, we recorded foraging data on only one individual of the pair.

For each foraging bout, we categorized foraging behavior using terminologies in Remsen and Robinson (1990). We recorded the number of searching movements made by the bird while searching for prey and the number of attack maneuvers directed toward prey. We identified trees within which birds foraged to species, and we estimated foraging height to the nearest 1 m. We measured the time during which an individual forager was in view with a stopwatch. The observer reported a running commentary on bird foraging activities to a second person, who recorded the sequence of events.

We classified search movements as hops, in which observed birds shift their position without extending their wings, and flights, in which birds change patches by flying. We obtained rates of movements per minute (Robinson & Holmes 1984), by tallying the numbers of each type of movement (hops or flights) and dividing it by the duration of the foraging bout (=hops or flights per minute) for each sunbird species.

We categorized two attack maneuvers as glean, in which a perched or hopping bird takes a prey from a nearby substrate, and hang-glean, in which a bird hangs upside down and tears apart or in some way manipulates the substrate. We used attack rates as an index of encounter rate with suitable prey (Robinson & Holmes 1984). Hang gleans occurred much less frequently than gleans. We obtained attack rates by tallying the number of glean and hang gleans and dividing this total by the duration of the foraging bout (=glean+hang glean per unit search time in minutes). We then obtained the ratio of attacks to hops to give the overall ease of finding food within a patch (food items per unit search movement), and the ratio of attacks to flights to give

the overall ease of finding food between patches (food items per unit search movement).

AGGRESSIVE INTERACTIONS..—We observed aggressive interactions between Amani and Collared Sunbird individuals when an individual of one species appeared to displace an individual of the other species from a foraging patch. For each interaction, we recorded which species was the aggressor, the height of the displacement, and the number of displacements.

FOOD RESOURCE ABUNDANCE AND DISTRIBUTION.—We evaluated whether invertebrate abundance in different tree species and at different tree heights influenced bird foraging techniques. We quantified abundance and distribution of invertebrates residing on leaves and associated twigs of the eight most common tree species. The surveys were conducted between 0600 and 1100   h, the period when birds were most active. The data were obtained from 21 individuals of each tree species for a period of 3 weeks between August and September 2003. Because birds foraged at both upper and lower levels of the trees, we used a full-body safety harness to climb trees and collect invertebrates within the trees' mid and upper canopies. We estimated height from which invertebrates were collected to the nearest 1 m, and then placed these into three height groups: understory 0–10 m; mid-canopy 11–20 m and canopy >20 m (Remsen & Robinson 1990). For the lower level we collected material while standing next to the tree. From each individual tree, we selected a branch and associated leaves for collection. A plastic bag (51   cm long and 61   cm wide) was placed around the branch, sealed, and then the branch was carefully cut taking care not to dislodge the invertebrates (see Ausden 1990 for similar procedure). The bags were lowered to the ground and transported to our residence where invertebrates were carefully removed, preserved in alcohol, labeled and later transported to the Entomology Department of the National Museums of Kenya. All invertebrates were counted and identified to the Family level (with the exception of spiders, Araneae and woodlice, Isopoda). We standardized abundances of invertebrates on the different tree species by reporting abundances per unit leaf area. Leaf areas were measured with model LI-COR-3100 area meter. Invertebrate density was expressed as numbers per cm^2 of leaf surface area, which eliminates the effects of differences in individual leaf sizes among the tree species (Holmes & Robinson 1981). Here we summarize the densities of all invertebrates (Araneae, Formicidae, Curculionidae, Gryllidae, Blattellidae, Geometridae and Isopoda).

