AN ABSTRACT OF THE THESIS OF

Schwann Tunhikorn for the degree of <u>Doctor of Philosophy</u> in <u>Fisheries and Wildlife</u> presented on <u>August 15, 1989.</u>

Title:	Resource Partitioning of Four Sympatric Mynas and					
	Starlings (Sturnidae) in Thailand					
Abstract approved:						
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Patterns of resource partitioning among 4 sympatric sturnids: [black-collared starling (Sturnus nigricollis), pied starling (S. contra), common myna (Acridotheres tristis) and crested myna (A. javanicus) were determined based on their food habits, foraging and nesting microhabitat selection, morphology and behavior. The study was conducted from March 1986 to June 1988 at and around Bang Pra Game Sanctuary, Cholburi, Thailand.

Diets of adults and nestlings of all species were significantly different. The 4 species exhibited significant differences in morphology, primarily in trophic (bill shape and length) and locomotive (wing shape and size) appendages that affect selection of foraging microhabitat and hence choice of diets.

Selection of nest site characteristics was significantly different among the species and was associated with types of tree i.e., palm vs non-palm (trees with forks or branches), distance of nest tree from human habitation and distance of nest tree from seasonal or permanent waters.

The pied starling, common myna and crested myna all selected different foraging habitats and used different techniques for foraging, however the black-collared starling shared foraging habitat with the other 3 species.

Breeding success, breeding chronology, and clutch sizes were similar for the 4 species.

These 4 sympatric sturnids partitioned their resources through differences in morphology, which, in turn, affected their foraging habitat selection and modes of foraging, and hence, differences in diet. Behavioral differences also segregated their foraging techniques and nest site selection.

Resource Partitioning of Four Sympatric Mynas and Starlings (Sturnidae) in Thailand

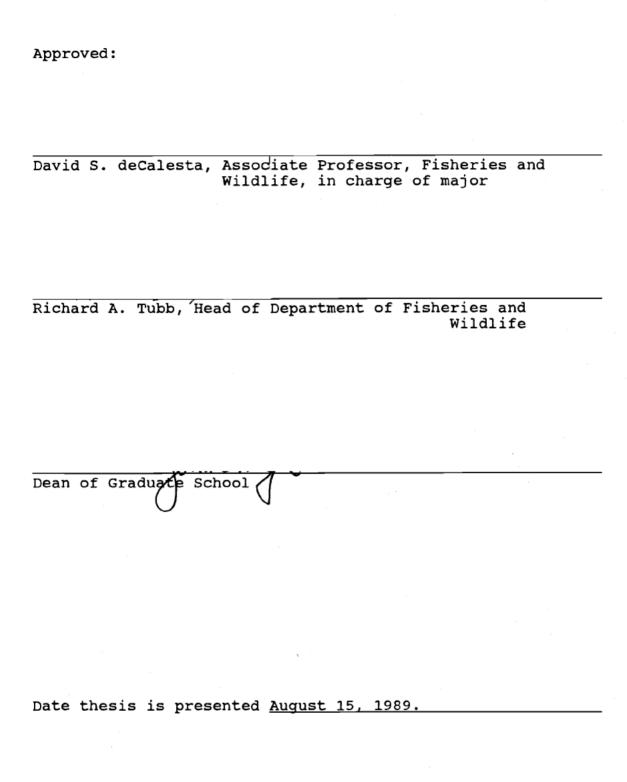
by

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A THESIS
submitted to
Oregon State University

Completed August 15, 1989

Commencement June 1990



DEDICATION

Dedicated to my parents, whose unending love, support and encouragement have seen me through many difficult times, and which have enabled me to come this far.

ACKNOWLEDGMENTS

My sincere appreciation to all my colleagues and friends who have helped make this study possible.

To Dr. David S. deCalesta, my major advisor, for his support and guidance during my study at Oregon State University, and for his assistance in preparing this disseration.

To Dr. Bruce E. Coblentz, who opened a new horizon for me to study and understand animal behavior.

To the members of my graduate advisory committee, Dr. William C. Kruger, Dr. Gordon E. Matzke, Dr. Joe B. Stevens, and Dr. Kim K. Ching for their advice and guidance.

To Dr. Pachijanut Siripanich who helped with the statistical aspects of this study.

Most importantly, I wish to thank my wife Bupphachart, for her devotion, patience and faith, and to my children, Maturawan, Tan and Tai who have made many sacrifices to share their frustrated father with his study.

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Resource Partitioning of Four Sympatric Mynas and Starlings (Sturnidae) in Thailand

INTRODUCTION

The principle of competitive exclusion maintains that no 2 species can coexist indefinitely if they use the same resources and if those resources limit their density. For sympatric species to coexist successfully, they must be segregated ecologically through the partitioning of resources by: 1) using different resources; 2) using the same resources at different resource states or at different times; or 3) using different areas in which resources are obtained (Diamond 1978, Lack 1971, MacArthur 1969a, Price 1975). In contrast, Connell (1975) and Weins (1977) argued that sympatric species can coexist without partitioning resources in cases where competition is intermittent, or factors such as harsh environmental conditions or predation maintain populations below densities where competition for resources would be limiting.

Birds appear to partition food resources in several different ways, thereby reducing competition. One way is by foraging behavior (Lack 1954, MacArthur 1958, Orians and Horn 1969). Examples of proferred resource partitioning have been documented for a wide variety of coexisting organisms (Schoener 1974), yet few, if any studies have

been conducted on sympatric avian species in the tropics.

Darwin (1859) and Welty (1975) pointed out that competition is most intense in the tropics. This view was supported by Connell (1975), who maintained that neither predation physical environments depress populations below competitive levels in the tropics. The close packing of competitive species in tropical ecosystems also tends to enhance the potential for resource partitioning as a survival tactic. The keenest competition occurs between conspecifics.

Similarly, closely-related species are likely to be more competitive than distant relatives (Wilson, 1975).

The importance of the structural configuration and local topography as determinants of habitat occupancy (and as a physical dimension for resource partitioning) by birds has been well studied (Klopfer 1963, Lack 1949, Svardson 1949). Lack (1949) and Svardson (1949) in particular proposed that habitat selection processes rely almost completely upon the bird's recognition of structural features of the environment. Both authors pointed out that structural cues are proximate factors and that ultimate factors, those concerned with survival value, must act through natural selection to delimit the spectrum of cues used by a species in habitat selection. Other researchers (Moermond 1979, Robinson and Holmes 1982) maintained that physical structure of the vegetation has been an important selective force in determining the patterns of bird locomotion, foraging behavior and resource exploitation.

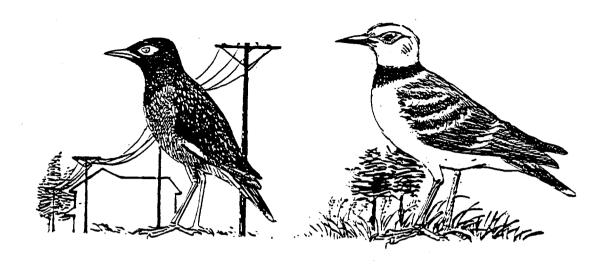
Avian reproductive success may be related to features of the nest tree (Best and Stauffer 1980) or the structural stability of the nest (Coon et al. 1981). Newton (1967) proposed that characteristics of the nest site as well as bird behavior are of significant importance in determining reproductive success. Osborne and Osborne (1980) related nesting success to characteristics of human disturbance and Klopfer (1963) maintained that early experiences with the environment may influence an individual bird's subsequent selection of habitat. Feare (1984), studying European starlings (S. vulgaris) concluded that good nesting sites consisted of a suitable cavity for the nest surrounded by a feeding area with sufficient food for the adults and their young. Selection of nesting sites represents another physical dimension of resource partitioning.

Ecologists have noted that within bird families, there are predictable relationships between morphology and ecology (Conant 1988, Grant 1986, Karr 1971, Karr and James 1975, Orians 1969, Schoener 1971). Mensural characters such as mass (Schoener 1968a) and trophic and locomotory appendages frequently have been used to make ecological inferences. Size and shape of trophic appendages are assumed to be related to the size of prey (Allaire and Fisher 1975, Cody 1968, Lack 1983) whereas relative size and shape of locomotory appendages such as wing and tarsus lengths have been related to the method of foraging for food (Baker 1979, Cody 1968, Cody 1974, Dilger 1956,

Fretwell 1969, Grant 1971, Keast 1970, Newton 1967, Osterhaus 1962). These morphological differences may represent physiological adaptations for resource partitioning.

The family Sturnidae is composed of over 100 species. Thirteen are native to Thailand, and 4 species (Fig. 1) of 2 genera [Acridotheres (A. tristis, common myna, and A. javanicus, crested myna) and Sturnus (S. nigricollis, black-collared starling, and S. contra, pied starling)] occur sympatrically over the entire country. They appear to be similar ecologically as they are of almost identical size and mass, occupy the same habitats, forage in similar ways, feed on similar foods, build similar nests and breed at the same time of year (Ali and Ripley 1972, Lekagul and Cronin 1974). These sturnids provide an excellent opportunity to study and document resource partitioning in terms of selection for foraging and nesting habitat, food selection, foraging strategies, reproductive success, and morphological differentiation.

The goal of this study was to determine whether partitioning of resources exists among these sturnids in a tropical setting where food was assumed abundant, the environment was not harsh, and a state of competition should exist.



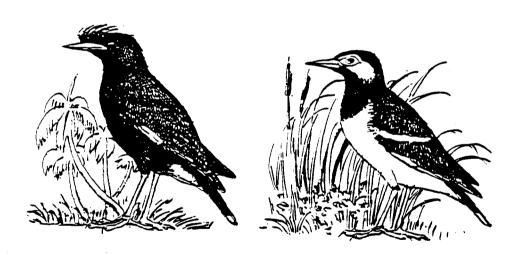


Figure 1. The 4 sympatric sturnids observed in this study. They are: A) the common myna (Acridotheres tristis); B) black-collared starling (Sturnus nigricollis); C) crested myna (A. javanicus); D) and pied starling (S. contra).

