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ARTICLE

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Predator avoidance as a function of flocking in the sexually dichromatic Hawaii akepa

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Abstract Hypotheses for joining a mixed-species bird flock consider each species as a single unit. In sexually dichromatic birds, differential conspicuousness between the sexes may result in differences in vigilance for predators. Aspects of the predator avoidance and foraging enhancement hypotheses for the selective value of joining a mixed-species flock were assessed for the strongly sexually dichromatic Hawaii akepa (*Loxops coccineus coccineus*). There was support for the primary predictions of the predator avoidance hypothesis: vigilance levels decreased with increasing group size, and with membership in a flock, but only for brightly colored adult males. There was little support for the hypothesis that the primary benefit of joining a mixed-species flock is to enhance foraging efficiency through "local enhancement".

Key words Predator avoidance · *Loxops coccineus* · Differential conspicuousness

Introduction

Extensive theoretical and empirical work on flocking point to two general hypotheses concerning its selective value: predator avoidance and foraging enhancement (Giraldeau and Caraco 2000; Krause and Ruxton 2002). Flocking may serve to decrease an individual's risk of predation through the "encounter" (Olson 1964; Inman and Krebs 1987) and "dilution" effects (Hamilton 1971; Foster and Treherne 1981; Cresswell 1994), the "confusion" effect (Allee 1938; Neill and Cullen 1974), or the "many eyes" effect (Pulliam 1973; Lima 1990, 1995). The encounter and dilution effects are purely probabilistic. The encounter effect favors being in a group by decreasing each individual's probability of detection by a predator while the dilution effect decreases each individual's probability of being attacked once detection has occurred. Under the confusion effect, a predator is less successful at tracking and catching a single prey when it is within a group of other moving individuals. Under the many eyes effect, individuals are safer in groups because the more eyes there are scanning the sky for predators, the better the chances that predators may be detected and avoided.

One aspect of the predator avoidance hypothesis that has been largely ignored is the effect of differential conspicuousness of individuals to predators. Between species, brighter males may be expected to be more conspicuous than duller males (Baker and Parker 1979). Within sexually dichromatic species, bright males are often more conspicuous than females. Quantitative aspects of vigilance may be expected to vary with conspicuousness as well as group size.

Alternatively, flocking may primarily serve to increase a group member's foraging efficiency through "local enhancement" (Turner 1964; Murton 1971; Krebs et al. 1972; Benkman 1988). Local enhancement is a form of information transfer between flock members regarding new types and concentrations of food resources, allowing flocking individuals to spend more time feeding and less time searching for food than non-flocking individuals.

The primary objective of this paper is to evaluate the predator avoidance and foraging enhancement hypotheses as they relate to flocking in a strongly sexually dichromatic "nuclear" species (sensu Moynihan 1962) within mixed-species flocks of Hawaiian forest birds. Previous work documented the structure of interspecific flocks of Hawaiian forest birds (Hart and Freed 2003). These flocks are seasonal, loosely structured social groupings that are highly variable in size and species composition. Some individual birds may spend time inside and outside of a flock on a given day or between days. This provides an opportunity to compare the behavior of birds in flocking and non-flocking status within the same habitat and at roughly the same times.

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The main predictions of the predator avoidance hypothesis tested here are: (1) vigilance levels should decrease with increasing group size, (2) vigilance levels for individuals in flocks should be less than for individuals out of flocks, and (3) bright males should show greater vigilance than duller females, with greater differences in vigilance depending on flock status. The first two predictions are related to the many eyes effect. The third prediction is based on differential conspicuousness. Because successful attacks by hawks on birds in this forest were rarely observed, it was not possible to directly assess the relevance of the encounter, dilution, or confusion effects to flocking. This difficulty has been encountered in all other studies on mixed-flocks of forest birds (Thiollay 1999).

The main prediction of the local enhancement hypothesis is that since flocking birds should locate high quality food patches more quickly, they should spend more time in fewer trees than non-flocking birds in the same area and season.