STATISTICAL ANALYSIS.—All statistical analyses were conducted using SYSTAT v.10.2 (SPSS Inc. 2000). We report values for bird morphology as mean ± SE, and invertebrate densities, foraging movements and attack methods as mean ± SE. We used two-sample t-tests to determine differences in the morphology of Amani and Collared Sunbird. We used a χ^2-test of heterogeneity to compare the distribution of foraging bouts by height in tree for the two sunbird species. To determine whether the sunbirds partitioned time of day for foraging, we compared the mean time

of a foraging bout between the sunbirds species using a t-test. We used multivariate analysis of variance (MANOVA) to examine the effects of bird species, tree species and foraging height on the foraging behaviors. Dependent variables were hops per minute, flights per minute, attacks per hop and attacks per flight. Independent variables were bird species, tree species, foraging height, and interactions of bird species × tree species, bird species × foraging height and tree species × foraging height. A significant or nearly significant ($P<0.10$) effect in the MANOVA was subsequently examined with a univariate F-test to investigate the specific treatment effect on the appropriate dependent variable. We used a goodness of fit test to determine if the frequency of displacement differed between the two species. We used an unpaired t-test with unequal sample sizes to compare the mean heights at which Collared Sunbirds displaced Amani Sunbirds ($N=19$) with those at which Amani Sunbirds displaced Collared Sunbirds ($N=3$). We used two-factor ANOVAs to examine effects of tree species and tree height on invertebrate prey. Independent variables were tree species and tree height. The dependent variable was invertebrate abundance.

RESULTS

BIRD MORPHOLOGY.—There were no differences in mean bill length between the two species, but significant differences occurred in body mass and absolute tarsus length (Table 2). The Collared Sunbird has a significantly larger body mass and a significantly longer absolute tarsal length than the Amani Sunbird. After adjusting for body mass, however, there are no differences in tarsal length between the species.

BIRD FORAGING MANEUVERS, SEARCH AND PREY ATTACK PATTERNS.—Both the Amani and the Collared Sunbird foraged predominantly in B. spiciformis (80% and 70%, respectively). The Amani Sunbird foraged more at mid-canopy and canopy levels (mean=19.8 ± 1.08 m) while the Collared Sunbird foraged more at mid-canopy and understory (mean=15.4 ± 1.9 m) (Fig. 1, =26.11, $P<0.01$). There was no significant difference in mean time of foraging bouts for the two sunbirds species ($t=1.67$, df=160, $P>0.10$).

TABLE 2. *Morphological characteristics of the Amani Sunbird and the Collared Sunbird. Only specimens from Arabuko-Sokoke Forest are included in the analysis. The measurements were obtained from collector tags on specimens at the American Museum of Natural History, Durban Natural Science Museum, National Museums of Kenya and the Smithsonian Institution.*

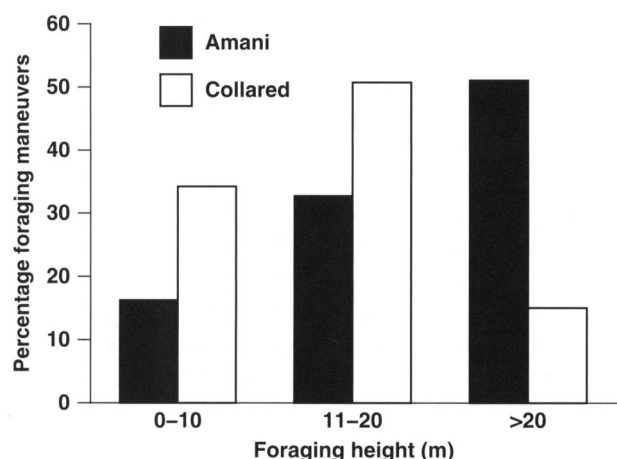| Variable	Amani Sunbird ± SE (N)	Collared Sunbird ± SE (N)	t	df	P
Body mass (g)	6.13 ± 0.42 (13)	6.74 ± 0.08 (42)	2.19	53	0.03
Bill length (mm)	12.73 ± 0.24 (15)	12.85 ± 0.18 (14)	0.44	27	0.66
Tarsal length (mm)	14.73 ± 0.39 (15)	15.81 ± 0.29 (21)	2.27	34	0.03
Relative leg length (tarsus/body mass$^{1/3}$)	8.11 ± 0.14 (13)	8.51 ± 0.19 (16)	1.67	27	0.11