Specifically, the objectives of this study were:

- 1. To compare the diets, foraging ecology, breeding biology and reproductive success of the 4 sympatric sturnids;
- 2. To compare nesting and foraging microhabitat among the 4 sturnids;
- 3. To compare morphological features that might allow the 4 sturnids to partition resources.

STUDY AREA

The study area, encompassing 27 km² was in Sri Racha District, located in Cholburi (Lat 13°N, Long 101°E), an eastern province approximately 115 km southeast of Bangkok, Thailand (Fig. 2). The study was concentrated on the 18.4 km² Bang Pra Wildlife Game Refuge administered by the Division of Wildlife Conservation and included approximately 17.8 km² of agricultural land surrounding the reservoir. About half of the 18.4 km² sanctuary is permanently flooded. Elevation of the site ranges from 12 to 35 m, and topography is primarily flat, with slope ranging from 0-5%. The weather follows a three-season pattern: a rainy season begins in June and lasts until October; a relatively cool winter from November to February; and an extremely hot, humid summer from late For the period 1984-1988, mean annual March until June. precipitation was 1347.6 mm, mean minimum temperature was 20.1°C occurring in December and January, and a mean maximum temperature was 35.3°C in March and April.

Approximately 35% of the refuge drier upland is dominated by shrub grassland interspersed by small to medium-sized trees [Siamese Rough Bush (Strebus asper), and Indian plum (Zizyphus mauritianna)]. The predominant grasses are lalang (Imperata sp.), Bermuda grass (Cynodon spp.), golden beardgrass (Chrysopogon aciculatus), and

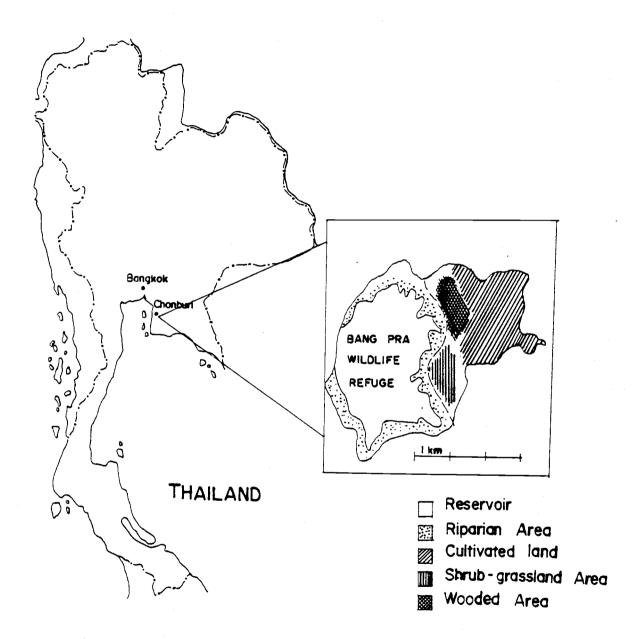


Figure 2. Map of Thailand with inset illustrating location of Study Area.

buffalo grass (<u>Brachiaria mutica</u>). Approximately 38% of the remaining area consists of stands of trees planted under the reforestation program of the Division of Wildlife Conservation, deserted coconut (<u>Cocos nucifera</u>) plantations, and riparian areas. Five feeder streams that originate from the Khao Kheiw Range to the north flow into a reservoir created by Bang Pra Dam. The banks of these streams and the reservoir are densely populated by bamboos (<u>Bambusa sp.</u>) and various species of reeds (<u>Arundo spp.</u>).

The highest portion of the refuge, located at the southern part of the study area, is covered by semipermanent and permanent ponds, with clusters of trees growing on the higher ground. Riparian grasslands were created where the ground gradually slopes down until it meets the water from the reservoir. In the rainy season, this area is generally flooded.

Areas under cultivation around the refuge included in the study are characterized by a mosaic of sugar cane (Saccharum officinarum), tapioca (Manihot esculenta), and coconut plantations. In addition, the study area is bordered on the north by rice paddies, and on the east by open fields where cattle were occasionally grazed.

The study area is divided into 4 major cover types, which were distributed as a mosaic of cultivated lands, riparian areas, shrub grasslands, and wooded areas.

<u>Cultivated Land</u>. This type approximated 64.0% of the study area and is composed of tapioca (45%), sugarcane

(41%), coconut (5.5%) and pineapple (Ananas comosus) (1%) plantations, corn (Zea Maize) fields (0.5%), rice paddies (Orysa sativa) (5%) and mixed orchard (2%).

Riparian Area. This area (making up approximately 12% of the study area) occurs where feeder streams flow into the reservoir, and around man-made impoundments. Riparian grassland occurs at the southwestern portion of the reservoir where the ground gently slopes down toward the reservoir. The vegetation in this area is composed mainly of various species of grasses (Imperata sp.), bamboos and figs (Ficus sp.) which were dominant along the banks. Scattered stands of Siamese Rough Bush patches occupied drier grounds. Grass height varies seasonally from 5-10 cm in summer to 75-80 cm in the rainy season. Portions of land along the southern boundary are grazed by livestock and grass height is kept consistently low (5-10 cm.) year round.

Shrub Grassland Area. This type covers 11% of the study area and occurs on higher and drier ground adjacent to the riparian area around the reservoir. This area is characterized by various species of grasses (Lalang sp.) creepers such as sensitive plant (Mimosa invisa), and shrubs such as Indian plum (Leucaena leucocephala), and Cassia tora. The dominant tree species are Siamese Rough Bush and figs.

Wooded Area. This type covers 13% of the study area and occurs on dry ground around the reservoir. Formerly a

shrub grassland community, it was planted with various species of trees under the reforestation program of the Wildlife Conservation Division. These trees, planted 4 m from each other, consisted of Yang (Dipterocarpus alatus), rain tree (Samanea saman), Catechu tree (Acacia catechu), Manila tamarin (Pithelcellobium dulce), agasta (Sesbania grandiflora) and wattle (Acacia auriculaeformis). They form dense patches of woodlands. Canopy coverage in these areas is 95-100%.

The soil in the refuge is classified as sandy and is infertile because of overuse. This area was once used to grow crops such as tapioca, sugar cane, and rice before it was foreclosed and flooded when Bang Pra Dam was completed.

This study area was chosen because all 4 sturnid species are resident year round, nest on the area, and have been observed feeding in mixed flocks.

METHODS

Diet Analysis

Adults of the 4 species were collected by shooting, and digestive system contents were examined to determine diets. From April 1986 to July 1988, collections of 5 individuals of each species from random sites were made at 2 week intervals. During breeding seasons, birds were collected in comparable habitats off the study area to avoid impacting concurrent evaluation of nesting ecology. Insofar as possible, I attempted to equalize the number of specimens taken with respect to cover type and time of Immediately after collection, each specimen collection. was weighed on a triple beam balance, and digestion was inhibited by forcing 2 ml of a 75% solution of alcohol down the throat. Within 2 hours of collection digestive tracts and gizzards were removed and stored in 70% alcohol for subsequent analysis.

Diet analysis began by examining the contents of the esophagus and gizzard with a stereomicroscope at 7x magnification. Food items were segregated into 4 categories: insects; non-insect invertebrates; vertebrates; and plant material. Plant and animal specimens were identified to Family, counted and volumes were measured. Because the birds broke larger insects into small pieces before swallowing, most identifications had to be made by entomologists using characteristic mandible, leg, head and

elytra parts. Sizes of these fragmented insect prey were estimated by comparing the size of characteristic body fragments with voucher specimens of known body size.

Initially, food habits of adults were analyzed by season. The study area is well irrigated, and virtually the same crops are grown year round, resulting, ostensibly, in little variation in availability of foods for the 4 sturnids. As there were no significant differences of foods eaten by the 4 sturnids among seasons, food habits data were pooled for all seasons into an annual diet.

In addition to stomach content analysis of adults of each species, food items brought to nestlings were recorded. Observations were obtained directly from blinds placed within 1.5-2.0 m of each nest. Food items were identified by comparison with reference collections. These observations were compared among species to determine if species-specific differences in nestling diets existed among the 4 species.

Diet composition (% occurrence) was compared between adults and nestlings within species to determine whether differences in diet existed.

Habitat Selection

Proportions of cover types and vegetative characteristics on the study area were determined by observation and from maps and aerial photographs.

Locations of birds in these habitats while foraging and

during breeding season were recorded to determine differences and similarities in habitat use when foraging and nesting.

Foraging Behavior and Selection of Foraging Habitat.

Behavior of birds that were actively foraging was quantified by following an individual or groups of individuals and recording cover type, tree species, ground cover, type of foraging behavior (flushing and chasing, darting and short flight after disturbed insect, slow searching, open-bill probing, hawking slow-flying insects and feeding in association with grazing livestock).

A bird was considered feeding if feeding duration was 3 minutes or more. These observations were made throughout the day, but mostly between 0600-1000 and 1500-1800 hours when birds were most active. I attempted to remain 30-50 m away from the birds to minimize influencing their activities and behavior.

Selection of Nesting Habitat. To assess possible partitioning of nesting habitat among species, I compared the characteristics of nest trees and vegetation surrounding nest trees among bird species.

During March-June of 1986-1988, nests were located by watching for birds carrying nesting materials or food to nests. Because black-collared and pied starlings build large, conspicuous dome-shaped nests that can be located

easily, searchers were stationed at various vantage points and systematically searched/observed for starling nests.

Common and crested mynas are cavity nesters, so their nests were located by searching dead coconut trees with broken tops, or by examination for nesting materials (hanging loose) where coconut fronds meet the trunk.

Vegetation structure and topography around nest trees were characterized by sampling 0.04 ha circular plots centered on the nest tree (James and Shugart 1970).