Materials and methods

Study site and bird species

This study was conducted during August 1997 within Hakalau Forest National Wildlife Refuge, at elevations of between 1,800 and 1,900 m on the northeast slope of Mauna Kea volcano, Island of Hawai'i (19°47′N–155°20′W). Hakalau contains relatively large populations of nine endemic forest bird species, including six species of Hawaiian honeycreepers (Aves: subfamily Drepanidinae), three of which are federally listed as endangered, as well as an endangered but locally common bird-eating hawk (Hawaiian hawk, *Buteo solitarius*). The canopy at Hakalau is 15–30 m in height and is comprised almost exclusively of old growth (>200 years) ohia, (*Metrosideros polymorpha*) and koa (*Acacia koa*) trees ranging from 20 to 140 cm in diameter at breast height (Hart 2000; Freed 2001).

The Hawaii akepa, a federally listed endangered honeycreeper, was the focal species for all behavioral observations reported here. Both sexes of akepa forage throughout the year primarily by prying open leaf buds on the terminal branch tips of ohia trees, making them particularly vulnerable to aerial predators. We have observed a hawk successfully prey on a bright adult male akepa, as well as a hawk capture and eat an akepa fledgling. The presumed predator surveillance behavior of akepa involves a quick (<0.5-s), periodic, sideways movement of the head about the vertebral axis, so that one eye is facing the sky directly. This 10- to 12-g, insectivorous honeycreeper is strongly sexually dichromatic. Males obtain an almost uniform, bright orange plumage at the end of their third year (Lepson and Freed 1995). Females are typically grayish-green with underparts varying from gray to orange-yellow, although some individuals have orange on the head and face (Lepson and Freed 1997). Other flock-joining honeycreeper species include the Hawaii creeper (*Oreomystis mana*), akiapolaau (*Hemignathus munroi*), iiwi (*Vestiaria coccinea*), apapane (*Himatione sanguinea*), and Hawaii amakihi (*H. virens virens*). In addition, the elepaio (*Chasiempis sandwichensis ridgwayi*) a Monarchine flycatcher, often joins flocks and functions as a "sentinel" species in the community (Hart and Freed 2003).

Twenty-three different flocks were encountered by walking a network of recently established trails and listening for singing or calling birds. Multi-specific associations were classified as mixed-species flocks if three or more birds of at least two species were traveling together between trees as a cohesive group (within a 10-m radius of each other) for a minimum of 15 min; otherwise they were considered temporary foraging aggregations. Flock size ranged from 5 to 75 birds, and generally contained slightly higher numbers of male than female akepa (Hart and Freed 2003). Over 75% of akepa observed in this study were individually color-banded, which allowed us to maximize the independence between observations.

Predictions

The predator avoidance hypothesis was assessed in two ways. First, the effect of group size (regardless of whether the bird was in a mixed-species flock or foraging aggregation) on vigilance behavior of 40 individual akepa was examined. Vigilance rates were calculated as the mean number of head cocks per 20-s period for each individual. All observations were recorded verbally with a continuously running hand-held mini-cassette recorder, and manually logged in the lab with a stop-watch. No observations were used that occurred within 0.5 h of a hawk detection, as this could greatly influence vigilance levels (Hart 2000). Focal birds were followed for as long as possible using 10 × 42 binoculars, and observation times ranged from 45.0 to 224.0 s. Group size was estimated as the number of near neighbors foraging within an approximate 10-m radius sphere of a focal individual. General linear model procedures (SYSTAT 10; SPSS 2000) were used to examine how vigilance rates varied with number of near neighbors (as a covariate) and sex (as a factor). The second assessment dealt with differences between males and females. Brightly colored males are expected to be more vigilant than females because they are more conspicuous to aerial predators. For this comparison, only adult male akepa were used, excluding four sub-adult males used in the previous analysis. In addition, 6 of the 40 birds were part of temporary aggregations, as opposed to clear, cohesive flocks. These birds were removed from the analysis so that flocking status was simply in or out of flock. A two-way analysis of variance (ANOVA, SYSTAT 10; SPSS 2000) was used to examine how flocking status and sex (bright adult males vs adult females) affected vigilance rates.

