RESEARCH ARTICLE

Interspecific Interactions between Primates, Birds, Bats, and Squirrels May Affect Community Composition on Borneo

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For several decades, primatologists have been interested in understanding how sympatric primate species are able to coexist. Most of our understanding of primate community ecology derives from the assumption that these animals interact predominantly with other primates. In this study, we investigate to what extent multiple community assembly hypotheses consistent with this assumption are supported when tested with communities of primates in isolation versus with communities of primates, birds, bats, and squirrels together. We focus on vertebrate communities on the island of Borneo, where we examine the determinants of presence or absence of species, and how these communities are structured. We test for checkerboard distributions, guild proportionality, and Fox's assembly rule for favored states, and predict that statistical signals reflecting interactions between ecologically similar species will be stronger when nonprimate taxa are included in analyses. We found strong support for checkerboard distributions in several communities, particularly when taxonomic groups were combined, and after controlling for habitat effects. We found evidence of guild proportionality in some communities, but did not find significant support for Fox's assembly rule in any of the communities examined. These results demonstrate the presence of vertebrate community structure that is ecologically determined rather than randomly generated, which is a finding consistent with the interpretation that interactions within and between these taxonomic groups may have shaped species composition in these communities. This research highlights the importance of considering the broader vertebrate communities with which primates co-occur, and so we urge primatologists to explicitly consider nonprimate taxa in the study of primate ecology. Am. J. Primatol. 75:170–185, 2013. © 2012 Wiley Periodicals, Inc.

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INTRODUCTION

For several decades, primatologists have been interested in the study of primate communities [Bourliere, 1984; Fleagle & Reed, 1996; Reed & Bidner, 2004]. A major component of studying primate communities has been to understand how species within communities are able to coexist over time. According to the principle of competitive exclusion, no two species can survive on the same limiting resource [Gause, 1934] and as a consequence no two species can occupy the same niche [Hutchinson, 1957]. A great deal of effort has therefore gone into understanding how niche space is divided among primate species within communities. Niche differentiation among primates has arguably led to differences in

diet, canopy use, habitat use, and body size among other dimensions [Bourliere, 1984; Fleagle et al., 1999]. In this research, primatologists have viewed primate communities as self-contained, and as a consequence, most of our understanding of primate

community ecology derives from the assumption that primates interact predominantly with other primates. However, the full set of species that compete with primates likely includes various nonprimate taxa [Emmons et al., 1983; Estrada & Coates-Estrada, 1985; French & Smith, 2005; Ganzhorn, 1999; Gautier-Hion et al., 1980; Marshall et al., 2009b; Strum & Western, 1982].

The extent to which primates may compete with other taxonomic groups likely varies across sites and biogeographic regions. Indeed there is substantial variation across continents in the proportion of mammals that are primates [Thalmann, 2007]. Intriguingly, primates compose 44% of nonvolant terrestrial mammalian species in Madagascar, whereas in other regions primates constitute only 8–12% of nonvolant land mammals [Jernvall & Wright, 1998]. This difference is particularly interesting in light of recent studies that are consistent with the interpretation that competition between primates is stronger in Madagascar than other regions [Beaudrot & Marshall, 2011; Kamilar & Guidi, 2010]. Given that primates comprise a larger portion of the vertebrate community in Madagascar, these animals may be competing more with each other on this island than in other regions where primates may be competing more with other animals. If competition for food resources is more severe between primates and other animals than among primates, then the effects of competition on community structure may be masked if primates are studied in isolation. Biogeographic regions other than Madagascar are therefore strong candidates for investigating the role of competition with nonprimate taxa in shaping primate communities.

Community ecologists have developed a suite of methods to examine interspecific interactions at the community level. These include metrics for quantifying patterns of species distributions expected to occur if competition and other interactions strongly affect the presence and absence of species across sites, or in other words, if species interactions structure patterns of species co-occurrence. Over the past few decades, there has been considerable advancement in the statistical rigor with which co-occurrence patterns are analyzed [Gotelli & Entsminger, 2011; Stone & Roberts, 1990]. Moreover, much research has incorporated these metrics to evaluate the importance of interspecific interactions in structuring communities, including a meta-analysis of 96 communities in which the strongest results were found for mammals and birds [Gotelli & McCabe, 2002]. Similar patterns occur in microorganisms, which suggests that co-occurrence patterns shaped by interspecific interactions may be present across a wide variety of life forms [Horner-Devine et al., 2007].

In this study, we investigated community assembly hypotheses for primate species in isolation and in addition to a larger community of vertebrates whose arboreal foraging and diet suggest a competitive relationship with sympatric primates. We focused on vertebrate communities in forested areas on Borneo, which is highly species-rich and is the world's second largest island. Of the biogeographic regions in which living primates occur, Asian primate communities are characterized by low species richness relative to other taxonomic groups and also in comparison to primate communities of other regions [Reed & Bidner, 2004; Thalmann, 2007]. Moreover, Ganzhorn [1999] has argued that competition between primates and other taxa is stronger on Borneo than in other regions based on analyses of body mass ratios. We examined to what extent communities are shaped by interspecific interactions when we examined communities of primates alone and in combination with other taxonomic groups. Specifically, we investigated three tests for detecting the effects of species interactions on communities: checkerboard distributions, guild proportionality, and Fox's assembly rule for favored states.

Checkerboard Distributions

One approach to evaluating species interactions is to look for evidence of significant patterning in the presence or absence of species across communities that has resulted from interactions between pairs of species. For example, a checkerboard distribution refers to the alternating presence of ecologically similar species on islands or other habitat patches, such as protected areas. In a checkerboard distribution, species A is present but species B is absent in some patches while species B is present but species A is absent in other patches (Fig. 1). Although there has been a long history in ecology of interpreting significantly checkerboard results as evidence of competition exclusion between pairs of species [Diamond, 1975; Gotelli & McCabe, 2002; Horner-Devine et al., 2007; Stone & Roberts, 1990], recent modeling efforts have suggested that interspecific interactions other than competition may produce significant checkerboard results [Ulrich & Gotelli, 2012]. Although interspecific competition is one
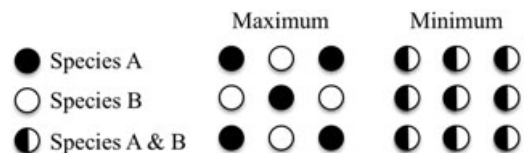
Fig. 1. Illustration of the maximum and minimum extent of a checkerboard distribution of two species. Each circle represents a site that contains either species A shown in black, species B shown in white, or both species. If species A and B are not found at the same site, then they exhibit a maximally checkerboarded distribution, whereas if species A and B consistently co-occur at the same site then they exhibit a minimally checkerboarded distribution.

potential causal factor driving checkerboard distributions, alternative explanations such as habitat checkerboard and historical effects are also possible and warrant additional consideration if analyses produce significant checkerboard results [Gotelli & McCabe, 2002]. We therefore investigated checkerboard distributions to evaluate the presence or absence of significant ecological structure in primate communities alone versus in the context of the broader vertebrate communities and suggest that results can direct future research towards understanding causal mechanisms.

Guild Proportionality

A guild refers to a group of species consuming the same class of resources [Fauth et al., 1996]. If competition affects species within communities at the guild level rather than at the level of individual species (i.e. if species within a guild are equivalent and guild-level resources are critical to determining the number of species that can persist in a guild), then the proportion of species in a guild should be relatively constant across communities irrespective of the identity of the species [Wilson, 1989]. For example, if we consistently find that each community consists of 50% frugivores, 30% insectivores, 20% omnivores, then the percentage of species in each guild is proportional across communities. Guild proportionality derives from the assumption that resource distribution is proportional across communities and because it is based strictly on the proportion of species, it does not take into account differences in species' body sizes that may affect resource use. There is evidence of guild proportionality in avian, ant, grassland, and saltmarsh communities [Feeley, 2003; Holdaway & Sparrow, 2006; Silva & Brandao, 2010; Wilson & Whittaker, 1995], but to our knowledge previous tests have not investigated mammals.