Measurements of vegetation were made as soon as the nest was found. Variables measured, or computed from measurements at each nest site (Morris and Lenon 1983) were:

- species and diameter at breast height (dbh) of all stems at least 1.5 m tall
- mean stem basal area (m²/ha)
- percent of ground cover of each forage class (grass, shrub)

The following characteristics of nest trees also were recorded:

- 1. species of nest tree
- height of nest tree
- 3. dbh of nest tree
- 4. height of nest from ground
- 5. height of lowest branch of nest tree to the ground

Topographic features at each nest site were measured to assess relationship of nest site to proximity of human influence, availability of potential foraging sites, and intra- and interspecific interactions. These included:

- 1. distance from nest tree to the nearest path or road
- 2. distance from nest tree to the nearest human habitation
- distance from nest tree to the nearest permanent or seasonal water source
- 4. distance from nest tree to the nearest active neighboring nest of similar or dissimilar species

Morphology

To assess the interrelationships between morphological patterns among the closely related sympatric species, 18 morphological characteristics were measured or calculated as follows:

- Body mass (weight) was measured with a triple-beam balance to the nearest 0.01 gm
- 2. Total length was measured from the tip of the bill to the tip of the tail with the bird on its back (Cramp and Simmons 1980)
- 3. Wing length was measured from the carpal joint to the tip of the longest primary (P 7) with the wing extended and pressed against the ruler

(Crunden 1963)

- 4. Wing span was measured with fully extended wings with the bird on its back
- 5. Wing area was measured by tracing the outline of the fully extended wing, and the wing area measured with a planimeter
- 6-8. Three bill measurements (Cody 1968, Cody 1974 and Hespenheide (1971) were taken to the nearest 0.01 mm with vernier calipers as follows: length (from the anterior edge of the nares to the tip of the culmen), width (culmen width at anterior edge of the nares), and depth (culmen depth at the anterior edge of the nares)
- 9. Tarsus length (Cody 1968, and Grant 1971) was
 measured from the tibio-tarsal joint to the joint
 between the tarsus and the middle toe of the
 folded leg (Cramp and Simmons 1980)
- 10. Foot span with claws was recorded as the distance from the tips of the hind and middle toes
- 11-14. Other morphological variables measured were the length of hind toe, inner toe, outer toe and tail.

Ratios of variables were calculated as follows:

- 15. Ratio 1 bill length/bill depth
- 16. Ratio 2 wing area/wing length
- 17. Ratio 3 bill length/bill width
- 18. Ratio 4 wing area/weight

Reproductive Success

Nests were located by observing birds carrying nesting material to nests or by observation of likely nest sites.

Once located, each nest was inspected every 2-3 days until all nestlings had fledged. If eggs or chicks disappeared or eggs failed to hatch, or the nest was destroyed, the nest was revisited at 1 week intervals for 2 weeks to determine if renesting occurred. Date, clutch size, incubation period, and fledging period were recorded and compared among species.

Statistical Analysis

Diet Analysis. Differences in proportions of diets comprised of the 4 major food types (insect, non-insect invertebrate, vertebrate, and plant material) for adults and nestlings were analyzed using Chi-square goodness-of-fit procedures (Snedecor and Cochran 1980). Proportion of diets comprised of diet items classified to family level were compared among sturnids using the Normal Approximation to Binomial (Z) test (Snedecor and Cochran, 1980).

Foraging Habitat Use. Foraging habitat selection among species was compared using the procedure of Neu et al. (1974). A Chi-square test was performed to test the hypothesis that individual species utilized cover types in proportion to their availability. If the null hypothesis was rejected, the selection for or avoidance of each cover type for each species was determined by constructing individual confidence intervals for the bird's proportion of use.

Morphology and Nest Site Selection. To test for differences of each morphological characteristic and of nesting site characteristics for all possible paired comparisons among species, univariate pairwise comparisons (Duncan's Multiple Range Test) were used. As a further refinement, stepwise discriminant function analysis (DFA) was used to select variables that most clearly differentiated morphological and nesting site characteristics among the 4 species according to sample

variance (Nie et al. 1975). The first function derived explains the greatest proportion of total variance, and each additional function accounts for successively less.

The stepwise discriminant function analysis selected, one at a time, those variables which best discriminated among the 4 sturnids for morphological and nest site vegetational and physical characteristics. Variables that provided maximum discrimination were also used to plot group centroids according to 2 canonical functions.

A classification of the original set of cases (morphological and site characteristics) was conducted to check the ability of discriminate function analysis to correctly assign birds to species according to morphological/nest site characteristics (Nie et al. 1975). Significance level used was $P \leq 0.05$ for all tests.

RESULTS

Food Analysis: Adults

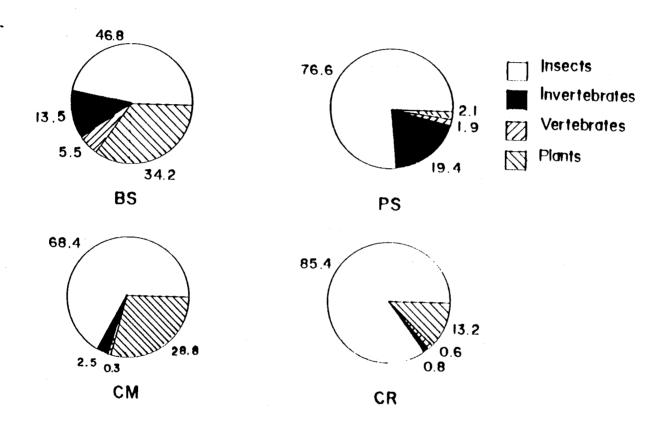
A total of 1,583 prey items, (1,301.8 ml), comprised of 1,092 insects, 151 invertebrates, 33 vertebrates and 307 plant materials (seeds, fruits, and roots) was identified from stomachs of 214 black-collared starlings, 213 pied starlings, 224 common mynas and 225 crested mynas. Chi-square tests revealed significant differences in the proportions of the 4 classes of food items among all 4 sturnids (Figure 3).

To further differentiate diets among the 4 species, tests for significance (Z-test) were performed on each prey type taken by all species as follows:

Insects. Insects of 8 different orders (23 families) were identified and made up the largest part of the diets of all 4 species by occurrence and volume. Pairwise comparisons (Z-test) among sturnids of insects consumed indicated significantly different diets among all pairs. The crested myna was the most insectivorous; Their primary insect prey were Orthoptera (41.2% occurrence, 65.5% by volume), Hemiptera (20.7% occurrence, 6.6% by volume) and Coleoptera (14.8% occurrence, 7.5% by volume).

The pied starling was the second most insectivorous (Fig. 3). Orthoptera and Coleoptera contributed 29.2% occurrence (46.3% by volume) and 25.0% occurrence (21.1% by volume) to their diet. The 2 major families of insects,

Diets of Adults (% Occurrence)



Diets significantly different (P < 0.01) among adults

Figure 3. Comparison of diets among black-collared starling (BS), pied starling (PS), common myna (CM), and crested myna (CR) based on 4 categories of food items. Bang Pra, Thailand. 1968-1988.

which together comprised 32.9% occurrence of the diet, were Gryllotalpidae (mole cricket, 16.7% occurrence, 33.1% by volume) and Carabidae (ground beetles, 16.2% occurrence, 6.8% by volume). Acrididae and Tettigoniidae (grasshoppers) contributed 10.7% occurrence (12.1% by volume) to the diet and Cydnidae (burrowing bug) of the order Hemiptera provided 10.6% occurrence ((5.8% by volume). The common myna's diet contained 68.4% occurrence (62.9% by volume) of insects but major food items, unlike that of the congeneric crested myna, were insects of the order Coleoptera (30% occurrence, 23.4% by volume),
Tenebrionid beetles (20.2% occurrence, 16.2% by volume) and orthoptera (19.2% occurrence, 25.8% by volume), of which grasshoppers contributed 17.7% occurrence (21.5% by volume).

The diet of black-collared starlings had the lowest occurrence of insects (Fig. 3). Orthoptera and Coleoptera contributed almost identical amounts to the diet (15.6% occurrence, 11.3% by volume and 15.9% occurrence and 18.9% by volume, respectively).

within the order Coleoptera, black-collared starlings ate more scarab beetles (Scarabidae) (9% occurrence 9.9% by volume) and ground beetles (Carabidae) (4.2% occurrence, 0.9% by volume) than other sturnids. Grasshoppers taken by black-collared starlings amounted to 9.7% occurrence (10.2% by volume), the lowest among the 4 sturnids.

Non-insect Invertebrates. Z-tests detected differences in % occurrence and % volume of invertebrates in diets of all species except between the common and crested mynas. Black-collared and pied starlings ate significantly more invertebrates than common and crested mynas (Fig. 3). Pied starling diets had the highest % occurrence and % volume of non-insect invertebrates. Oligocheata (earthworm, 12.7% occurrence, 9.8% by volume and Gastropoda (fresh-water snail of the family Thiaridae, 3.2% occurrence, 1.5% by volume) were the 2 major orders taken. Arachnida (spiders and scorpions) and Diplopoda (pill millipedes) contributed smaller portions (1.9% and 1.6% respectively).

The diet of black-collared starlings also contained a high % of invertebrates, and differed from the pied starling's diet in that, they consumed more crustaceans (rice field crab, family Parathelphusidae, 3.7% occurrence). Common and crested mynas included few invertebrates in their diets (0.8% occurrence, 3 small fresh-water shrimps), 1.8% occurrence (snails) respectively.

Vertebrates. Black-collared and pied starlings ate significantly more vertebrate food than the mynas. Vertebrates obviously were not a staple food of any of the 4 sturnids, as they constituted relatively small proportion of total diets (Fig. 3). The highest frequency of occurrence of vertebrates in sturnid diets was frogs,

family Ranidae (22 in black-collared starling, 8 in pied starling and 1 in common myna diets).

Plant Materials. Vegetative composition of the diet varied significantly ($P \le 0.01$) among species except between the black-collared starling and the common myna.

Black-collared starlings had the most vegetarian diet (Fig. 3). They ate fruits and seeds of 8 different plant families, the majority being <u>Ficus</u> sp. and <u>Strebus asper</u> (Moraceae) (9.4% occurrence, 18.9% by volume, combined), Leguminaceae (6% occurrence), cucumbers (Cucurbitaceae) (5.5% occurrence) and Flacourtiaceae (6.2% occurrence). Pied starlings had the smallest proportion of plant material in their diet (Fig. 3).

The second most frequent item in the diet of the common myna was vegetative material (28.8% and 34.7% by volume), consisting chiefly of commercial poultry and livestock foods and kitchen scraps, such as cooked rice (Gramineae). These 2 types of man-made food comprised about 10.2% occurrence and 12.3% by volume of the total diet. The common myna also had the most diverse plant material diet, as vegetative parts (fruits, seeds and flesh) of 11 different plant families were found in its diet. Four major families (Moraceae, Passifloraceae, Leguminaceae and Euphorbiaceae) made up 15.3% occurrence (18.7% by volume) of the diet.