FIGURE 1.   The percentage of foraging bouts by the Amani Sunbird and the Collared. Sunbird within three vegetation strata: 0–10 m=understory (N=12 Amani and 42 collared); 11–20 m=mid-canopy (N=61 Amani and 44 Collared); 20 m=canopy (N=27 Amani and 11 Collared). The Amani Sunbird foraged predominantly within the mid-canopy and the canopy strata while Collared Sunbird foraged predominately within the mid-canopy and the understory (χ_2^2=26.11, P<0.01).

The foraging movements and attack methods of the Amani Sunbird and Collared Sunbird were mostly similar and they varied little with tree species and foraging height. In the MANOVA, there was no significant main effect of bird species (Wilk's $\lambda_{5,156}$=0.963, P=0.31), but in the associated univariate F tests, attacks per flight differed significantly between species ($F_{1,160}$=4.7, P=0.04). Amani Sunbird had 2.8 times more prey attacks per flight than the Collared Sunbird (Amani: 3.72 ± 0.67 attacks/flight; Collared: 1.24 ± 0.84 attacks/flight). There was no significant effect of tree species (Wilk's $\lambda_{5,156}$=0.982, P=0.72), nor foraging height (Wilk's $\lambda_{10,\ 312}$=0.982, P=0.98). There was no significant interaction of bird species × tree species (Wilk's $\lambda_{5,156}$=0.987, P=0.83), nor between tree species × foraging height (Wilk's $\lambda_{10,312}$=0.969, P=0.89). There was a nearly significant interaction of bird species × foraging height (Wilk's $\lambda_{10,312}$=0.90, P=0.08). Univariate tests indicated that this interaction was due to differences among hops/min ($F_{2,160}$=2.8, P=0.06), search flights/min ($F_{2,160}$=4.9, P<0.01), and prey attacks/min ($F_{2,160}$=4.9, P<0.01). In the Amani Sunbird, hops/min, flights/min and attacks/min within the understory were almost three times those at the mid-canopy and the canopy, whereas in the Collared Sunbird, the rates were low and virtually uniform across the vertical strata (Fig. 2).

AGGRESSIVE INTERACTIONS.—We observed Collared Sunbirds displacing Amani Sunbirds from their feeding sites on 22 occasions. In contrast, we observed Amani Sunbirds displacing Collared Sunbirds on only three occasions (χ_1^2=14.4, P<0.001). Displacements of Amani Sunbirds by Collared Sunbirds (mean=14.2 ± 0.8 m; range=8–20 m) occurred at significantly lower heights (unpaired t-test, t_{20}=3.49, P<0.003) than those in
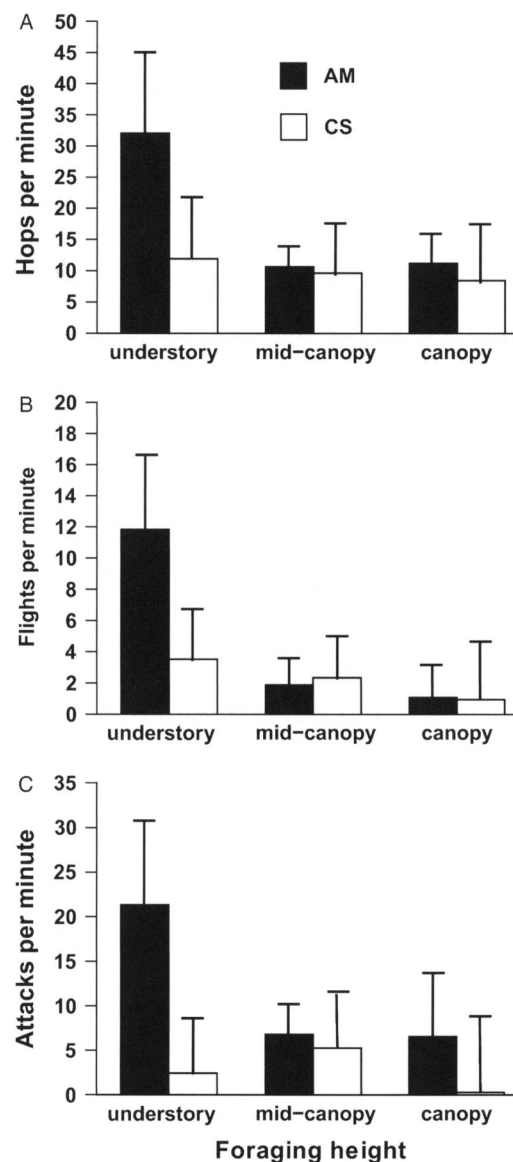