Fox's Assembly Rule for Favored States

According to Fox's assembly rule [Fox, 1987], interspecific competition should favor the entry and persistence of species that are most distinct from those already present in a community. The rule predicts that an incoming species will more likely persist if it belongs to a guild not represented in the community than if it attempts to divide niche space with species of the same guild that are already present. If interspecific competition favors the entry of species that are most distinct from members already present in the community, then communities will contain an equal number of species in each guild more often than is expected by chance. The rule defines a site as favored (i.e. in support of the assembly rule) if and only if species fill each guild evenly such that no guild has two or more representatives than an-

other guild. For example, according to the rule a site with three frugivores, three omnivores, and four insectivores is favored whereas a site with three frugivores, three omnivores, and five insectivores is unfavored.

Fox's assembly rule is similar to guild proportionality in that it assumes that the distribution of resources is even across sites, however it also requires the more strict assumption that resource distribution is even within sites. Hence, Fox's assembly rule assumes that the distribution of all resources is homogeneous and therefore that the number of species at each site in each guild should be more homogeneous than expected by chance. For a group of sites, if more sites meet the test for "favored" than are expected based on a null model, then the sites support the assembly rule.

METHODS
Data Collection

We compiled species presence–absence data on bats, birds, primates, and squirrels (Table I) from a combination of published and unpublished sources for 21 forested sites located throughout Borneo [Struebig et al., 2010]. We included as many sites for which we could obtain reliable species lists of all four taxonomic groups. The sites include all major naturally occurring habitat types found in Borneo (i.e. mangrove, swamp, lowland, hill, montane, and karst forests). For a subset of the analyses, we restricted the number of sites to include only those with the same broad habitat types to control for variation in habitat. These sites included lowland, hill, and montane forest (Fig. 2).

We used published descriptions to classify each species based on arboreality (terrestrial or nonterrestrial), activity pattern (diurnal or nocturnal), resident status (resident or nonresident), and diet (folivore, frugivore, frugivore/folivore, insectivore, or omnivore;). We included only resident, arboreal species because these species are most likely to interact with primates. To assign species to guilds, we used broad dietary categories to code for the presence or absence of items in the diet of each species based on qualitative diet descriptions. We defined folivores as species whose diets contained consistently available items, such as vegetation, moss, lichen, fungus, bark, or roots. We defined frugivorous species as those species for which the diet contains fruit, nectar, seeds, buds, or flowers. We designated species with dietary items in both of these categories as frugivore/folivores. Insectivores included species that exclusively fed on insects or other invertebrates. Omnivores included species that fed on both plant and animal matter. We excluded any species with a diet containing vertebrates because the diet would unlikely overlap with primates unless the diet also contained plant

TABLE I. List of species included in the study

Class	Order	Family	Genus	Species	No. of Sites	Guild	Invert	Fruit	Act
Aves	Accipitriformes	Accipitridae	*Aviceda*	*jerdoni*	7	NA	0	0	D
Aves	Apodiformes	Apodidae	*Aerodramus*	*fuciphagus*	9	IN	1	0	D
Aves	Apodiformes	Apodidae	*Aerodramus*	*maximus*	10	IN	1	0	D
Aves	Apodiformes	Apodidae	*Aerodramus*	*salangana*	2	IN	1	0	D
Aves	Apodiformes	Apodidae	*Apus*	*affinis*	9	IN	1	0	D
Aves	Apodiformes	Apodidae	*Collocalia*	*esculenta*	10	IN	1	0	D
Aves	Apodiformes	Apodidae	*Cypsiurus*	*balasiensis*	4	IN	1	0	D
Aves	Apodiformes	Apodidae	*Hirundapus*	*gigateus*	9	IN	1	0	D
Aves	Apodiformes	Apodidae	*Hydrochorous*	*gigas*	3	IN	1	0	D
Aves	Apodiformes	Apodidae	*Rhaphidura*	*leucopygialis*	11	IN	1	0	D
Aves	Apodiformes	Hemiprocnidae	*Hemiprocne*	*comata*	14	IN	1	0	D
Aves	Apodiformes	Hemiprocnidae	*Hemiprocne*	*longipennis*	14	IN	1	0	D
Aves	Bucerotiformes	Bucerotidae	*Anthracoceros*	*albirostris*	8	OM	1	1	D
Aves	Bucerotiformes	Bucerotidae	*Anthracoceros*	*malayanus*	14	OM	1	1	D
Aves	Bucerotiformes	Bucerotidae	*Berenicornis*	*comatus*	11	OM	1	1	D
Aves	Bucerotiformes	Bucerotidae	*Buceros*	*rhinoceros*	16	OM	1	1	D
Aves	Bucerotiformes	Bucerotidae	*Rhinoplax*	*vigil*	17	OM	0	1	D
Aves	Bucerotiformes	Bucerotidae	*Rhyticeros*	*corrugatus*	15	OM	1	1	D
Aves	Bucerotiformes	Bucerotidae	*Rhyticeros*	*undulatus*	11	OM	1	1	D
Aves	Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*affinis*	1	IN	1	0	N
Aves	Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*concretus*	3	IN	1	0	N
Aves	Columbiformes	Columbidae	*Ducula*	*aenea*	7	FR	0	1	D
Aves	Columbiformes	Columbidae	*Ducula*	*badia*	6	FR	0	1	D
Aves	Columbiformes	Columbidae	*Ducula*	*bicolor*	5	FR	0	1	D
Aves	Columbiformes	Columbidae	*Ducula*	*pickeringii*	2	FR	0	1	D
Aves	Columbiformes	Columbidae	*Macropygia*	*emiliana*	5	FR	0	1	D
Aves	Columbiformes	Columbidae	*Macropygia*	*ruficeps*	5	FR	0	1	D
Aves	Columbiformes	Columbidae	*Ptilinopus*	*jambu*	8	FR	0	1	D
Aves	Columbiformes	Columbidae	*Ptilinopus*	*melanospilus*	1	FR	0	1	D
Aves	Columbiformes	Columbidae	*Treron*	*capellei*	14	FR	0	1	D
Aves	Columbiformes	Columbidae	*Treron*	*curvirostra*	12	FR	0	1	D
Aves	Columbiformes	Columbidae	*Treron*	*fulvicollis*	4	FR	0	1	D
Aves	Columbiformes	Columbidae	*Treron*	*olax*	10	FR	0	1	D
Aves	Columbiformes	Columbidae	*Treron*	*vernans*	7	FR	0	1	D
Aves	Coraciiformes	Meropidae	*Nyctyornis*	*amictus*	14	IN	1	0	D
Aves	Cuculiformes	Cuculidae	*Cacomantis*	*merulinus*	11	OM	1	1	D
Aves	Cuculiformes	Cuculidae	*Cacomantis*	*sonneratii*	8	IN	1	0	D
Aves	Cuculiformes	Cuculidae	*Cacomantis*	*variolosus*	4	IN	1	0	D
Aves	Cuculiformes	Cuculidae	*Chrysococcyx*	*minutillus*	4	IN	1	0	D
Aves	Cuculiformes	Cuculidae	*Chrysococcyx*	*russatus*	1	IN	1	0	D
Aves	Cuculiformes	Cuculidae	*Chrysococcyx*	*xanthorhynchus*	8	OM	1	1	D
Aves	Cuculiformes	Cuculidae	*Hierococcyx*	*fugax*	12	OM	1	1	D
Aves	Cuculiformes	Cuculidae	*Hierococcyx*	*vagans*	6	IN	1	0	D
Aves	Cuculiformes	Cuculidae	*Phaenicophaeus (Rhopodytes)*	*diardi*	11	IN	1	0	D
Aves	Cuculiformes	Cuculidae	*Rhinortha*	*chlorophaea*	13	IN	1	0	D
Aves	Cuculiformes	Cuculidae	*Surniculus*	*lugubris*	15	OM	1	1	D
Aves	Cuculiformes	Cuculidae	*Zanclostomus*	*javanicus*	11	IN	1	0	D
Aves	Falconiformes	Falconidae	*Microhierax*	*latifrons*	3	NA	0	0	D
Aves	Passeriformes	Acanthizidae	*Gerygone*	*sulphurea*	11	IN	1	0	D
Aves	Passeriformes	Aegithinidae	*Aegithina*	*tiphia*	7	IN	1	0	D
Aves	Passeriformes	Aegithinidae	*Aegithina*	*viridissima*	13	IN	1	0	D
Aves	Passeriformes	Campephagidae	*Coracina*	*fimbriata*	13	OM	1	1	D
Aves	Passeriformes	Campephagidae	*Coracina*	*larvata*	5	OM	1	1	D
Aves	Passeriformes	Campephagidae	*Coracina*	*striata*	9	IN	1	0	D
Aves	Passeriformes	Campephagidae	*Hemipus*	*hirundinaceus*	15	IN	1	0	D
Aves	Passeriformes	Campephagidae	*Hemipus*	*picatus*	8	IN	1	0	D
Aves	Passeriformes	Campephagidae	*Lalage*	*nigra*	4	IN	1	0	D
Aves	Passeriformes	Campephagidae	*Pericrocotus*	*flammeus (speciosus)*	14	IN	1	0	D