Foraging enhancement

This study was done in an area where the canopy was predominantly discontinuous, and individual trees could be easily discerned from their neighbors. Previous work at Hakalau (Fretz 2000) demonstrated high variability between trees in foliage arthropods; consequently, each tree was viewed as a discrete food patch. Aspects of patch choice were examined for 14 individual akepa foraging in different flocks and 11 akepa out of flocks. Each focal individual was followed by a single observer (P.J.H.) for a mean of 19 min (range = 8.0–54.1 m) in a minimum of 5 successive trees, for a total of 466 min in 170 different trees. Variables measured were time spent by an individual per tree, flocking status (in or out of flock), and tree volume [estimated as the volume of a box (maximum length × width × height of the canopy), and as the volume of a semisphere $(2/3 \times \pi \times r^3)$]. These methods likely under- and overestimated true canopy volume, respectively, in order to bracket patch size of a single tree. Each is relatively unbiased because akepa visited only ohia trees during the course of the study. The main assumption was that patch (tree) occupation time reflects density of arthropod prey within the patch (e.g., Charnov 1976). Time spent in tree was analyzed through analysis of covariance with tree volume as a covariate and flocking status as a factor (SYSTAT 10; SPSS 2000). This is important because time spent in tree could be a function of tree volume as well as density of food per forager.

Results

Predator avoidance

Combining the sexes, there was a decrease in vigilance levels as the number of near neighbors increased ($F = 7.8$, $df = 1$, $P = 0.008$; Fig. 1). There was no significant heterogeneity of slopes with levels of sex in analysis of covariance ($F = 2.47$, $df = 1$, $P = 0.124$).

For adult females and brightly colored adult males clearly foraging in or out of flocks, there was a significant interaction between sex and flocking status on vigilance levels ($F = 10.1$, $df = 1$, $P = 0.004$; Fig. 2). Males outside of flocks had much higher vigilance rates than males in flocks, while females showed insignificant changes.

Foraging enhancement

There was no interaction between tree volume (using either measure) and levels of flocking status, nor was there an effect of flocking status on time spent in tree. However, there was an increase in time spent in tree with tree volume ($F = 23.2$, $df = 1$, $P < 0.01$ for volume estimated as a box; $F = 21.3$, $df = 1$, $P < 0.01$ for volume estimated as a semisphere). There was little difference in number of trees visited per unit time for individuals in versus out of flocks (23.00 vs 20.44 trees/h respectively, $T = 0.69$, $df = 156$, $P = 0.49$).

Discussion

The decrease in individual vigilance levels with increasing group size, and the strong effect of flocking status on vigilance levels (for bright adult males) provides support for the predator avoidance hypothesis. There was little evidence that flocking birds accrued direct foraging benefits through local enhancement. Here, we explore the relationship between vigilance, plumage brightness, and sex. Finally, the local enhancement hypothesis will be further evaluated as it relates to akepa in Hawaiian flocks.

Vigilance, brightness, and sex

A significant result of this study was that bright orange adult akepa males were much more vigilant than the more cryp-

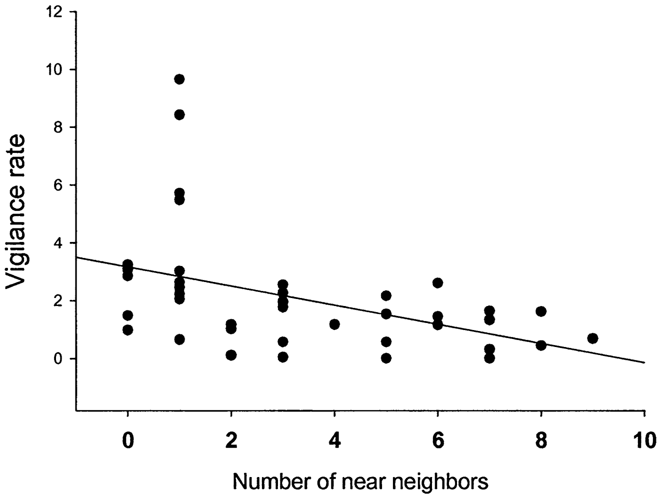

Fig. 1. The relationship between vigilance levels (number of head cocks per 20-s period) and the number of neighbors foraging within an imaginary 10-m sphere of focal male and female akepa in summer 1997