The crested myna's diet contained 13.2% occurrence

(6.4% by volume) vegetable matter. Moraceae,
Passifloraceae, Leguminoceae and Cucurbitaceae contributed
3.9% occurrence (12.4% by volume), 2% occurrence (0.4% by
volume), 2.5% occurrence (1.5% by volume) and 2.5%
occurrence (0.6% by volume) respectively.

Food Analysis: Nestlings

A total of 6,680 feedings was recorded from 29 nests. Chi-square tests indicated significant differences (<0.01) in the proportions of the 4 categories of food (insects, non-insect invertebrates, vertebrates, plant material) fed to nestlings among all species (Fig. 4).

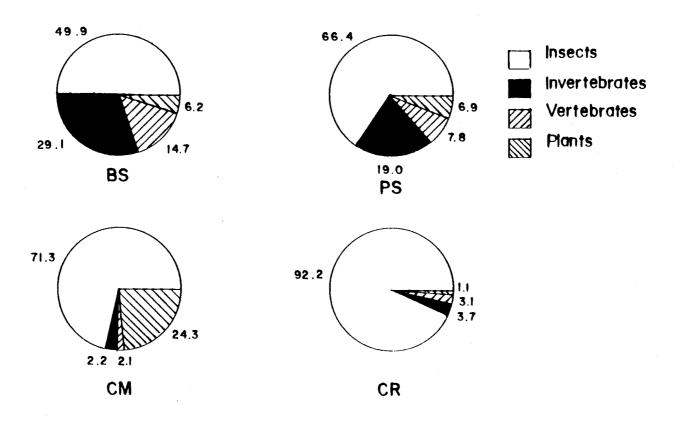
Z-tests were used to test for significance of food brought back to nestlings among all species.

Insects. Number of insects fed to nestlings differed significantly among all 4 species (Fig.4). Crested myna nestlings were fed the highest proportion of insects (92.2% occurrence), of which grasshoppers made up 64.9% and Lepidopteran caterpillars 24.6% of the feedings.

Insects comprised 71.3% of common myna feedings;
Orthopterans (grasshoppers) were 45.1% and Lepidopterans
16.4%.

Pied starling young received 66.4% occurrence of insects of which Orthopterids comprised 32.3% and Lepidopteran larvae 22.9%. Within the Orthopterans, the important food items brought to pied starling nestlings

Diets of Nestlings (% Occurrence)



Diets significantly different ($P < O \cdot OI$) among nestlings

Figure 4. Comparison of food of 4 categories fed to nestlings among black-collared starling (BS), pied starling (PS), common myna (CM), and crested myna (CR). Bang Pra, Thailand. 1986-1988.

were crickets (Gryllidae) 19.5%, and grasshoppers (Acrididae and Tettigoniidae) 9.7%. occurrence.

Black-collared starling young, by contrast, were fed insects in only 49.9% of feedings, comprised of 16.5% Lepidopterans larvae, 16.1% grasshoppers (Acrididae and Tettigoniidae) and 10.4% Coleopteran beetles (Cerambicidae and Carabidae).

Non-Insect Invertebrates. Amounts of non-insect invertebrates in the nestlings' diets were significantly different among all species (Fig. 4). The starlings utilized significantly greater amounts of invertebrates in nestling diets than mynas (black-collared starling, 29.2%; pied starling 19%; common myna 2.2%; and crested myna 3.7%) (Fig. 4).

Within the genus Sturnus, black-collared starlings heavily exploited earthworms (Oligocheata) (23.3%), while pied starlings divided their invertebrate diet almost equally between spiders (Arachnida, 7.2%) and earthworms (8.7%).

Vertebrates. Pairwise comparison of % occurrence of vertebrate prey in all species' diets revealed significant differences among all pairs except between common and crested mynas.

As with adult diets, species in the genus Sturnus utilized higher percentages of vertebrates in nestling

diets than mynas (Fig. 4). Black-collared and pied starlings fed significantly more amphibians (Ranidae) to nestlings than common and crested mynas (13.4% and 7.8% compared to 0.9% and 2.7%, respectively). Common mynas secured the most reptilian prey (1.2% for both species).

Pied starling and crested myna young were fed almost negligible amounts of vertebrates (0.2% and 0.4%, respectively).

Between the black-collared starling and common myna, which exploited almost equal percentages of reptilian prey, the black-collared starling's most common prey was lizards of the family Lacertidae, whereas the common myna secured mostly small house lizards of the family Gekkonidae, that live in or close by human settlements.

In addition the 2 starling exploited fish that were stranded or trapped in shallow water. Pied starlings brought 6 small Cyprinid fish (0.4% of the total diet) to nestlings, and a black-collared starling was observed feeding a small fish (0.1% of the diet) to its nestling. By contrast, mynas were never observed exploiting fish as food for adults or nestlings.

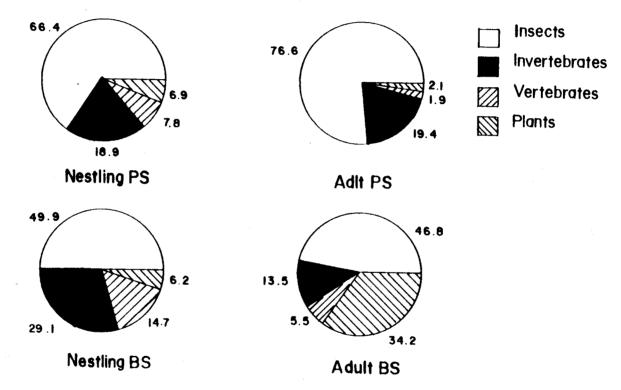
<u>Plant Materials</u>. Comparison of amounts of vegetative materials brought back to nests revealed highly significant differences ($P \le 0.01$) among all species except between black-collared and pied starlings. Common myna nestlings received the diet highest in plant matter (24.3%) and

crested myna the lowest (1.1%). Black-collared and pied starling young were fed similar amounts of plant materials (6.3 and 6.9%, repectively). The high % of plant material in the common myna diet was comprised of commercial livestock and poultry pellets (4.9%), kitchen scraps (mostly cooked rice and, on 6 occasions, noodles: 8.1%). Common mynas also utilized figs and fruits of Strebus asper (both belong to the family Moraceae, 8.9%).

<u>Diets of Adult vs Nestlings of the Same Species</u>. Diet composition between adults and nestlings of the same species was significantly different for all species (Fig. 5-6).

Generally, diets of nestlings had higher frequencies of insects, non-insect invertebrates and vertebrates than those of the adults. This was probably due to high protein requirements of nestlings during the rapid growth period. However, adult pied starlings had diets higher in insects and lower in plant material frequencies than nestlings, which may have been the result of the high availability of Strebus asper fruits, a major component in diets of nestling pied starlings (6.2% occurrence). Average volume of this fruit as fed to nestlings was 0.1-0.2 ml and insignificant when compared to the volume of crickets and grasshoppers fed to nestlings, which each had volumes of 0.5-2 ml (19.5 and 9.7% occurrence, respectively). Had nestling diets been compared volumewise (impossible because

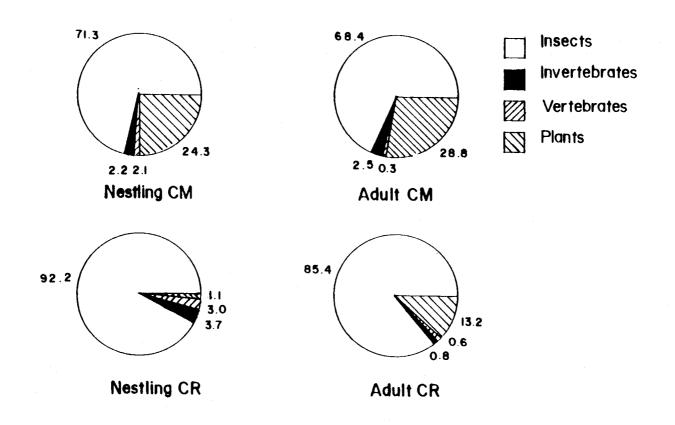
Diets of Adult VS Nestling Starlings'



Diets significantly different between adults and nestling within species

Figure 5. Differences in proportions of diets of adults and nestlings of black-collared starling (BS), and pied starling (PS). Bang Pra, Thailand. 1968-1988.

Diets of Adult VS Nestling Mynas¹



Diets significantly different between adults and nestlings within species

Figure 6. Differences in proportions of diets of adults and nestlings of common myna (CM), and crested myna (CR). Bang Pra, Thailand. 1986-1988.

I was unable to obtain volumes of foods fed to nestlings), nestling diets likely would have had higher volumes of insects and lower volumes of plant material.

Common mynas exhibited higher similarity of diets between adults and nestlings ($\underline{P} < 0.05$) than the other three species (Fig. 5-6). This similarity might have stemmed from their feeding habits; they often lived and foraged close to human habitation, utilizing exotic foods such as kitchen scraps and animal feeds for themselves and their nestlings.

Diets of adult and nestling black-collared starlings did not differ in composition of insects (46.8% occurrence vs 49.9% occurrence) but were significantly different in frequencies of non-insect invertebrates, vertebrates, and plant material (P \leq 0.01). Nestlings had higher frequencies of non-insect invertebrates and vertebrates than adults (29.1% and 14.7% vs 13.5 and 5.5%, respectively). They also had significantly lower frequencies of plant material in their diet than adults (6.2% vs 34.2%). It is worth noting that although the black-collared starling is the most frugivorous species of the group (Fig. 3), nestlings were fed a diet low in plant composition (6.2% occurrence) (Fig. 5). Black collared starling young were the heaviest of the 4 sturnids, and might have required a higher protein diet for growth.

The diet of crested myna nestling's also had higher insect, non-insect invertebrate and vertebrate, and lower

plant material frequencies than those of adults (Fig. 6).