TABLE I. Continued

Class	Order	Family	Genus	Species	No. of Sites	Guild	Invert	Fruit	Act
Aves	Passeriformes	Campephagidae	*Pericrocotus*	*igneus*	10	IN	1	0	D
Aves	Passeriformes	Campephagidae	*Pericrocotus*	*solaris*	2	IN	1	0	D
Aves	Passeriformes	Chloropseidae	*Chloropsis*	*cochinchinensis*	13	OM	0	0	D
Aves	Passeriformes	Chloropseidae	*Chloropsis*	*cyanopogon*	16	OM	0	0	D
Aves	Passeriformes	Chloropseidae	*Chloropsis*	*sonnerati*	15	OM	1	1	D
Aves	Passeriformes	Corvidae	*Cissa*	*thalassina*	1	IN	1	0	D
Aves	Passeriformes	Corvidae	*Dendrocitta*	*cinerascens*	4	OM	1	1	D
Aves	Passeriformes	Corvidae	*Platylophus*	*galericulatus*	13	IN	1	0	D
Aves	Passeriformes	Corvidae	*Platysmurus*	*leucopterus (aterrimus)*	11	IN	1	0	D
Aves	Passeriformes	Dicaeidae	*Dicaeum*	*agile*	2	OM	1	1	D
Aves	Passeriformes	Dicaeidae	*Dicaeum*	*chrysorrheum*	12	OM	1	1	D
Aves	Passeriformes	Dicaeidae	*Dicaeum*	*concolor (minullum)*	10	OM	1	1	D
Aves	Passeriformes	Dicaeidae	*Dicaeum*	*cruentatum*	11	OM	1	1	D
Aves	Passeriformes	Dicaeidae	*Dicaeum*	*everetti*	4	OM	1	1	D
Aves	Passeriformes	Dicaeidae	*Dicaeum*	*monticolum*	6	OM	1	1	D
Aves	Passeriformes	Dicaeidae	*Dicaeum*	*trigonostigma*	13	OM	1	1	D
Aves	Passeriformes	Dicaeidae	*Dicaeum*	*trochileum*	3	OM	1	1	D
Aves	Passeriformes	Dicaeidae	*Prionochilus*	*maculatus*	15	FR	1	0	D
Aves	Passeriformes	Dicaeidae	*Prionochilus*	*percussus*	7	FR	1	0	D
Aves	Passeriformes	Dicaeidae	*Prionochilus*	*thoracicus*	11	OM	1	1	D
Aves	Passeriformes	Dicaeidae	*Prionochilus*	*xanthopygius*	13	OM	1	1	D
Aves	Passeriformes	Dicruridae	*Dicrurus*	*aeneus*	12	IN	1	0	D
Aves	Passeriformes	Dicruridae	*Dicrurus*	*hottentottus*	6	IN	1	0	D
Aves	Passeriformes	Dicruridae	*Dicrurus*	*leucophaeus*	5	IN	1	0	D
Aves	Passeriformes	Dicruridae	*Dicrurus*	*paradiseus*	18	IN	1	0	D
Aves	Passeriformes	Eurylaimidae	*Calyptomena*	*hosei*	4	OM	1	1	D
Aves	Passeriformes	Eurylaimidae	*Calyptomena*	*viridis*	16	OM	1	1	D
Aves	Passeriformes	Eurylaimidae	*Calyptomena*	*whiteheadi*	4	OM	1	1	D
Aves	Passeriformes	Eurylaimidae	*Cymbirhynchus*	*macrorhynchos*	14	OM	1	1	D
Aves	Passeriformes	Eurylaimidae	*Eurylaimus*	*javanicus*	15	IN	1	0	D
Aves	Passeriformes	Eurylaimidae	*Eurylaimus*	*ochromalus*	18	IN	1	0	D
Aves	Passeriformes	Eurylaimidae	*Psarisomus*	*dalhousiae*	2	IN	1	0	D
Aves	Passeriformes	Hirundinidae	*Hirundo*	*tahitica*	14	IN	1	0	D
Aves	Passeriformes	Irenidae	*Irena*	*puella*	13	OM	1	1	D
Aves	Passeriformes	Monarchidae	*Hypothymis*	*azurea*	16	IN	1	0	D
Aves	Passeriformes	Monarchidae	*Terpsiphone*	*paradisi*	18	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Copsychus*	*malabaricus*	14	OM	1	1	D
Aves	Passeriformes	Muscicapidae	*Copsychus*	*stricklandii*	4	OM	1	1	D
Aves	Passeriformes	Muscicapidae	*Culicicapa*	*ceylonensis*	9	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Cyornis*	*banyumas*	5	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Cyornis*	*caerulatus*	6	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Cyornis*	*concretus*	8	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Cyornis*	*rufigastra*	3	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Cyornis*	*superbus*	13	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Cyornis*	*turcosus*	11	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Cyornis*	*unicolor*	7	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Eumyias*	*indigo*	3	OM	1	1	D
Aves	Passeriformes	Muscicapidae	*Eumyias*	*thalassinus*	5	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Ficedula*	*dumetoria*	11	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Ficedula*	*westermanni*	6	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Muscicapella*	*hodgsoni*	4	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Rhinomyias*	*olivaceus*	4	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Rhinomyias*	*ruficauda*	7	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Rhinomyias*	*umbratilis*	16	IN	1	0	D
Aves	Passeriformes	Muscicapidae	*Trichixos*	*pyrropygus*	15	IN	1	0	D
Aves	Passeriformes	Nectariniidae	*Aethopyga*	*siparaja*	14	OM	1	0	D

