Seeds in droppings of Bare-necked Umbrellabird *Cephalopterus glabricollis* in Monteverde, Costa Rica: analysis of overlap in fruit diet

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Se colectaron muestras fecales de machos de *Cephalopterus glabricollis* durante la época reproductiva en Costa Rica, para determinar de manera preliminar la sobreposición en el consumo de frutas. La misma puede reflejar competencia por recursos alimenticios. Se colectó un total de 30 muestras fecales de tres individuos de un arena de despliegue (lek). El 70% de estas muestras contenían semillas y pulpa de frutos. Entre 50% y 83% de las muestras fecales de cada individuo contenía semillas. Se encontraron semillas de cinco familias en las heces (Asteraceae, Cecropiaceae, Marcgraviaceae, Passifloraceae y Piperaceae), además de semillas no identificadas. Algunas muestras fecales contenían semillas de hasta cuatro especies de plantas, la media por muestra varió entre 1,5 y 1,8. En comparación con un modelo nulo hubo poca sobreposición en el consumo de frutos, probablemente debido a diferencias en la utilización de los recursos. Análisis preliminares sugieren que los individuos de *C. glabricollis* dividen los recursos especialmente (p.e. formando territorios en las arenas) durante el período reproductivo.

Introduction

Bare-necked Umbrellabird *Cephalopterus glabricollis* is an altitudinal migrant on the Caribbean slope of northern Costa Rica[8]. Costa Rican land-use practices, converting forest habitat to single-family plots, pastures and monocrops, have resulted in lowland deforestation[6] and eliminated large tracts of non-breeding territory for *C. glabricollis*. Habitat degradation coupled with small population sizes and a narrow distribution (Costa Rica to western Panama[9]) make *C. glabricollis* vulnerable to extinction. Much of the information concerning *C. glabricollis* comes from the work of Fogden & Fogden[2] in the Peñas Blancas Valley on the Caribbean slope of the Tilaran Mountains in northern Costa Rica. Their research, over a ten-year period, was the first detailed account of *C. glabricollis* behaviour, including lekking activity, feeding behaviour, vocalisations and the first recorded active nest.

The aim of this paper is to present preliminary analysis of overlap in resource and fruit consumption based on faecal samples collected during the breeding season from male *C. glabricollis*. Such an evaluation is an important first step in determining the role of competition and resource utilisation as mechanisms for explaining overlap in diets. The degree to which birds overlap in fruit diet may reflect possible competition for food resources. High overlap does not necessarily mean competition is operating, as resources may not be abundant. Conversely, low overlap as observed in *C. glabricollis* may result from individuals partitioning resources spatially (e.g. 'lekking' territories). My research was conducted from 19 May to 18 June 1998 in El Bosque Eterno de los Niños, San Gerado Valley, Costa Rica. This area of pre-montane rain forest, at 1,200 m, is maintained by the Monteverde Conservation League and located on the Caribbean slope of the Continental Divide adjacent to Santa Elena Reserve.

Behavioural observations

C. glabricollis spends the majority of the year (June to mid-March) in the lowlands (100–500 m) and migrates upslope to breed at 800–2,000 m in mid-March to June. At San Gerado, three males occupied a widely spaced display area in an 'exploded lek', with each male having a distinct territory (c.60 x 100 m) within audible distance of the others. Males commence calling at dawn (05h00) for a period of 10–20 minutes (see Fogden & Fogden[2] for calling details) and usually do not vocalise during the rest of the day. Temporal variability in rate and duration of calls was noted for different males within the lek from the beginning to the end of the breeding season, and further investigation might provide insight on the intersexual behaviour of males within a lek. Males spend most of the day on 2–3 favourite perches, 10–15 m above ground, within their territory when not foraging in fruiting trees. *C. glabricollis* is largely frugivorous, feeding on fruits from Arecaceae, Lauraceae, Flacourtaceae and Cecropiaceae, but supplements its diet with anoles, frogs and large insects[9]. One male was observed at San Gerado vigorously beating a frog against a tree.