Insect prey brought to nests of all 4 species were generally much larger in estimated size than those found in diets of adults. Grasshoppers consumed by common myna adults were normally 1.2-2 cm long, those brought to nestlings were estimated to be 4-6 cm long. Black-collared starlings also brought prey to nestlings that was larger than normally consumed by adults.

This behavior of bringing larger prey for nestlings probably reflected an effort to maximize energy gain for nestlings per foraging trip. This finding was consistant with that of Tinbergen (1981), who found that parents of European starlings (Sturnus vulgaris) swallowed small items and collected the larger ones for the nestlings.

Foraging Habitat Use

None of the sturnids except the black-collared starling utilized cover types in proportion to their availabilities. Instead, they exhibited strong selection for open cultivated land (Fig. 7). Of the 4 species, black-collared starlings most frequented woodlands while pied starlings foraged in woodlands the least (Fig. 7). In open cultivated land, each species exhibited distinct selection for different foraging habitat. Black-collared starlings and common mynas selected sparsely- covered and short to medium ground vegetation (height = 2-10 cm), and

Proportion of Use of Foraging Habitat

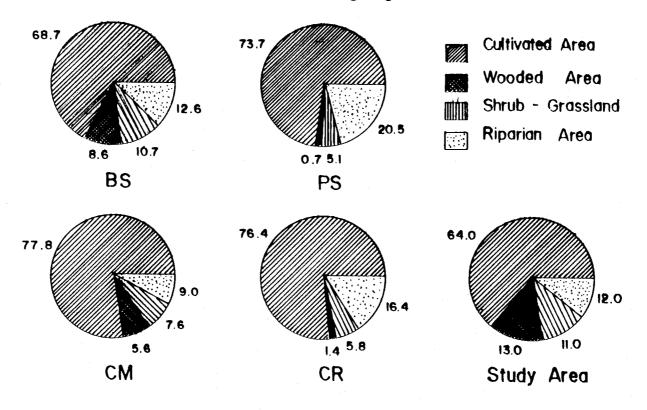


Figure 7. Comparison of availability and use of 4 foraging habitats by the black-collared starling (BS), pied starling (PS), common myna (CM), and crested myna (CR). Bang Pra, Thailand. 1986-1988.

selected for drier ground. Pied starlings and crested mynas, in contrast, foraged in tall grass (15-30 cm) as readily as in short grass. Furthermore, pied starlings clearly selected for moist or marshy habitat, and were rarely seen feeding far from water.

Neu's procedure revealed that the black-collared starling was the only species that used all cover types in proportion to availability (Fig. 7). It foraged in cultivated areas as well as in wooded, shrub-grass and riparian areas. In wooded areas, however, black-collared starlings foraged mainly at the edges or at the edge of openings inside these wooded areas. When foraging in riparian areas or in rice paddies where the substrate was wet and soft, black-collared starlings tended to forage on drier and firmer ground than did the pied starling and crested myna.

Pied starlings selected for open fields of agricultural land, especially in wet or moist rice paddies or flooded grasslands. They also selected for wet, marshy habitat around riparian areas (Fig. 7). Pied starlings were seldom observed foraging far from water, and when feeding in mixed flocks, tended to forage on wetter and softer ground, utilizing tall ground vegetation as long as the substrate was soft.

Frequency of use of cultivated areas by common mynas was greater than expected and less than expected for wooded areas. Common mynas utilized grass-shrub habitats and

riparian areas in proportion to their availabilities (Fig. 7). They selected for short to moderate ground vegetation (5-15 cm) and avoided tall and dense grassland. When foraging in rice paddies, common mynas tended to feed on firmer and drier portions.

Crested mynas selected for open cultivated areas and moist, marshy habitats around riparian areas (Fig. 7) and avoided dense woodlands. Shrub-grasslands received little use except when cattle were present. Of the times crested mynas were observed feeding in shrub-grasslands (n=25), 21 (84%) were associated with grazing cattle.

Nest Site Selection

A total of 157 nests was located, of which 48 were black-collared starling, 40 were pied starling, 40 were common myna and 29 were crested myna. Common and crested mynas are predominantly secondary cavity nesters while black-collared and pied starlings build dome-shaped nests. Nesting material of the latter 2 species consisted mainly of grass, creeper stems, small plants, and, occasionally, pieces of paper, rags and discarded plastic bags.

Analysis of variance of nesting site variables of all possible pairs indicated differences among species of sturnids in all variables except dbh of nest tree, basal area, % grass coverage and % of bare ground (Table 1).

Table 1. Comparison of nest site characteristics among the black-collared starling (BS), pied starling (PS), common myna (CM) and crested myna (CR).

	BS	CM	CR	PS
Height of nest t	ree (m)			
X S.D. F - test	3.3	3.8	11.2 3.6 , PS * CR; BS	2.2
dbh of nest tree	(m)			
X S.D. F - test	0.14	0.07	0.29 0.09 r all possible	0.23
Basal area (m²)				
	0.08	0.02	0.08 0.07 r all possible	0.1
Height to lowest	branch (m)			
	4.2	3.0 S; PS * CM	7.2 2.8 ; PS * CR; BS	1.2
Nest height (m)				•
X S.D. F - test	2.6	3.0	6.9 2.2 ; CR * BS; CR	2.1
Distance to house	e (m)			
X S.D. F - test	146.2 131.2 CM * B		122.0	173.7 132.2
Distance to road				
X S.D. F - test		11.2 16.4 S: PS * CM		28.9 29.8

Table 1. (continued)

	BS	СМ	CR	PS
Distance to water	(m)			
$\bar{\mathbf{x}}$	164.7	101.3	168.4	40.6
S.D.	146.5			77.7
F - test	PS	* BS; PS * CM; *CR		
Percent tree cove	rage			
\bar{x}	26.9	43.0	19.9	22.3
		26.6		18.8
F - test	CM	* BS; CM * CR;	CM * PS	
Percent shrub cov	erage			
$\overline{\mathbf{x}}$	11.9	24.5	23.6	8.1
		22.8		
F - test	BS	& CM; BS * CR;	PS & CM; PS	& CR
Percent grass cov	erage			
$\bar{\mathbf{x}}$	50.9	53.9	48.4	52.4
S.D.		29.2		
F - test	not s	ignificant in a	ll possible p	airs
Percent bare area				
\bar{x}	34.5	28.4	26.7	31.8
S.D.	26.9	18.5	20.4	32.1
		ignificant in a		

^{* =} significant difference ($P \le = 0.05$)

BS * CM * CR * PS = significant different in all possible
 pairs

Pied starlings used trees with forked branches exclusively, while black-collared starlings utilized trees with branching limbs (52%) as well as coconut palms (48%) which have no branches. Common and crested mynas, on the other hand, depended almost entirely on coconut trees as nesting sites; all except 2 of the common myna nests found were on coconut trees, either in holes or in the cup-shaped pockets at the junction of the fronds and the trunk.

The crested myna is more strictly a cavity nester.

Its favorite nesting sites were openings in the top of dead coconut trees where the crown was broken off, or cavities between clusters of coconut fruits and the trunk, behind layers of hanging dead fronds.

Common myna nests were found significantly closer to human habitation than the other 3 species, and, because most of the nests were built on crowns of coconut trees, the height of nest and lowest branch from ground, and height of nest tree were the greatest among the species.

Pied starlings built their nests significantly closer to water and at greater distances from houses than those of the other sturnids. Because tall trees in marshy habitat were uncommon, pied starling nests were found at a lower height.

Black-collared starlings sometimes built their nests on coconut trees, but always at greater distances from human habitation than the common myna. Because black-collared starling nests were found on palm and non-palm

trees, they shared nest site characteristics with pied starlings and common mynas.

Crested mynas, in contrast, were limited to natural cavities found mostly in dead coconut trees with broken crowns. Their nest sites had the lowest % canopy coverage, and most nests were relatively farther away from human habitation than those of the common myna and the black-collared starling.

Stepwise discriminant function analysis of nesting site characteristics resulted in 3 discriminant functions (Table 2). The first function, which accounted for the greatest proportion of the total variance (81.3%), was associated with species of nest tree, height of lowest branch from ground, height of nest tree, distance from nest tree to road and % grass coverage around the nest tree. This function clearly was correlated with species of nest trees, and separated species nesting on palm (coconut) trees from those nesting in non-palm trees. Pied starlings were never found nesting on coconut trees, whereas black-collared starlings nested on palm and non-palm trees, and all common and crested myna nests were found on coconut trees. Palm (coconut) trees were associated with close proximity to roads or foot paths, sparsely covered ground, greater tree height and higher lowest branch.

The second function explained an additional 10.5% of the total variance and was correlated with nest height, % shrub coverage and % bare ground.

Table 2. Pooled-within-groups correlations between discriminating nest site variables and canonical discriminant functions.

<u>Variables</u>	Function	1	Function 2	Function	3
Nest tree	0.8073	*	0.1802	-0.0444	
Lowest branch	0.6538	*	0.0067	0.3313	
Tree height	0.4454	*	0.3439	0.2658	
Distance to road	-0.2341	*	-0.0833	0.0256	
% grass cover	-0.0761	*	-0.0070	-0.0351	
		-			
Nest height	0.2081		0.5291	** 0.3910	
% shrub coverage	0.2294		-0.2425 *	** -0.1235	
<pre>% bare ground</pre>	-0.0512		0.1900	-0.0017	
% canopy coverage	0.1286		0.0725	 0.7854	***
Distance to water	0.2083		0.4517	-0.4827	***
Distance to house	-0.0676		-0.0375	0.3604	***
Basal area	-0.0613		-0.0470	-0.0735	***
Nest tree dbh.	0.0228		0.0004	-0.0268	***

^{*} Variables discriminanted by discriminant Function 1

^{**} Function 2

^{***} Function 3

The third function accounted for 8.2 percent of the total variation and was identified by canopy coverage, nest tree dbh, basal area and distance from nest to the nearest water. This function was also correlated with type of nest tree. A non-palm tree would normally have greater canopy coverage, greater dbh and basal area, and, when chosen as nest tree, tended to be closer to water.