TABLE I. Continued

Class	Order	Family	Genus	Species	No. of Sites	Guild	Invert	Fruit	Act
Aves	Passeriformes	Nectariniidae	*Aethopyga*	*temminckii*	11	OM	1	1	D
Aves	Passeriformes	Nectariniidae	*Anthreptes*	*malacensis*	10	OM	1	1	D
Aves	Passeriformes	Nectariniidae	*Anthreptes*	*rhodalaemus*	8	OM	1	1	D
Aves	Passeriformes	Nectariniidae	*Anthreptes*	*simplex*	11	OM	1	1	D
Aves	Passeriformes	Nectariniidae	*Arachnothera*	*affinis*	12	OM	1	0	D
Aves	Passeriformes	Nectariniidae	*Arachnothera*	*chrysogenys*	12	OM	1	1	D
Aves	Passeriformes	Nectariniidae	*Arachnothera*	*crassirostris*	14	OM	1	0	D
Aves	Passeriformes	Nectariniidae	*Arachnothera*	*flavigaster*	14	OM	1	1	D
Aves	Passeriformes	Nectariniidae	*Arachnothera*	*juliae*	5	NA	0	0	D
Aves	Passeriformes	Nectariniidae	*Arachnothera*	*longirostra*	17	OM	1	0	D
Aves	Passeriformes	Nectariniidae	*Arachnothera*	*modesta*	1	OM	1	0	D
Aves	Passeriformes	Nectariniidae	*Arachnothera*	*robusta*	13	OM	1	0	D
Aves	Passeriformes	Nectariniidae	*Chalcoparia*	*singalensis*	13	OM	1	1	D
Aves	Passeriformes	Nectariniidae	*Cinnyris*	*jugularis*	8	OM	1	0	D
Aves	Passeriformes	Nectariniidae	*Hypogramma*	*hypogrammica*	14	OM	1	1	D
Aves	Passeriformes	Nectariniidae	*Leptocoma*	*calcostetha*	6	IN	1	0	D
Aves	Passeriformes	Nectariniidae	*Leptocoma*	*sperata*	12	NA	0	0	NA
Aves	Passeriformes	Oriolidae	*Oriolus*	*chinensis*	2	OM	1	1	D
Aves	Passeriformes	Oriolidae	*Oriolus*	*cruentus*	2	OM	1	1	D
Aves	Passeriformes	Oriolidae	*Oriolus*	*xanthonotus*	15	OM	1	1	D
Aves	Passeriformes	Oriolidae	*Oriolus*	*xanthornus*	1	OM	1	1	D
Aves	Passeriformes	Pachycephalidae	*Pachycephala*	*cinerea (grisola)*	5	IN	1	0	D
Aves	Passeriformes	Pachycephalidae	*Pachycephala*	*hypoxantha*	5	IN	1	0	D
Aves	Passeriformes	Paridae	*Parus*	*major*	1	OM	1	0	D
Aves	Passeriformes	Pityriaseidae	*Pityriasis*	*gymnocephala*	13	IN	1	0	D
Aves	Passeriformes	Pycnonotidae	*Criniger*	*bres*	13	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Criniger*	*finschii*	12	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Criniger*	*ochraceus*	8	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Criniger*	*phaeocephalus*	14	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Hemixos*	*flavala*	8	NA	0	0	D
Aves	Passeriformes	Pycnonotidae	*Iole*	*olivacea*	12	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Ixos*	*malaccensis*	12	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*atriceps*	15	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*brunneus*	5	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*cyaniventris*	14	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*erythropthalmos*	12	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*eutilotus*	15	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*melanicterus (flaviventris)*	3	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*melanoleucos*	9	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*nieuwenhuisii*	3	FR	0	0	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*plumosus*	12	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*simplex*	14	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Pycnonotus*	*squamatus*	8	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Setornis*	*criniger*	9	OM	1	1	D
Aves	Passeriformes	Pycnonotidae	*Tricholestes*	*criniger*	13	OM	1	1	D
Aves	Passeriformes	Rhipiduridae	*Rhipidura*	*albicollis*	6	IN	1	0	D
Aves	Passeriformes	Rhipiduridae	*Rhipidura*	*javanica*	14	IN	1	0	D
Aves	Passeriformes	Rhipiduridae	*Rhipidura*	*perlata*	14	IN	1	0	D
Aves	Passeriformes	Silviidae	*Abroscopus*	*superciliaris*	8	IN	1	0	D
Aves	Passeriformes	Silviidae	*Phylloscopus*	*trivirgatus*	4	IN	1	0	D
Aves	Passeriformes	Silviidae	*Seicercus*	*montis*	4	IN	1	0	D
Aves	Passeriformes	Sittidae	*Sitta*	*frontalis*	15	IN	1	0	D
Aves	Passeriformes	Sturnidae	*Aplonis*	*panayensis*	7	FR	0	1	D
Aves	Passeriformes	Sturnidae	*Gracula*	*religiosa*	16	OM	1	1	D
Aves	Passeriformes	Timaliidae	*Alcippe*	*brunneicauda*	15	OM	1	1	D
Aves	Passeriformes	Timaliidae	*Garrulax*	*lugubris (calva)*	3	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Garrulax*	*mitratus*	4	OM	1	1	D

TABLE I. Continued

Class	Order	Family	Genus	Species	No. of Sites	Guild	Invert	Fruit	Act
Aves	Passeriformes	Timaliidae	*Garrulax*	*palliatus*	5	OM	1	1	D
Aves	Passeriformes	Timaliidae	*Macronous*	*ptilosus*	17	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Malacopteron*	*affine*	13	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Malacopteron*	*albogulare*	9	NA	0	0	D
Aves	Passeriformes	Timaliidae	*Malacopteron*	*cinereum*	15	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Malacopteron*	*magnirostre*	16	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Malacopteron*	*magnum*	16	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Pteruthius*	*flaviscapis*	4	OM	1	1	D
Aves	Passeriformes	Timaliidae	*Stachyris*	*erythroptera*	16	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Stachyris*	*leucotis*	5	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Stachyris*	*maculata*	15	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Stachyris*	*nigriceps*	8	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Stachyris*	*nigricollis*	14	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Stachyris*	*poliocephala*	12	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Stachyris*	*rufifrons*	6	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Trichastoma*	*abboti*	6	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Trichastoma*	*bicolor*	13	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Trichastoma*	*perspicillatum*	1	NA	0	0	D
Aves	Passeriformes	Timaliidae	*Trichastoma*	*sepiaria*	11	IN	1	0	D
Aves	Passeriformes	Timaliidae	*Yuhina*	*everetti*	7	IN	1	0	D
Aves	Passeriformes	Turdidae	*Chlamydochaera*	*jefferyi*	4	OM	1	1	D
Aves	Passeriformes	Zosteropidae	*Chlorocharis*	*emiliae*	4	OM	1	0	D
Aves	Passeriformes	Zosteropidae	*Zosterops*	*atricapilla*	2	OM	1	1	D
Aves	Passeriformes	Zosteropidae	*Zosterops*	*everetti*	3	IN	1	0	D
Aves	Passeriformes	Zosteropidae	*Zosterops*	*flavus*	1	IN	1	0	D
Aves	Passeriformes	Zosteropidae	*Zosterops*	*palpebrosus*	2	IN	1	0	D
Aves	Piciformes	Indicatoridae	*Indicator*	*archipelagicus*	6	IN	1	0	D
Aves	Piciformes	Picidae	*Blythipicus*	*rubiginosus*	15	IN	1	0	D
Aves	Piciformes	Picidae	*Celeus*	*brachyurus*	12	OM	1	1	D
Aves	Piciformes	Picidae	*Chrysocolaptes*	*lucidus*	1	IN	1	0	D
Aves	Piciformes	Picidae	*Dendrocopos*	*canicapillus*	10	OM	1	1	D
Aves	Piciformes	Picidae	*Dinopium*	*javanense*	4	IN	1	0	D
Aves	Piciformes	Picidae	*Dinopium*	*rafflesii*	12	IN	1	0	D
Aves	Piciformes	Picidae	*Dryocopus*	*javensis*	13	IN	1	0	D
Aves	Piciformes	Picidae	*Hemicircus*	*concretus*	14	OM	1	1	D
Aves	Piciformes	Picidae	*Meiglyptes*	*tristis*	16	IN	1	0	D
Aves	Piciformes	Picidae	*Meiglyptes*	*tukki*	16	IN	1	0	D
Aves	Piciformes	Picidae	*Mulleripicus*	*pulverulentus*	15	IN	1	0	D
Aves	Piciformes	Picidae	*Picus*	*mentalis*	12	OM	1	1	D
Aves	Piciformes	Picidae	*Picus*	*miniaceus*	11	IN	1	0	D
Aves	Piciformes	Picidae	*Picus*	*puniceus*	17	IN	1	0	D
Aves	Piciformes	Picidae	*Reinwardtipicus*	*validus*	17	IN	1	0	D
Aves	Piciformes	Ramphastidae	*Calorhamphus*	*fuliginosus*	15	OM	1	1	D
Aves	Piciformes	Ramphastidae	*Megalaima*	*australis*	16	OM	1	1	D
Aves	Piciformes	Ramphastidae	*Megalaima*	*chrysopogon*	12	OM	1	1	D
Aves	Piciformes	Ramphastidae	*Megalaima*	*eximia*	8	FR	0	1	D
Aves	Piciformes	Ramphastidae	*Megalaima*	*henricii*	12	FR	0	1	D
Aves	Piciformes	Ramphastidae	*Megalaima*	*monticola*	7	OM	1	1	D
Aves	Piciformes	Ramphastidae	*Megalaima*	*mystacophanos*	16	OM	1	1	D
Aves	Piciformes	Ramphastidae	*Megalaima*	*pulcherrima*	4	OM	1	1	D
Aves	Piciformes	Ramphastidae	*Megalaima*	*rafflesii*	14	OM	1	1	D
Aves	Psittaciformes	Psittacidae	*Loriculus*	*galgulus*	16	FR	0	1	D
Aves	Psittaciformes	Psittacidae	*Psittacula*	*longicauda*	8	FR	0	1	D
Aves	Psittaciformes	Psittacidae	*Psittinus*	*cyanurus*	10	FR	0	1	D
Aves	Psittaciformes	Psittacidae	*Tanygnathus*	*lucionensis*	2	FR	0	1	D
Aves	Strigiformes	Strigidae	*Otus*	*rufenscens*	8	IN	1	0	N
Aves	Trogoniformes	Trogonidae	*Harpactes*	*dardii*	14	IN	1	0	D
Aves	Trogoniformes	Trogonidae	*Harpactes*	*duvaucelii*	16	NA	0	0	D
Aves	Trogoniformes	Trogonidae	*Harpactes*	*kasumba*	14	OM	1	1	D