FIGURE 2.   Rates of movement ($\bar{x}$ ± SE) by sunbirds at the tree understory, mid-canopy and the canopy. (A) Rate of movement within tree branches, corresponding to within micropatch movements (hops/min; $F_{2,160}$=2.8, P=0.06); (B) Rate of movement between tree branches, corresponding to micropatch change rate (flights/min; $F_{2,160}$=4.9, P<0.01); and (C) prey attack rate (attacks/min; $F_{2,160}$=4.9, P<0.01). Rates of both foraging movements and attack rates of the Amani Sunbird increased when foraging within the understory. These rates were low and uniform across strata for the Collared Sunbird.

which Amani Sunbirds displaced Collared Sunbirds (mean=21.67 ± 1.7 m; range=20–25 m).

FOOD RESOURCE ABUNDANCE AND DISTRIBUTION.—Invertebrate densities varied among tree species ($F_{2,\ 162}$=7.12, P<0.01). Mean density of invertebrates was higher in H. verrucosa and B. spiciformis compared with each of six other tree species (Fig. 3). The other tree species were Julbernardia magnistipulata, Manilkara sansibarensis,
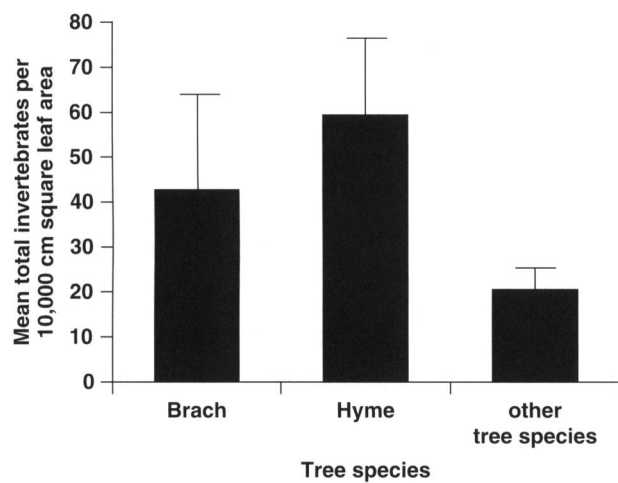
FIGURE 3.   The relative density of invertebrates ($\bar{x} \pm$ SE) among tree species ($F_{2, \ 162}$=7.12, P<0.01). Brach, *Brachystegia spiciformis*; Hyme, *Hymenaea verrucosa*. Other tree species include six tree species combined; *Julbernardia magnistipulata, Manilkara sansibarensis, Mimusops obtusifolia, Lannea schweinfurthii, Afzelia quanzensis* and *Strychnos madagascariensis*.

Mimusops obtusifolia, Lannea schweinfurthii, Afzelia quanzensis and *Strychnos madagascariensis*. Height from which invertebrates were collected had no significant effect on invertebrate density ($F_{2, \ \ 162}$=2.10, P=0.13).