Faecal analysis

The use of faecal samples to determine overlap of fruit consumption in birds is an effective tool, although there are inherent disadvantages. Differential passage rates of seeds could produce an overestimation of the importance of small-seeded fruits in diets of some species[1]. In addition, some

seeds are regurgitated rather than defecated, resulting in an underestimation of those fruits in the diet. Analysis of faecal samples is not prone to the biases intrinsic in direct observation of fruit consumption. Often, visual records of fruit consumption are incomplete, owing to difficulties in observing birds through dense vegetation. Faecal sample analysis when used properly provides an unbiased technique with which to compile quantitative data to determine overlap in fruit consumption.

To quantify diet, faecal samples were collected on 19 May–18 June 1998 from leaves of understorey plants after observing a male defecate. These samples were individually wrapped in filter paper, labelled and stored in small plastic bags for subsequent identification. A dissecting scope was used to separate seeds from each sample and a reference collection established for identification to genus or species. A total of 30 faecal samples was collected: eight, 16 and six from males A, B and C. Seeds and pulp occurred in 70% of all faecal samples, while pulp alone appeared in 30%. Only three samples contained insect exoskeleton fragments (two from male A and one from male B).

Individual faecal samples contained seeds from as many as four species of plants with two or fewer species being the norm. Seeds of at least five families and one unknown family were identified: Asteraceae, *Asteracea* sp.; Cecropiaceae, *Cecropia polyphlebia*; Marcgraviaceae, *Marcgravia* sp.; Passifloraceae, *Passiflora* sp.; Piperaceae, *Piper* sp.; and one unknown. Male B possessed the most samples containing seeds from all six families, except Piperaceae. No significant difference was found in plant species diversity among males A, B and C when using a rarefaction simulation.

Analysis of overlap in fruit consumption was performed running simulations (1,000 repetitions) on EcoSim[4] using a Pianka Index and randomisation algorithm 1, which replaces the observed utilisations with a uniform random variate. This assumes that utilisation of any resource item is possible and equiprobable[5]. The observed mean (0.56) was significantly less than the expected null mean (0.78, $p < 0.05$), indicating a low fruit consumption overlap among *C. glabricollis* males. It is unlikely that each resource is equally available within each male's territory, resulting in intraspecific differences.

Discussion

Null models are useful in determining whether observed niche overlap is more or less than expected by chance, but do not distinguish between ecological niche shifts and evolutionary character displacement[7]. It is not possible to infer the mechanisms responsible for higher or lower overlap in fruit diet without quantitative data on resource abundance. High overlap in fruit diet may reflect an over-abundance of resources or the absence of competition[3]. Conversely, low overlap in fruit diet could result from competition or from differences in resource availability.

Low overlap in fruit diet consumption among male *C. glabricollis* provides the framework for further investigation of the relationships between intrasexual competition and resource utilisation. Determination of foraging strategies (e.g. whether males leave their territory to forage) is essential to the interpretation of these relationships. If *C. glabricollis* males forage solely within their territory, then low overlap may simply reflect differences in food resource availability. Given that males provide no parental care, the establishment of territories may reflect competition for access to females in an 'exploded lek' system. Direct competition for territories may indirectly influence low overlap of fruit diet of *C. glabricollis* males. Differences in availability and diversity of food resources within 'lekking' territories may result in differences in utilisation of these resources, resulting in low overlap in fruit consumption. Further research, conducted over longer periods, is necessary to determine *C. glabricollis* foraging habits and to corroborate this hypothesis.

Conversion of tropical forests to single-family plots, monocrops or extensive cattle pastures is increasingly prevalent in this region of Central America. Understanding the relationship between land-use changes in habitat structure and *C. glabricollis* populations is increasingly important in their acquisition of resources (e.g. fruit and 'lekking' territories). With a population estimated at 80–100 individuals in the Peñas Blancas Valley[2], active management of critical habitat is essential for the conservation of *C. glabricollis* in Costa Rica.

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