TABLE I. Continued

Class	Order	Family	Genus	Species	No. of Sites	Guild	Invert	Fruit	Act
Aves	Trogoniformes	Trogonidae	*Harpactes*	*oreskios*	8	NA	0	0	D
Aves	Trogoniformes	Trogonidae	*Harpactes*	*orrophaeus*	9	NA	0	0	D
Aves	Trogoniformes	Trogonidae	*Harpactes*	*whiteheadi*	5	IN	1	0	D
Aves	(unclear)	INCERTAE SEDIS	*Erpornis*	*zantholeuca*	10	OM	1	1	D
Aves	(unclear)	INCERTAE SEDIS	*Orthotomus*	*atrogularis*	14	IN	1	0	D
Aves	(unclear)	INCERTAE SEDIS	*Orthotomus*	*ruficeps*	13	IN	1	0	D
Aves	(unclear)	INCERTAE SEDIS	*Philentoma*	*pyrrhoptera*	15	IN	1	0	D
Aves	(unclear)	INCERTAE SEDIS	*Philentoma*	*velata (velatum)*	11	IN	1	0	D
Aves	(unclear)	INCERTAE SEDIS	*Tephrodornis*	*gularis*	14	IN	1	0	D
Aves	(unclear)	Podargidae	*Batrachostomus*	*cornutus*	3	NA	0	0	N
Mammalia	Chiroptera	Emballonuridae	*Emballonura*	*alecto*	10	NA	0	0	N
Mammalia	Chiroptera	Emballonuridae	*Emballonura*	*monticola*	9	NA	0	0	N
Mammalia	Chiroptera	Hipposideridae	*Coelops*	*robinsoni*	2	IN	1	0	N
Mammalia	Chiroptera	Hipposideridae	*Hipposideros*	*ater*	6	IN	1	0	N
Mammalia	Chiroptera	Hipposideridae	*Hipposideros*	*bicolor*	4	IN	1	0	N
Mammalia	Chiroptera	Hipposideridae	*Hipposideros*	*cervinus*	11	IN	1	0	N
Mammalia	Chiroptera	Hipposideridae	*Hipposideros*	*cineraceus*	6	IN	1	0	N
Mammalia	Chiroptera	Hipposideridae	*Hipposideros*	*diadema*	8	IN	1	0	N
Mammalia	Chiroptera	Hipposideridae	*Hipposideros*	*doriae (sabanus)*	3	IN	1	0	N
Mammalia	Chiroptera	Hipposideridae	*Hipposideros*	*dyacorum*	6	IN	1	0	N
Mammalia	Chiroptera	Hipposideridae	*Hipposideros*	*galeritus*	9	IN	1	0	N
Mammalia	Chiroptera	Hipposideridae	*Hipposideros*	*larvatus*	4	IN	1	0	N
Mammalia	Chiroptera	Hipposideridae	*Hipposideros*	*ridleyi*	5	IN	1	0	N
Mammalia	Chiroptera	Nycteridae	*Nycteris*	*tragata (javanica)*	8	IN	1	0	N
Mammalia	Chiroptera	Pteropodidae	*Aethalops*	*aequalis (alecto)*	4	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Balionycteris*	*maculata*	15	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Chironax*	*melanocephalus*	3	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Cynopterus*	*brachyotis*	15	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Cynopterus*	*horsfieldii*	3	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Cynopterus*	*sphinx*	1	NA	0	0	N
Mammalia	Chiroptera	Pteropodidae	*Dyacopterus*	*spadiceus*	5	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Eonycteris*	*major*	1	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Eonycteris*	*spelaea*	7	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Macroglossus*	*minimus*	11	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Megaerops*	*ecaudatus*	5	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Megaerops*	*wetmorei*	2	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Penthetor*	*lucasi*	8	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Pteropus*	*vampyrus*	13	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Rousettus*	*amplexicaudatus*	2	FR	0	1	N
Mammalia	Chiroptera	Pteropodidae	*Rousettus*	*spinalatus*	1	FR	0	1	N
Mammalia	Chiroptera	Rhinolophidae	*Rhinolophus*	*acuminatus*	3	IN	1	0	N
Mammalia	Chiroptera	Rhinolophidae	*Rhinolophus*	*affinis*	4	IN	1	0	N
Mammalia	Chiroptera	Rhinolophidae	*Rhinolophus*	*borneensis*	15	IN	1	0	N
Mammalia	Chiroptera	Rhinolophidae	*Rhinolophus*	*creaghi*	4	IN	1	0	N
Mammalia	Chiroptera	Rhinolophidae	*Rhinolophus*	*luctus*	7	IN	1	0	N
Mammalia	Chiroptera	Rhinolophidae	*Rhinolophus*	*philippinensis*	2	IN	1	0	N
Mammalia	Chiroptera	Rhinolophidae	*Rhinolophus*	*pusillus*	2	IN	1	0	N
Mammalia	Chiroptera	Rhinolophidae	*Rhinolophus*	*sedulus*	12	IN	1	0	N
Mammalia	Chiroptera	Rhinolophidae	*Rhinolophus*	*trifoliatus*	14	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Kerivoulininae)	*Kerivoula*	*hardwickii*	8	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Kerivoulininae)	*Kerivoula*	*intermedia*	9	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Kerivoulininae)	*Kerivoula*	*minuta*	7	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Kerivoulininae)	*Kerivoula*	*papillosa*	12	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Kerivoulininae)	*Kerivoula*	*pellucida*	8	IN	1	0	N