DISCUSSION

We used a comparison of the foraging behaviors and resource exploitation systems of Amani and Collared Sunbirds to gain insights into mechanisms allowing the two congeners to coexist within the Arabuko-Sokoke Forest. We used foraging theory as a conceptual framework (Table 1) to guide our quantification of foraging behavior. One species, the Amani Sunbird, has a highly restricted distribution, found only in Arabuko-Sokoke Forest in Kenya, and two montane forests (East Usambaras and Ud-zungwa escarpment) in Tanzania. The other species, the Collared Sunbird, is widespread throughout Africa occurring in diverse habitats below 2800 m elevation. This regional distributional pattern of the two species is mirrored within the Arabuko-Sokoke Forest as the Amani Sunbird exhibited a narrower realized niche than the Collared Sunbird. The Amani Sunbird foraged predominantly in the upper canopy, and it foraged almost exclusively on a single tree species, *B. spiciformis*. In contrast, the Collared Sunbird foraged predominantly in the understory and mid-canopy, and it used two tree species extensively for foraging, *B. spiciformis* and *H. verrucosa* (Oyugi 2005). Overall, the Amani Sunbird exhibited higher search and prey attack rates than the Collared Sunbird. The differences between the two sunbird species in distribution and habitat use emerge from differences in their resource exploitation systems, which in turn may reflect differences in foraging costs and aptitudes. In the following, we explain how the foraging costs of Amani and Collared Sunbirds may emerge from differ-

ences in their search and attack strategies and morphology, and from interspecific interactions.

SEARCH AND ATTACK STRATEGIES.—The most striking difference in foraging behavior between the Amani Sunbird and the Collared Sunbird was the number of attacks per flight, a metric that reflects the ratio of prey consumption rate to frequency of movement among foraging patches. The Collared Sunbird, with its low attacks per patch, suggests a strategy of increased patch movement and cursory exploitation of invertebrates within a patch. In contrast, the Amani Sunbird, with its high attacks per patch, suggests a strategy of reduced travel and more thorough exploitation of invertebrates within a patch. The two species appear to coexist when the cursory feeder (Collared Sunbird) moves among patches faster and depletes patchily distributed resources to a lesser extent than the thorough feeder (Amani Sunbird).

FEEDING RATES AND HEIGHT SEGREGATION.—The two sunbird species used different microhabitat-specific feeding rates when foraging within the different foliage strata. The search and prey attack rates of the Amani Sunbird were three times greater within the understory than within either the mid- or upper-canopies. In contrast, the Collared Sunbird exhibited virtually the same feeding rate across all three of these foliage strata. These findings could suggest that the understory presents the Amani Sunbird with a more conducive foraging environment than the mid- and upper-canopies, whereas there are no such differences for the Collared Sunbird. Prey abundance did not, however, differ between the understory and the upper canopy. Moreover, if the understory was a better foraging environment, we would expect the Amani Sunbird to spend its greatest amount of time foraging there rather than in the mid- and upper-canopies, as we observed.

Based on foraging theory, we expect high feeding rates in patches or microhabitats where prey abundances are high (Charnov 1976). Alternatively, patches or microhabitats with high foraging costs will be utilized by a forager only when it supports sufficiently high harvest rates to offset the costs (Brown 1988). Given that we found no difference in prey abundances among the vegetative strata, we attribute the high foraging rate of the Amani Sunbird in the understory to increased foraging costs, and the lower foraging rates in the upper strata to reduced foraging costs. We hypothesize that the greater foraging costs for the Amani Sunbird in the understory arises from the dominance relationships between the two species. Based on aggressive interactions, the larger Collared Sunbird is dominant over the smaller Amani. Thus, we hypothesize that interference competition from the Collared Sunbird in the understory raises the foraging costs of the Amani Sunbird within that stratum, and this elevated foraging cost drives the increased search and prey attack rates exhibited by the Amani when foraging there. The observed displacements of Amani Sunbirds by Collared Sunbirds occurred at the lower strata, offering support to this idea. In contrast, the Collared Sunbird appears to experience similar foraging costs across all strata while biasing its overall foraging activity to the understory and mid-canopy strata.