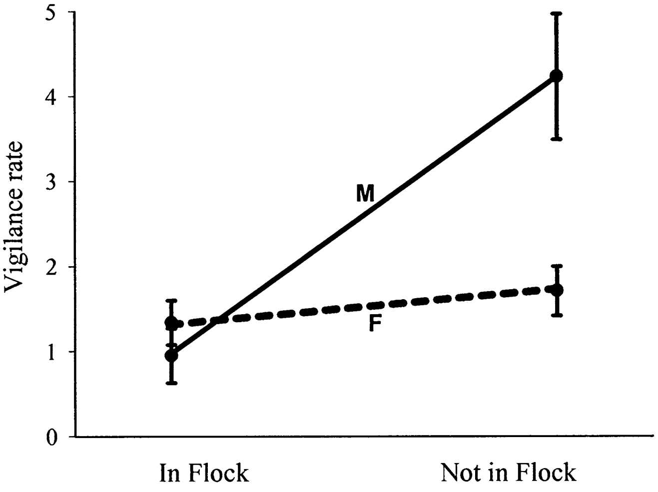

Fig. 2. The variation in vigilance rate (number of head cocks per 20-s period) as a function of sex (*M*, *F*) and flocking status (in vs out of flock) for akepa in summer 1997 ($n = 18$ males and 16 females)

tically colored females outside of flocks (Fig. 2). The bright orange plumage of these males is relatively unusual in birds and likely a result of sexual selection. Sexual selection and other processes favor bright colors (Andersson 1994), which are usually assumed to be conspicuous and therefore selected against by increased predation (Slagsvold et al. 1995; Götmark and Olsson 1997). However, Baker and Parker (1979) suggested that the brighter birds within a population may be unprofitable, possibly by being more vigilant or agile. These latter ideas have been supported by Götmark (1992, 1995), and may be relevant to akepa because these birds exhibit extreme intra and inter-sexual variation in color (Lepson and Freed 1997). It would be useful to compare the vigilance behavior of duller second year and third year males with that of adult males, and of females that vary considerably in expression of the male plumage character.

Slagsvold et al. (1995) and Götmark and Olsson (1997) found increased levels of predation on the more brightly colored members of bird populations. The data presented here provide further evidence that increased vigilance (when not in a flock) is an apparent additional cost to brightness. Bright males may have a higher probability than cryptic females of being preyed upon, and this is reflected in their higher vigilance levels for predators outside of flocks. Presumably, the cost of these higher vigilance levels is a decreased rate of food intake (e.g., Caraco 1979). When bright males join a flock, their risk of predation is decreased (through the dilution, confusion, and many eyes effects), and their vigilance levels become similar to those of females in flocks.

There was only a slight, insignificant trend toward decreased vigilance levels for females in versus out of flocks (Fig. 2). This raises the possibility that the proximate benefits of joining a flock differ between the sexes. Females may join flocks to be with their mates, or to decrease their risk of predation primarily through the dilution effect.

Local enhancement

The amount of time individuals spent in a tree increased with canopy volume, but there was little difference in tree size usage or patch occupation time for birds in versus out of flocks. These data indicate that the variability in arthropod abundance between trees may not be great enough to drive flocking through local enhancement in this area.

Local enhancement is an inherently difficult process to demonstrate in the field for canopy foraging insectivores, and its importance is still debated. For mixed-species flocks of insectivores, there is little empirical evidence for a general increase in foraging efficiency for a majority of the species involved (but see Hino 2000). In addition, the generally restricted home ranges of, and high food niche diversity among, insectivorous mixed-flock participants minimize the potential for information transfer leading to a local enhancement effect (Powell 1985). Most of these birds have small home ranges and visit all parts of their range frequently (Buskirk et al. 1972; Munn and Terborg 1979; Powell 1979; Gradwohl and Greenberg 1980; Powell 1985; Jullien and Thiollay 1998). Therefore, they can regularly monitor food availability and probably maintain a high degree of familiarity with food resource distributions within their home ranges. Foraging enhancement benefits through information exchange may apply primarily to monospecific flocks of frugivores or granivores, whose food often occurs in localized and ephemeral clumps (Krebs et al. 1972; Powell 1985).

Of course, a more direct evaluation of the foraging enhancement hypothesis as it relates to Hawaiian forest birds would include measurements of food intake rates. These measurements should also take into account the inherent increase in time available to feed that would accompany any reduction in time allocated to vigilance for birds within flocks. A positive relationship between group size and food intake rates would be evidence that flocking may also benefit individuals through local enhancement.

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