TABLE I. Continued

Class	Order	Family	Genus	Species	No. of Sites	Guild	Invert	Fruit	Act
Mammalia	Chiroptera	Vespertilionidae (Kerivoulininae)	*Kerivoula*	*whiteheadii*	1	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Kerivoulininae)	*Phoniscus*	*atrox*	4	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Kerivoulininae)	*Phoniscus*	*jagorii*	2	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Murininae)	*Harpiocephalus*	*harpia*	1	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Murininae)	*Murina*	*aenea*	3	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Murininae)	*Murina*	*cyclotis*	4	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Murininae)	*Murina*	*rozendaali*	3	IN	1	0	N
Mammalia	Chiroptera	Vespertilionidae (Murininae)	*Murina*	*suilla*	10	IN	1	0	N
Mammalia	Primates	Cercopithecidae	*Macaca*	*fascicularis*	21	OM	1	1	D
Mammalia	Primates	Cercopithecidae	*Nasalis*	*larvatus*	10	FO	0	1	D
Mammalia	Primates	Cercopithecidae	*Presbytis*	*cristata*	10	FO	0	1	D
Mammalia	Primates	Cercopithecidae	*Presbytis*	*frontata*	6	FO	0	0	D
Mammalia	Primates	Cercopithecidae	*Presbytis*	*hosei*	7	FO	0	0	D
Mammalia	Primates	Cercopithecidae	*Presbytis*	*melalophos*	3	FO	0	0	D
Mammalia	Primates	Cercopithecidae	*Presbytis*	*rubicunda*	16	FO	0	0	D
Mammalia	Primates	Hominidae	*Pongo*	*pygmaeus*	13	FR	1	1	D
Mammalia	Primates	Hylobatidae	*Hylobates*	*agilis*	5	FRFO	0	1	D
Mammalia	Primates	Hylobatidae	*Hylobates*	*muelleri*	17	FR	0	1	D
Mammalia	Primates	Lorisidae	*Nycticebus*	*coucang*	12	OM	1	1	N
Mammalia	Primates	Tarsiidae	*Tarsius*	*bancanus*	14	IN	1	0	N
Mammalia	Rodentia	Sciuridae	*Aeromys*	*tephromelas*	4	FRFO	0	1	N
Mammalia	Rodentia	Sciuridae	*Aeromys*	*thomasi*	4	FR	0	1	N
Mammalia	Rodentia	Sciuridae	*Callosciurus*	*adamsi*	3	NA	0	0	D
Mammalia	Rodentia	Sciuridae	*Callosciurus*	*baluensis*	3	NA	0	0	D
Mammalia	Rodentia	Sciuridae	*Callosciurus*	*notatus*	16	OM	1	1	D
Mammalia	Rodentia	Sciuridae	*Callosciurus*	*orestes (formerly nigrovittatus)*	4	OM	1	1	D
Mammalia	Rodentia	Sciuridae	*Callosciurus*	*prevostii*	19	OM	1	1	D
Mammalia	Rodentia	Sciuridae	*Exilisciurus*	*exilis*	15	OM	1	0	D
Mammalia	Rodentia	Sciuridae	*Exilisciurus*	*whiteheadi*	6	FO	0	0	NA
Mammalia	Rodentia	Sciuridae	*Glyphotes*	*simus*	3	NA	0	0	D
Mammalia	Rodentia	Sciuridae	*Hylopetes*	*lepidus*	1	NA	0	0	N
Mammalia	Rodentia	Sciuridae	*Hylopetes*	*spadiceus*	1	NA	0	0	N
Mammalia	Rodentia	Sciuridae	*Iomys*	*horsfieldi*	3	NA	0	0	N
Mammalia	Rodentia	Sciuridae	*Nannosciurus*	*melanotis*	12	NA	0	0	D
Mammalia	Rodentia	Sciuridae	*Petaurista*	*elegans*	1	NA	0	0	N
Mammalia	Rodentia	Sciuridae	*Petaurista*	*petaurista*	5	FRFO	0	1	N
Mammalia	Rodentia	Sciuridae	*Petinomys*	*genibarbis*	3	NA	0	0	N
Mammalia	Rodentia	Sciuridae	*Petinomys*	*hageni*	1	NA	0	0	N
Mammalia	Rodentia	Sciuridae	*Petinomys*	*setosus*	1	NA	0	0	N
Mammalia	Rodentia	Sciuridae	*Petinomys*	*vordermanni*	1	NA	0	0	N
Mammalia	Rodentia	Sciuridae	*Pteromyscus*	*pulverulentus*	1	NA	0	0	N
Mammalia	Rodentia	Sciuridae	*Ratufa*	*affinis*	18	FRFO	0	0	D
Mammalia	Rodentia	Sciuridae	*Sundasciurus*	*brookei*	6	NA	0	0	D
Mammalia	Rodentia	Sciuridae	*Sundasciurus*	*hippurus*	14	OM	1	1	D
Mammalia	Rodentia	Sciuridae	*Sundasciurus*	*jentinki*	4	NA	0	0	D
Mammalia	Rodentia	Sciuridae	*Sundasciurus*	*lowii*	14	OM	1	1	D
Mammalia	Rodentia	Sciuridae	*Sundasciurus*	*tenuis*	7	OM	1	1	D

Species attribute data and taxonomy: guild assignments include insectivore (IN), omnivore (OM), frugivore (FR), folivore (FO), frugivore/folivore (FRFO), and unknown (NA). Invert and fruit columns indicate the presence (1) or absence (0) of invertebrates or fruits in the diet respectively. Activity patterns include diurnal (D), nocturnal (N), or unknown (NA).
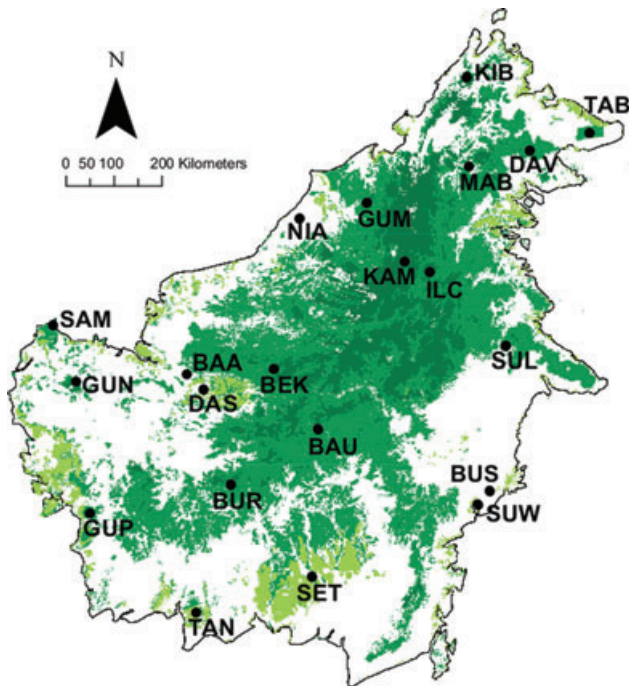
Fig. 2. Locations of sites on Borneo in Southeast Asia: BAU: Barito Ulu; BAA: Batang Ai National Park; BEK*: Betung Kerihun National Park; BUR*: Bukit Raya-Bukit Baka National Park; BUS: Bukit Soeharto Wildlife Reserve; DAS: Danau Sentarum National Park; DAV: Danum Valley Conservation Forest; GUM: Gunung Mulu National Park; GUN: Gunung Niut Wildlife Reserve; GUP: Gunung Palung National Park; ILC: Inhutani Logging Concession; KAM*: Kayan Mentarang National Park; KIB*: Kinabalu National Park; MAB*: Maliau Basin Conservation Area; NIA: Niah National Park; SAM: Samunsam Wildlife Sanctuary; SET: Sebangau National Park; SUL*: Sungai Lesan Protection Forest; SUW: Sungai Wain Protection Forest; TAB: Tabin Wildlife Reserve; TAN: Tanjung Puting National Park. Sites with similar forest types included in the habitat analysis are indicated with an asterisk. Forest cover according to Miettinen et al. [2011]. Light shading represents swamp forests and mangroves, dark shading represents montane forest and all other shading represents lowland forests.

matter, in which case we classified the species as an omnivore.

All data compilation and analysis for this study took place at the University of California, Davis beginning in August 2010. We collected no new field data and as such there were no applicable institutional animal care committee protocols to be approved. All research adhered to the legal requirements of the United States and to the American Society of Primatologists principles for the ethical treatment of nonhuman primates.

Analysis

Our objective was to determine the extent of ecological structure present in communities of primates and in the broader vertebrate communities in which primates live. We therefore investigated each co-occurrence pattern using all species combined as well as several subsets of the data, which included

analyzing each taxonomic group individually (primates, birds, bats, or squirrels), or grouped as nonvolant species (primates and squirrels), mammals (primates, squirrels and bats), diurnal species (diurnal primates, squirrels and birds), and all species.

There has been substantial debate on the subject of determining α values in statistical testing [Rice, 1989; Roback & Askins, 2005]. We agree with the argument that authors should reject correction factors in ecological studies and instead report exact *P*-values and interpret results reasonably [Moran, 2003; Nakagawa, 2004]. We therefore report exact *P*-values and base our interpretation of the data on the α = 0.05 level.