A discriminant function analysis classification of the original set of cases within each group was conducted to check the adequacy of the discriminant function to predict bird species based on nest site characteristics (Table 3). The discriminant function analysis indicated that nest site micro-habitats of these sturnids were separated primarily (81%) by 5 habitat variables: species of nest tree (palm vs non-palm) (which was directly correlated to the other variables); height of lowest branch; height and % of grass cover at base of nest tree; and distance of nest tree from roads. Twenty-seven % of black-collared starling nests, 68% of common myna nests, 83% of crested myna nests, and 95% of pied starling nests were correctly classified using these criteria.

Scatterplots (Fig. 8) displaying nest site requirements of the 4 sturnids demonstrate that the black-collared starling has the most generalized nest site requirements.

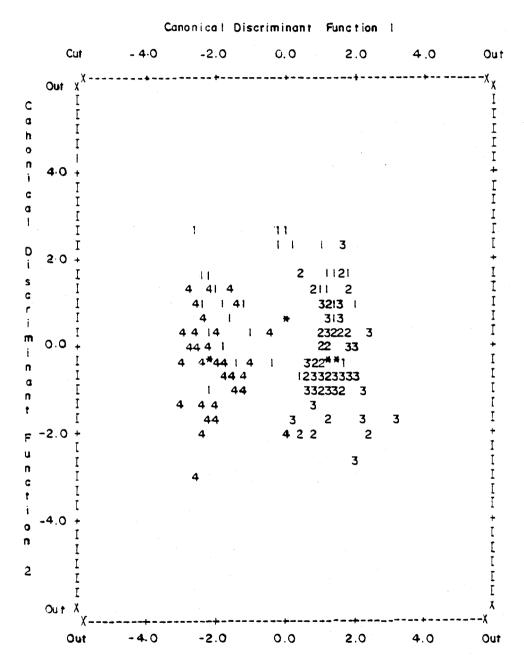


Figure 8. Scatterplot of the first and second canonical functions derived from Discriminant Function Analysis of nest site characteristics for the 4 sturnids. Black-collared starling = 1, common myna = 2, crested myna = 3, pied starling = 4.

Table 3. Discriminant Function Analysis classification by nest site characteristics of black collared starling (BS), pied starling (PS), common myna (CM) and crested myna (CR): accuracy of prediction.

Actual species	No. of cases		Predicted	species	
		BS	CM	CR	PS
BS1	48	13 27.1%	<u>_7</u>	13 27.1%	<u>15</u> 31.3%
		27.1%	14.6%	27.1%	31.3%
CM	38	<u> </u>	26 68.4%	11 28.9%	<u> </u>
		2.6%	68.4%	28.9%	0%
CR	29	_1_	13.8%	24	<u>0</u> 0%
.\$		3.4%	13.8%	82.8%	0%
PS PS	40	_1	08	_1	<u>38</u> 95%
		2.5%	0%	2.5%	95%

Percent of "grouped" cases correctly classified = 65.16%

The pied starling had relatively different nest site requirements and had virtually no nest site characteristics in common with common and crested mynas.

Crested and common mynas had high similarity of nest site characteristics as derived from discriminant function analysis. Both are cavity nesters and had to rely on palm trees for nest sites (Table 4).

All 4 species are edge species, selecting for nesting trees along the edge of a stand or an isolated tree in the middle of a field. Densely wooded areas were not selected for by any of the 4 sturnids.

Pied starlings selected nest sites where wet, marshy or riparian areas, or rice cultivation were nearby regardless of height or canopy coverage to the nest tree. Pied starling nests had the lowest mean nest height, lowest mean nest tree height, lowest mean lowest branch height, and had the lowest number of trees with the nesting site plot. The critical factor in selection of nest trees by pied starlings was distance of nest tree to the nearest water.

These factors characterized pied starling nesting habitat as open riparian or marshy areas and areas adjacent to rice cultivation with scattered small to medium trees far from human habitation and with relatively dense ground vegetation. The behavior of placing its nest a short height above the ground, and with little concealment, reflects the affinity of pied starlings to marshy habitat

Table 4. Species of tree used for nesting by black-collared starling (BS), pied starling (PS), common myna (CM), and crested myna (CR).

Tree Species	BS	PS	CM	CR
Coconut palm	231	· -	38	27
Palmypa palm	-	-	-	2
Siamese rough bush	13	24		-
Indian plum	3	7	-	-
Bamboo	-	5	_	-
Other non-palm trees	9	4	-	-
Houses	-	-	2	-

¹ Number of nests found in each tree per sturnid.

where tall trees are rare and ground predator accessibility is low (Joern and Jackson 1983).

Black-collared starlings were less selective in choosing nesting sites. Their nests were found on crowns of coconut trees as well as on branching trees such as Siamese Rough Bush, and generally were at greater distances from marshy habitats or water impoundments and higher above ground than pied starling nest sites. Black-collared starlings also selected nest sites on the fringe or edge of a tree stand or coconut plantation and in isolated trees in the middle of rice fields.

Common and crested mynas had similar nest site characteristics and both are secondary cavity nesters. Additionally, common mynas utilized holes in buildings and house eaves. Five percent (2 of 40) of common myna nests examined were found on houses or buildings; the remaining 38 were on coconut trees. The high percentage of nests in cococuts indicated selection for these trees, probably because coconuts were the only tree providing pocket-shaped nest sites and because they were close to human habitation.

Nesting in coconut trees by the mynas suggested that they chose close proximity to human habitation where foods are more abundant (the mean distance of common myna nest trees to human habitation was the closest of the 4 species).

The crested myna selected coconut trees that either had been dead for awhile and had broken-off crowns which

created opened- top vertical cavities, or coconut trees that had layers of hanging dead fronds. Crested myna nests were farther from human habitation than those of the common myna (Table 1) and crested mynas were never observed foraging around houses or entering building or roofed livestock pens to feed on livestock feeds.

Morphology and Behavior

A total of 876 sturnids (214 black-collared starlings, 213 pied starlings, 224 common and 225 crested mynas) was collected. Univariate pairwise comparisons revealed significant differences in many morphological characteristics among the 4 species (Table 5). The black-collared starling was the largest of the 4 species, had the longest and most rounded wings, and the second longest and heaviest bill. The pied starling was the smallest species of the group, but had the longest, thinnest, and narrowest bill. It also had the most pointed wings and the lowest wing loading (high ratio wing area/body weight).

Common and crested mynas shared several morphological characteristics but differed in weight, and shape of bill and wing. Common mynas were significantly heavier, had thicker and broader bills and higher wing loading that crested mynas.

Presumably, the large size and relatively long wings of the black-collared starling, which consumes more fruit

Table 5. Comparison of morphological characteristics among the black-collared starling (BS), pied starling (PS), common myna (CM) and crested myna (CR).

	BS		CM	CR	PS
Weight (gm)					
X S.D. F - test			113.55 10.38 * CR * P	10.58	83.27 6.28
Total length (cm)					
X S.D. F - test	27.85 1.24 BS		1.31	25.10 0.90	24.12 0.97
Wing length (cm)					
X S.D. F - test	21.34 0.82 BS		19.06 0.79 * CR * P	18.68 0.62 S	17.37 0.63
Wing span (cm)					
X S.D. F - test	1.55		42.84 1.33 * CR * P	1.26	38.80 1.07
Tail length (cm)					
X S.D. F - test	9.21 0.82 BS		8.56 0.59 * CR * P	8.16 0.61 S	7.84 0.49
Bill length (cm)					
X S.D. F - test	2.90 0.18 BS	* CM	2.17 0.12 * CR * P	2.34 0.15 S	2.96 0.18
Bill width (cm)					
X S.D. F - test			0.83 0.05 * CR * P		0.74

Table 5. (continued)

<u> </u>				
	BS	CM	CR	PS
Bill depth (cm)				
X S.D. F - test	0.06	0.82 0.05 S; PS * CM;	0.81 0.05 PS * CR; BS	0.05
Tarsus length (cm)				
X S.D. F - test	0.23	0.18 S; BS * CM;	3.35 0.20 BS * CR; PS	0.21
Hind toe (cm)				
X S.D. F - test	0.26	0.23	2.75 0.22 PS * CR; CM	0.19
Inner toe (cm)				
X S.D. F - test	0.17	0.17	2.25 0.14 PS * CR; BS	0.12
Outer toe (cm)				
X S.D. F - test	0.28	0.22 S; PS * CM;	2.35 0.18 PS * CR; CF	0.21
Foot span (cm)				
X S.D. F - test	0.22	6.50 0.21 M * CR * PS	6.83 0.23	5.93 0.20
Wing area (cm ²)				
X S.D. F - test	12.64	134.62 9.80 M * CR * PS	10.74	119.82 10.08

Table 5. (continued)

	BS	CM	CR	PS
Bill length/bill	width			
$\overline{\mathbf{x}}$	3.23	2 66	2 22	
S.D.	0.19	2.66 0.18		3.81
F - test		CM * CR * P	0.19 S	0.27
Bill length/bill	width			
$\overline{\mathbf{x}}$	3.40	2.63	2 01	
S.D.	0.20	0.17	2.91	4.0
F - test		CM * CR * PS	0.18	0.31
Wing area/wing l	ength (cm ² /c	cm)		
$\overline{\mathbf{x}}$	7.29	7 06	6.80	ć 00
S.D.		0.46		6.90
F - test		CM; BS * CR;	0.52	0.61
	CM * I	es cr	D5 * P5; C1	1 * CR;
Wing area/Weight	(cm^2/gm)			
$\overline{\mathbf{x}}$	1.12	1.19	1.29	1.44
S.D.	0.12	0.11	0.12	0.14
F - test		M; BS * CR;		0.14

^{* =} significant difference ($P \le 0.05$)

BS * CM * CR * PS = significant different in all possible pairs

than the other 3 sturnids, are adaptations that enable it to make the long flights between widely scattered fruit trees.

The black-collared starling possessed the second longest, widest, and deepest bill, which enabled it to secure larger and heavier prey items such as the 5-6 cm cerambid beetles, and small frogs (one frog 11 cm long was recovered from a nestling). The larger size also allowed the black-collared starling to carry heavier foods to the nest. On several occasions black-collared starlings were observed carrying balls of entwined earthworms to the nest. The weight of the worms sometimes was so great that the birds had to stop 1-2 times to readjust their holds, and it was obvious they were under tremendous strain. Longer and stouter bills gave the black-collared starlings an advantage of digging deeper into substrates and in moist grasslands it appeared to be the most efficient worm digger of the group.