Morse (1974) noted that if an interspecific dominance hierarchy exists, a subordinate should shift its resource use to decrease overlap with the dominant. The dominance hierarchy may manifest via outright aggression, in which case the dominant displaces the subordinate (Morse 1976, Sherry 1979, Alatalo 1981) or avoidance of the dominant by the subordinate in areas in which the dominant is present (Morse 1974). In accordance with these expectations, larger species are typically dominant to smaller ones (Morse 1974, Schoener 1983, Alatalo & Moreno 1987). In Europe, several species of tits (*Parus* spp) frequently coexist, forming mixed species flocks (Norberg 1979). The formation of these mixed-species flocks is permitted because each species restricts its foraging to a subset of available foliage volume (Alatalo *et al.* 1986). For example, in an aviary experiment, both the smaller Coal Tit (*Parus ater*) and the larger Willow Tit (*Parus montanus*) foraged preferentially on inner tree parts when each species foraged in the absence of the other (Alatalo & Moreno 1987). But when individuals of the two species were together, Willow Tits retained their preference for inner tree parts, while Coat Tits altered their foraging, taking an increasing amount of prey from outer tree parts. Similarly, in a removal experiment conducted in a coniferous forests, smaller Coal Tit (*P. ater*) and Goldcrest (*Regulus rugulus*) shifted their niche to inner canopies when larger Willow Tit (*P. montanus*) and Crested Tit (*Parus cristatus*) were removed, but used outer tree layers in their presence (Alatalo *et al.* 1985).

A similar relationship may hold for the Amani and Collared Sunbirds within Arabuko-Sokoke Forest. Based on their similar morphologies and close relatedness, the two species should experience strong competition for food resources. The larger Collared Sunbird is behaviorally dominant over the Amani Sunbird, making their competition asymmetric. Hence, much like the willow tit in the above examples, we hypothesize that the Amani Sunbird biases its foraging to the upper canopy to avoid interference from the Collared Sunbird (also see Robinson 1981). Unfortunately, given the conservation status of the Amani Sunbird, experimental manipulations are not permitted.

Alternatively, some other factor such as habitat specific predation risk, or interference from some other bird species could explain the pattern of foraging costs. While a viable alternative, we place less credence on this hypothesis as it would require that the predator or competitor influence the two sunbird species in very different ways. We feel it is more parsimonious to hypothesize that the Collared Sunbird poses a direct foraging cost on the Amani Sunbird.

In conclusion, this study provides critical information on the relationship between foraging behavior, habitat characteristics and morphological traits in a rare and a common sunbird species. Cursory foragers (Kotler & Brown 1988, Brown 1989) like the Collared Sunbird tend to be less efficient foragers that gain priority to high-quality patches and habitats through interference competition (Persson 1985). Thorough foragers (Kotler & Brown 1988, Brown 1989) like the Amani Sunbird forage more efficiently, and are superior at exploitative competition. Using a comparative approach, we demonstrate that measures of foraging rates indicate that the Amani Sunbird is a thorough forager within the upper canopy, where it moves infrequently, as opposed to the lower canopy, where it moves more frequently. In contrast, the Collared Sunbird is a cursory forager across the vertical strata, moving frequently between feeding patches. The foraging ecology of Amani and Collared Sunbirds leads us to hypothesize that the critical habitat variables for the coexistence of the two species within the Arabuko-Sokoke Forest reduce to a single tree species, *B. spiciformis*, and the ability of the sunbird species to partition foraging effort by height. We further hypothesize that persistence of the Amani Sunbird appears dependent upon continued existence of tall *B. spiciformis* trees within the canopy of the Arabuko-Sokoke Forest.

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