Checkerboard Distributions

To test for checkerboard distributions, we used the co-occurrence analysis in the program EcoSim [Gotelli & Entsminger, 2011] to calculate *C*-scores [Stone & Roberts, 1990]. We compared observed scores to a null distribution model based on 5,000 permutations with fixed column and row totals. A *C*-score measures the mean number of "checkerboard units" based on all possible pairs of species in a presence–absence matrix. A checkerboard unit refers to a 2×2 site by species submatrix in which one site contains only one species and the other site only contains the other species such that the two species do not co-occur at either site [Gotelli & Entsminger, 2011]. EcoSim follows Stone and Roberts [1990] in calculating a checkerboard unit as $CU_{ij} = (r_i - S_{ij})(r_j - S_{ij})$, where r_i and r_j are the total number of occurrences across sites of species i and j and S is the number of sites where the two species co-occur. The *C*-score is the mean of the *CU*-values for all species pairs in a matrix. If the observed matrix has a significantly higher *C*-score than matrices under the null model, this suggests evidence of significant ecological structure in the community, which can result from species segregation, aggregation, or turnover [Ulrich and Gotelli, 2012]. While even the most conservative measure suggests that significant *C*-scores are typically the result of species segregation, which is consistent with the traditional *C*-score interpretation of competitive exclusion, further analyses at the species–pair level are necessary to determine the causal factor [Ulrich and Gotelli, 2012]. If nonprimate vertebrate species importantly interact with primate species, then we expect to find higher *C*-scores when we include nonprimates in the analysis than when we examine primates alone.

Because species responses to variation in habitats (i.e. habitat checkerboards) can also cause significant *C*-scores [Gotelli & McCabe, 2002], we performed additional analyses to control for the effects of variation in habitat on checkerboard distributions. We conducted the analysis with a subset of six of the total sites because they encompassed the same
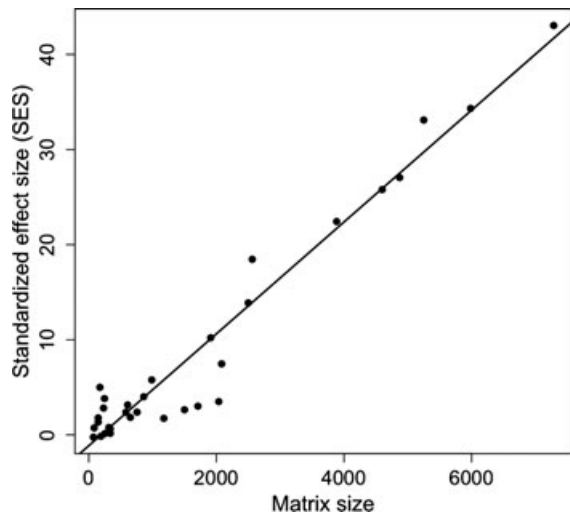
Fig. 3. Linear relationship between matrix size and SES in *C*-score analysis for all communities. There is a significant positive linear relationship between the SES and the size of the presence–absence matrix, which is defined as the number of species times the number of sites (linear regression, $df = 30$, $R^2 = 0.94$, $P < 0.001$). Because the SES scales with matrix size, we limit direct comparisons of SES values and instead rely on the patterning of significant *C*-score values across communities.

broad habitat types of lowland, hill, and montane forest. To examine the effects of interactions related to specific types of resources, we also conducted the co-occurrence analysis separately using only species whose diets include invertebrates and again using only species whose diets include fruit.

For all checkerboard analyses, we report the standardized effect size (SES) and the probability that the observed *C*-score is greater than the expected *C*-score given the simulated data (*P*). We calculate the SES as the (observed index − mean of simulated indices) / standard deviation of simulated indices. Published guidelines note that the SES allows for comparisons between different tests because it scales the results of each test in units of standard deviations [Gotelli & Entsminger, 2011]. However, there is a significant positive linear relationship between the SES and the size of the presence–absence matrix, which is defined as the number of species times the number of sites (linear regression, $df = 30$, $R^2 = 0.94$, $P < 0.001$; Fig. 3). We therefore do not interpret relative differences in SES values between communities as biologically meaningful. We focus on the comparison of expected and observed *C*-score values for each community and we examine the patterning of significantly checkerboarded communities based on analyses of all sites and when we controlled for habitat and diet characteristics.

Guild Proportionality

To test for guild proportionality, we conducted *G*-tests of independence [McDonald, 2009] using the function g.test [Hurd, 2011] in the software R 2.13.0

TABLE II. Number of species included in analyses

	Bats	Birds	Primates	Squirrels
(**a**) Foraging guild				
Folivores	0	0	6	1
Frugivores	15	23	2	1
Frugivore/Folivores	0	0	1	3
Insectivores	34	112	1	0
Omnivores	0	94	2	7
Unknown	3	11	0	15
Total	52	240	12	27
(**b**) Diet				
Fruit	15	103	7	9
Invertebrates	34	205	4	7

Number of species included in analyses for each taxonomic group (a) for each foraging guild used in the analyses for guild proportionality and Fox's assembly rule for favored states and (b) with diets containing fruits or invertebrates used in the analyses for checkerboard distributions based on species whose diets contained fruit or invertebrates, respectively. Overall checkerboard analyses included species from all foraging guilds including unknown, but guild proportionality analyses excluded species with unknown foraging guilds.

[R Development Core Team, 2012]. If the proportion of species in guilds changes significantly across sites, then $P < 0.05$. If the proportion of species in guilds is fixed, then $P > 0.95$. If $0.05 < P < 0.95$, then the proportion of guilds remains constant but with noise [Feeley, 2003]. If nonprimate vertebrates are more important competitors of primates than other primates, then we expect to find greater evidence of guild proportionality when we include nonprimate vertebrates. We excluded species for which dietary data were unavailable from the guild-level analyses (Table II).

Fox's Assembly Rule

We compared the observed number of favored states to the distribution of favored states expected under the null model using the favored states option within the guild analysis in EcoSim [Gotelli & Entsminger, 2011]. We implemented the recommended program settings for column and row totals. If nonprimate vertebrates are stronger competitors of primates than other primates, then we expect to find greater evidence in support of Fox's assembly rule when we consider nonprimate vertebrates at the same time as primates than when we consider primates in isolation.

RESULTS
Checkerboard Distributions

Significantly high checkerboard scores are consistent with the interpretation that species interactions have structured co-occurrence patterns across communities. When we included all sites ($N = 21$), observed checkerboard scores were greater than expected for all communities analyzed (Fig. 4); this
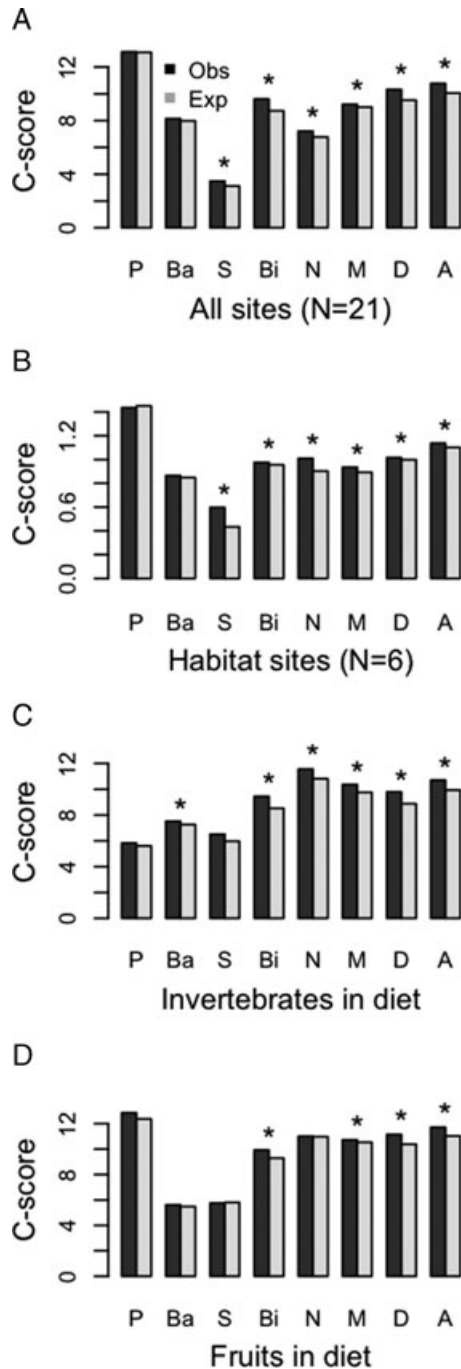
Fig. 4. Comparison of observed and expected checkerboard scores in dark gray and light gray, respectively, for (**A**) all sites (**B**) and sites with similar habitat (**C**) and for fruit-eating species and (**D**) invertebrate eating species (Ba: bats; Bi: birds; P: primates; S: squirrels; N: nonvolant; M: mammals; D: diurnal; A: all species). If an observed matrix has a significantly higher *C*-score than expected given the null model indicated by an asterisk, then species pairs co-occur less often than expected by chance. When interpreting the graph of the observed versus expected c-scores, it is the relative difference between observed and the expected rather than the absolute c-score values that is meaningful. Significantly high *C*-scores are consistent with the interpretation that there is significant ecological structure within communities.