When using the open-bill probing method, blackcollared starlings were able to dislodge larger and heavier
chunks of earth to expose subterranean prey. [In birds
that employ open-bill probing, the protractor muscle is
greatly developed, reaching its maximum in the genus
Sturnus, especially in the pied starling. Open-bill
probing is conducted by thrusting the closed bill into the
substrate and then forcing it open with an upward movement
of the upper mandible, exposing insects and non-insect

invertebrates. Birds with this ability have the anterior portion of the skull pinched in to allow the eyes to move forward during probing, enabling the bird to see where it is probing without having to tilt its head to obtain optimum viewing (Beecher 1978].

The pied starling had the longest bill despite the fact that it was the smallest of the 4 species. Its long and slender bill required it to feed in softer, moist substrates, and it was seldom observed foraging far from marshy habitat, waterholes or rice paddies. The pied starling used open-bill probing the most frequently of the 4 species, and differed from the black-collared starling (which fed on drier, firmer ground) by jabbing and poking into crevices, under chunks of earth, and into clumps of grasses. Its diet featured soft-bodied non-insect invertebrates and insects, which live in wet environments, like mole crickets. Pied starlings moved slowly and methodically as they searched the ground for food, appearing more thorough and deliberate than the other 3 species.

Bills of the common and crested mynas are similar in size and shape, but the common myna's is slightly shorter and wider, which presumably allows it to feed on a more generalized diet. It is the most agile of the 4 species, and is capable of rapid darting and short flights after flushed insects.

Although all 4 species used open-bill probing, pied

starlings used it the most extensively, (Table 6) possibly because they fed primarily in wet, marshy areas where the ground was softer and more amenable to this foraging technique. Black-collared starlings used this feeding method slightly less than the pied starling, but were able to dislodge larger pieces of earth because of their larger bill size.

Common and crested mynas used open-bill probing considerably less often than black-collared starlings. The crested myna employed a "beater" tactic of feeding in large flocks. Feeding mynas stirred up insects by walking around or leap-frogging over each other. Crested mynas used grazing livestock as beaters to flush insects, ostensibly seeking out grazing cattle. Common mynas also used cattle as beaters, but not as extensively as crested mynas (proportion of frequencies of crested and common myna were feeding in association with cattle was 7:3). Black-collared and pied starlings, by contrast, were never observed using grazing cattle as beaters. They fed in the vicinity of grazing cattle but never ventured close enough to feed on insects flushed by the cattle.

The crested myna had the longest hind toe and its foot span was slightly longer than the black-collared starling's, even though the black-collared starling was 30% heavier (Table 5).

Table 6. Percent open-bill probing on different foraging micro-habitats of black-collared starling (BS), pied starling (PS), common myna (CM), and crested myna (CR).

	Sparsely covered soft substrate	Short grass (5-10 cm.)
PS	80 - 90	85 - 95
BS	80 - 85	85 - 90
CM	<40	<30
CR	<40	<30

The black-collared starling, which consumed the highest proportion of fruit, in contrast, had the second-longest hind toe and foot span.

Black-collared starlings, as the heaviest species, could not reach fruits growing on long, thin branches of plants such as <u>Securinega virosa</u>, on which crested mynas fed in large flocks.

The pied starling had the shortest hind toe and foot span and was rarely seen feeding in trees, except when Eugenia sp. and Atreblus asper (which have large, sturdy branches), were fruiting.

Common mynas, with intermediate hind toe and foot span lengths, selected dry, sparsely-covered ground for foraging and were rarely seen feeding on soft, wet or partially-flooded rice paddies.

Stepwise discriminant function analysis produced 3 functions for segregating the 4 species on the basis of morphology (Table 7). The first function explained 57% of the total variance and was associated with bill shape (bill length/bill depth and width) and bill length. This function separated birds with long, straight, narrow bills from those with shorter, broader, and slightly curved bills.

The second function accounted for 35% of variance and was associated with weight, total length and wing span,

Table 7. Pooled-within-groups correlations between discriminating morphological variables and canonical discriminant functions.

<u>Variables</u>	Function 1	Function 2	Function 3
Bill length/Bill width	0.6965 *	-0.2794	-0.1798
Bill length/Bill depth	0.5805 *	-0.1943	-0.1434
Bill length	0.5328 *	-0.5017	-0.2260
Tarsus length	-0.3132 *	-0.2485	-0.2209
Inner toe	-0.1876 *	-0.0994	-0.0678
Outer toe	-0.1599 *	-0.0734	0.0131
Wing span	-0.2878	-0.7714 **	-0.0421
Wing length	-0.2223	-0.6245 **	-0.1105
Weight	-0.2540	-0.5965 **	0.1677
Wing area	-0.1206	-0.4168 **	0.0619
Bill depth	-0.0461	-0.2747 **	-0.0497
Tail length	-0.0997	-0.2506 **	0.0907
Wing area/Weight	0.1965	0.2290 **	-0.1176
Bill width	-0.1546	-0.1756 **	0.0113
Total length	-0.0329	-0.0495 **	0.0343
Foot span	-0.3140	-0.0956	-0.6941 ***
Hind toe	-0.1381	-0.0469	-0.1985 ***
Wing area/Wing length	-0.0175	-0.1216	0.1318 ***

^{*} Variables discriminanted by discriminent Function 1

^{**} Function 2

^{***} Function 3

wing length, wing area, and wing loading, which relates to speed of flight.

The third function accounted for 8% of the variance and was associated with foot span and shape of wing, which related to maneuverability during flight.

A classification of the original set of cases within each group was conducted to check the adequacy of the discriminant functions to correctly identify birds on the basis of morphological features. On average, discriminant function analysis correctly classified 96.5% of the cases (Table 8).

Scatterplots (Fig. 9) indicated that crested and common mynas shared many morphological characteristics, as did the black-collared and pied starlings.

Breeding Ecology

A total of 157 nests was located. Common mynas and pied starlings bred earlier (February) than either the black-collared starling (March), or crested myna (late March-early April).

Clutch sizes of the 4 species ranged from 2-5 eggs (Table 9). Incubation periods ranged from 14-16 days for the pied starling to 16-18 days for the black-collared starling. Common and crested mynas had similar incubation periods of 15-18 days. Pied starlings fledged slightly faster (20-24 days) than black collared starlings (23-26 days). Common and crested mynas had similar fledging

Table 8. Discriminant Function Analysis classification by morphological characteristics of black-collared starling (BS), pied starling (PS), common myna (CM) and crested myna (CR): accuracy of prediction.

		-couracy	or breatcrio	11.	
Actual species	No. of cases		Predicted species		
		BS	CM	CR	PS
BS ¹	214	212 99.0%	2 1.0%	_ <u>0</u> 0%	_0 0%
CM	224	<u>0</u>	220 98.2%	<u>4</u> 1.8%	<u> </u>
CR	225	0	20 9.0%	205	0
PS	213	0% 	9.0% 0 0%	91% 0 _0%	0% <u>213</u> 100%

Percent of "grouped" cases correctly classified - 96.5 percent

Canonical Discriminant Function 1 Out -8.0 4.0 8.0 Out x C a п 0 8.0 C 3 32332 333 C 333 323333333 2 22222333333333 2232223333*333333 m 22223*3333333 i 22222323732 n 2222222 Œ 22 n 1 1 111 11111 F 111*1111 u 11111111 n 1111111 C 1111 1 -8.0 . 2

Figure 9. Scatterplot of the first and second canonical funtions derived from Discriminant Function Analysis for the morphological characteristics of the 4 sturnids. Black-collared starling = 1, comon myna = 2, crested myna = 3, pied starling = 4.

0

4.0

9.0

Out

Out

-8.0

-4.0

periods, from 22-25 days (Table 9).

Common mynas averaged 3.4 eggs per clutch and had the highest hatching success (73.1%) and fledging success (53.9%) while crested mynas and pied starlings had similar hatching (64.0% and 64.3%) and fledging successes (46.1% and 46.0% respectively). Black-collared starlings had the lowest hatching success (57.5%). (Table 9).

Black-collared starlings suffered 23.5% (12 nests) of nests lost to weather and depredation while pied starlings had the highest clutch size $(\bar{X}=4)$, but the lowest percentage of fledging success (46.0%) (Table 9). Pied starlings lost 29% (9 nests) of their nests to heavy rain and predation (Table 9). Pied starling nests and nestlings have a foul odor and are not sought after as pets. Nevertheless, 12 nestlings from 4 nests were removed by humans.

The crested myna, because of its specific nest site requirements, was confined to a narrower range of nesting substrates. The crested myna had an average clutch size of 3.3 eggs/nest (Table 9), hatching and fledging 64.0% and 46.1% of its young, rates that were almost identical to those of the pied starling. It also suffered the highest nest loss (8 nests, 29.6%) (Table 9) due to weather and removal by man (the crested myna is sought after as a pet because it is a good mimic).

Table 9. Hatching and fledging rates of black-collared starlings (BS), pied starlings (PS), common myna (CM), and crested myna (CR).

	No. Nests	Range	Clutch	size	Percent Hatched	Percent Fledged	Percent Nest Lost
BS	51	2-5	2.8	1.18	57.5	52.5	23.5
PS	31	2-5	4.0	0.82	64.3	46.3	29.0
CM	38	2~5	3.4	0.86	73.1	53.9	28.9
CR -	27	2.5	3.3	0.78	64.0	46.1	29.6

DISCUSSION

Results of this study suggested that two pairs of closely related sympatric mynas and starlings achieved ecological separation through differences in morphology and behavior, which, in turn, were manifested by differences in diet, foraging ecology and habitat selection as proposed by Orians (1969), Schoener (1971), and Karr (1971) for tropical species.

Differences in trophic appendages, such as bill size and shape, and in locomotory appendages (size and shape of wings and toe lengths) of these 4 sturnids, reinforced by food habits and behavior, innate or learned, dictated where and how the species foraged and nested. According to Klopfer (1973), differences in feeding behavior or feeding structure, such as specialized feeding apparatus and learning, resulted in differences in diets, and may be used to infer responses to interspecific competition.

However, Diamond (1978) and Schoener (1982) warned against interpreting ecological systems on the basis of a limited number of interactions among a small number of members of a community. Because ecological systems are so multi-layered and complex, they may be influenced by temporal or spatial changes in the environment, chance events, parasites or predators, competition mutualism, or by the complicated interplay of all these factors. He suggested that one cannot look for overall general theories but must look for influences that are more important in one

setting as against another.

On the other hand, ecological separation of sympatric species observed in this study might be caused by ongoing interspecific competition in which one species is in the process of being crowded out by the other(s), such as might be inferred by the rapid range expansion of the common myna (Baker 1926, Ali and Ripley 1972).

The common myna, a commensal of humans, is capable of colonizing formerly virgin areas developed by man, even far out into the jungle (Baker, 1926) It was rarely seen far from human settlement, and was opportunistic and aggressive. Of the 4 species observed in my study, the common myna was found in the greatest numbers in and around cities, towns and human settlements (personal observation). Aagaard (1930) reported that common mynas were rare in and around Bangkok in the period 1910-1925, but were becoming more and more numerous. At the same time, pied starlings, which had been numerous in Bangkok, were declining in number.

At present, common mynas share with the tree sparrow (Passer montanus) the distinction of being the commonest and best known birds in Thailand. The tameness (or boldness) of the common myna is likely to carry selective advantage and has probably contributed to the urbanization of this species over the last 60-70 years. High abundance of food year round in the vicinity of human settlement likely produced the high breeding density of common mynas

in urban habitats.

The crested myna shared many of the common myna's traits. Although it selected for open, cultivated areas, it was also found in cities and towns, only not as numerous as the common myna. I was told during interviews with long-time local farmers that crested mynas and pied starlings were found in greater numbers in the study area 30-40 years ago, but as more and more rice paddies were replaced by tapioca and sugar cane plantations crested mynas and pied starling numbers had declined considerably, while numbers of common mynas increased, probably due to the increase in human settlement and decline of marshy habitat, a situation favoring expansion of common myna range.

Alternatives different patterns of resource use under different settings may exist. For example, Weins (1974), and Rotenberry (1980) presented evidence of broad dietary overlaps, unpredictable species composition and poor correlations between diet and morphology in shrub-steppe grasslands with small-sized bird communities. They argued that stochastic environmental affects might be important for many animal communities, whereas interspecific competition might be insignificant despite the fact that Schoener (1965) pointed out that smaller birds can tolerate greater dietary overlap than larger birds because smaller birds feed upon smaller prey which are more abundant.

Wilson (1975) also stated that competition is more common

in stable than in unstable ecosystems, and even when it occurs, it can be suspended for long periods of time by the intervention of density-dependent factors, especially unfavorable weather conditions.

Direct competition was not evident in this study; however, all four species under study were segregating their food resources, and food might have been limiting. Most animals species increase at geometric rates, and numbers are checked only by food supply (Lack, 1966, Wynne-Edwards, 1962). Ashmole (1968) and Torborgh (1977) maintained that food habits of coexisting species diverge during the most difficult season thereby reducing competition.

At all times during this study all 4 species differed markedly in their feeding micro-habitats and were consuming different types of food secured by different behaviors. Only under certain circumstances, when food was suddenly highly abundant for a short period, such as when prey was exposed by plowing, would all 4 species consume similiar food. Food segregation by these 4 species suggested that food in the tropical setting of this study was not as abundant as it was thought to be and interspecific competition might be operating.

Results of this study suggested that differences in body mass, size and shape of trophic and locomotory appendages, and, ultimately, patterns of resource segregation among the 4 sturnids may have diverged as a

result of interspecific competition. Wherever related bird species overlapped in range, they were either different in size of body or beak, or they used different methods of seeking food (Diamond, 1973).

Differences in shapes of bills and wings identified by this study were corroborated by different feeding techniques and selection for different foraging habitats. Pied starlings segregated according to food habits (utilized more non-insect invertebrates and exhibited a distinct length/bill width ratio) and foraging habitat (use of soft, marshy and muddy habitat).

Black-collared starlings, also segregated on the basis of food habits (larger prey, a different bill length/bill width ratio, possibly related to use of drier and firmer substrates for open-bill probing) and foraging habitat (relatively rounder wings added maneuverability for flight in dense, wooded areas).

Common and crested mynas had shorter and broader bills than the starlings and open-bill probed less frequently. The common myna, with the shortest bill, open-bill probed the least, adapting instead a feeding behavior characterized by dashing and jabbing after ground prey and flights after disturbed insects. It also fed on kitchen scraps, livestock feeds, and entered buildings to forage on poultry feed.

Crested mynas, on the other hand, adapted a behavior independent of morphology preferring to feed in association

with grazing livestock, and captured insects stirred up by the grazing disturbance. Heatwole (1965) discovered that cattle egrets that fed in association with cattle were about two and a half times more efficient than egrets that did not.

The relatively longer hind toe and foot span of the crested myna were reflected in the better clinging or gripping ability of the crested myna which foraged readily in dense, tall grasses and reeds (Leisler and Winkler, 1985). The crested myna fed on flower nectar: longer toes would certainly enable it to cling to smaller branches and favor access to fruits and flower nectar. Long foot span and toes would also enable crested mynas to walk on soft mud and rice paddies.

Difference in nest site selection among these 4 species also suggested ecological segration through difference in behavior which is independent of morphology.

The mynas nested exclusively on palm trees while starlings nested on (non-palm) branching trees, although black-collard starlings built their nests on palm trees as well as branching trees.

As a secondary cavity nesting bird, and a commensal species of man, the common myna was able to use natural and man-made artificial cavities. The common myna adapted a nest-selection behavior (nesting in "opened" or cup-shaped cavities), that gave it an advantage over the crested myna as the crested myna required a complete hole to build its

nest in. This behavior enabled common mynas to have less restrictive nest site requirements, and a broader nesting site substrate to select from.

Pied starlings built their nests on small to medium size trees close to water or marshland. Pied starlings had the highest clutch size $(\bar{X}=4)$, but the lowest percentage of fledging success (46.0%). This was probably due to the placement on exposed, forked branches with little or no concealment (this study and Baker 1926). Such placement exposed nests to unfavorable weather and predation (Lill, 1974). Pied starlings lost 29% (9 nests) of their nest due to heavy rain and predation.

Pied starlings displayed a trait that was not observed in the other 3 species; placing objects that have a strong odor such as fish heads, small mammal bones, or discarded snake skins not intended as nesting material on top of the entrance tunnel of the nest. These objects were perhaps used to camouflage the strong odor of the nest, as food to divert potential predators from nestling, or as a repellent in cases when snake skins were used.

Black-collared starlings had the lowest clutch size $(\bar{X}=2.8)$ because they were parasitized by the koel (Eudynamys scolopacea). The female koel removes a host species' egg and replaces it with 1 of her own [host parents are lured away from the nest by the male koel, (Ali and Ripley 1972)]. The fledging success of black-collared starlings, when not parasitized by koel was 52.5% as

opposed to 48% when parasitism occurred. Of 51 blackcollared starling nests found, 17 (30%) were parasitized. Eggs in 3 nests were totally replaced by koel eggs. black-collared starling was the only species parasitized by koel, probably for 3 reasons: 1) the black-collared starling was the largest species of the group (wt = 140 gm, total length = 28 cm), hence the higher probability of survival of koel chicks whose adult size was 220-250 gm in weight, and 35 - 45 cm in length. (Smaller species such as pied starlings (wt = 84 gm, total length = 24 cm) would have difficulty finding adequate amounts of food for the parasite chicks); 2) the koel is a secretive species, rarely venturing out into open areas, and most blackcollared starling nests found were located along edges of orchards and woodlands, thus increasing the chances of being parasitized; and 3) it is impossible for a bird the size of the koel to enter nests of common and crested myna because these 2 species are cavity nesters. This left only the black-collared starling as the only member of the group to be parasitized by koel.

Although no nest depredation was witnessed, potential predators in the study area were snakes and humans. The black-collared starling has become a popular pet species, because it has the ability to mimic voices and has a diverse repertoire of songs. Another factor responsible for the high percentage of black-collared starling nest losses was that the koel is also a popular pet species, and

koel nestlings make a loud, rattling hunger call that can be heard up to 60 - 70 m. This call increased the chances of black-collared starling nest depredation by attracting humans.

This study suggested that patterns of resource segregation among the 4 sturnids may have diverged as a result of interspecific competition, with an undetermined level of interference by man.

When studying members of an animal community living in a disturbed, human-altered environment, one cannot overlook the impact of human activities on the ecosystem. Human activities favor one species at the expense of others, and this may hasten the competitive process or even eliminate a species which does not compete well, changing the momentum and direction of the evolutionary process in some species (Lack, 1971).

Sturnids, as a family, have been successful in competing with other bird species because they have abilities to diversify their diets by modification of behavior and morphology (alteration of skull and masculature which enable them to feed on subterranean organisms using open-bill probing technique). Man has also assisted sturnid range expansion by clearing forests and replacing them with open cultivated land which provided artificial foods and nesting sites. Moreover, man has helped expand sturnid range by introducing them to places outside their original ranges (Feare, 1984).

The history of human activity concerning land use, habitat disturbance, and interference with the biotic communities should be considered together with interactions occurring among members of the animal community for a better understanding of patterns of resource partitioning.

CONCLUSION

Results of this study indicated that these 4 species of closely-related sympatric mynas and starlings partitioned their resources effectively through differences in morphological and behavioral characteristics; each species has its own area of specialization.

In this study, four sympatric species were found to differ markedly in several morphological characteristics, foraging ecology and composition of diet, nesting and foraging habitat selection.

The above results are consistent with certain ecological theories and are reasonably convincing that ecological segregation among the 4 coexisting sturnids was achieved by difference in size, habitat selection, feeding micro-habitat, foraging technique, and type of prey.

It is difficult to address resource partitioning without knowledge of the evolutionary history of these sturnids (which is lacking), and the interactions among members of the avian community. Most important of all, perhaps, is the impact on the ecology of these species caused by man's activities. Further study should be directed at resource utilization (partitioning) at the community level, based on interactions of members of the community (parasitism, predation, mutualism, and competition) and human activities.

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