patterning was significant when we analyzed individual taxonomic groups of birds (SES = 33.10, $P < 0.001$) or squirrels (SES = 3.15, $P < 0.001$), but not bats (SES = 1.74, $P = 0.053$) or primates (SES = 0.14, $P = 0.437$). In the communities with taxonomic groups combined, checkerboard scores were significant for all combinations. This included significant *C*-scores for nonvolant species (SES = 4.01, $P = 0.002$), mammals (SES = 3.50, $P < 0.001$), diurnal species (SES = 34.32, $P < 0.001$), and all species combined (SES = 43.04, $P < 0.001$; Fig. 4A).

In the analysis of sites with similar habitat ($N = 6$), the patterns were consistent with the results for all sites. Observed checkerboard scores were greater than those expected under the null models for all communities analyzed except for primates; this patterning was significant when we analyzed individual taxonomic groups of birds (SES = 2.64, $P = 0.017$) or squirrels (SES = 5.00, $P < 0.001$), but not bats (SES = 0.65, $P = 0.235$) or primates (SES = –0.24, $P = 0.604$). Among combined taxonomic groups, checkerboard scores were significant for all combinations, including nonvolant species (SES < 3.82, $P = 0.003$), mammals (SES = 2.38, $P = 0.025$), diurnal species (SES = 3.02, $P = 0.001$) and all species (SES = 7.47, $P < 0.001$) (Fig. 4B).

We also ran the checkerboard analysis for a subset of species based on the presence of broad dietary items in their diets. For species with fruit in their diets, birds were the only taxonomic group with significant checkerboard distributions when considered in isolation (SES = 10.21, $P < 0.001$). Although primates considered in isolation were marginally significant (SES = 1.79, $P = 0.060$), the other taxonomic groups did not exhibit significant checkerboard scores (bats: SES = 0.78, $P = 0.222$); squirrels: SES = –0.15, $P = 0.522$) nor did the nonvolant species (SES = 0.16, $P = 0.400$). We found significantly high checkerboard scores for fruit-eating mammals (SES = 1.84, $P = 0.046$), diurnal species (SES = 13.88, $P < 0.001$), and all species combined (SES = 18.46, $P < 0.001$; Fig. 4C).

For species with invertebrates in their diets, checkerboard distributions were significant in communities of bats (SES = 2.39, $P = 0.015$), birds (SES = 22.43, $P < 0.001$), mammals (SES = 5.78, $P < 0.001$), nonvolant species (SES = 2.82, $P = 0.012$), diurnal species (SES = 25.79, $P < 0.001$), and all species combined (SES = 27.05, $P < 0.001$), but not in primates (SES = 0.73, $P < 0.241$) or squirrels (SES = 1.35, $P = 0.110$) (Fig. 4D).

Guild Proportionality

We found results consistent with "fixed" guild proportionality in primates ($G = 32.70$, χ^2 $df = 80$, $P = 1.00$), squirrels ($G = 28.02$, χ^2 $df = 60$, $P = 1.00$), birds ($G = 19.14$, χ^2 $df = 40$, $P = 0.998$), and nonvolant species (primates and squirrels combined;

TABLE III. Guild proportionality results

Taxa	Log-likelihood ratio statistic (G)	χ^2 degrees of freedom	P-value
All species	89.04	80	0.23
Bats	44.06	20	<0.01
Birds	19.14	40	1.00
Diurnal	66.09	80	0.87
Mammals	108.59	80	0.02
Nonvolant	35.58	80	1.00
Primates	32.70	80	1.00
Squirrels	28.02	60	1.00

Guild proportionality results for G-tests of independence. Guild proportionality is consistent with competition at the guild level structuring communities when resources are distributed homogeneously across sites. $P < 0.05$ suggests the proportion of guilds changes significantly across sites. $P > 0.95$ suggests the proportion of guilds changes is fixed. If $0.05 < P < 0.95$, then the proportion of guilds remains constant but with noise [Feeley, 2003].

$G = 35.58$, χ^2 $df = 80$, $P = 1.00$). Significant departure from guild proportionality was evident for bats ($G = 44.06$, χ^2 $df = 20$, $P = 0.001$) and mammals ($G = 108.59$, χ^2 $df = 80$, $P = 0.018$). Results for guild proportionality in diurnal species ($G = 66.09$, χ^2 $df = 80$, $P = 0.868$) and all species combined ($G = 89.04$, χ^2 $df = 80$, $P = 0.229$) were nonsignificant (Table III).

Fox's Assembly Rule for Favored States

We did not find support for Fox's assembly rule for any of the communities (all species, $P = 1.00$; bats, $P = 0.796$; birds, $P = 0.806$; diurnal species, $P = 1.00$; mammals, $P = 0.995$). Initial analysis was not applicable for primates, squirrels, or nonvolant vertebrates because these communities did not contain multiple species from each guild. We did not find support for the rule when the guilds with one species or less were omitted (primates, $P = 0.989$; squirrels, $P = 0.222$; nonvolant species, $P = 0.340$).

DISCUSSION

We evaluated the extent to which species interactions shape vertebrate communities, specifically communities of primates, birds, bats, and squirrels in Borneo. We investigated co-occurrence patterns consistent with interactions structuring the presence or absence of species in communities. Our results suggest that consideration of the broader mammalian and avian communities in which primates live is of central importance for understanding the distribution of primate species and the composition of communities. We found strong support for checkerboard distributions (i.e. the alternating presence or absence of species across sites), particularly when taxonomic groups were combined, and we found the same patterns after accounting for habitat heterogeneity. We also found significant evidence of checkerboard distributions when we analyzed communities defined by dietary characteristics by examining species whose diets include fruits or invertebrates. We found evidence of guild proportionality in birds, primates, squirrels, and the nonvolant species, but did not find support for Fox's assembly rule in any of the communities examined. These results demonstrate the presence of significant ecological structure, which indicates that these communities are nonrandom assemblages of species, and are consistent with the interpretation that species interactions within and between these taxonomic groups may have shaped both species distributions and community structure. Moreover, these results suggest that interactions between primates and other taxonomic groups can have important effects on primate community composition and future research should take account of them.

Variation in the size and habitat heterogeneity of the protected areas is a potential alternative explanation for the significant checkerboard scores because habitat checkerboards, in addition to species interactions, are known to drive checkerboard species patterns [Gotelli et al., 2010; Gotelli & McCabe, 2002]. Given that the sites included in this study cover all major forest types found on Borneo, it is possible that our checkerboard results may reflect habitat checkerboards. Complementary analysis with a subset of the data restricted to similar habitat types, however, yielded consistent results. Thus, while it is likely that habitat heterogeneity contributes to the checkerboard distributions we found when we considered all sites, it is unlikely that it can explain them entirely.

With the notable exceptions of primate communities and bat communities, we found that all other communities examined were significantly checkerboarded when we included species with all diet types. However, we note that communities of insecteating bats were significantly checkerboarded. Previous research on rhinolophoid bats in southeast Asia demonstrated that competition has led to niche differentiation within this insectivorous guild [Kingston et al., 2000], although recent research on North Borneo and the Malay peninsula suggests that insectivorous bat assemblages are relatively homogenous over substantial geographic distances [Struebig et al., In review; Struebig et al., 2011]. Thus, primates are particularly noteworthy for their lack of significant checkerboard distributions when considered in isolation and for the presence of significant C-scores when analyzed with other taxa. These results suggest that there is less interspecific interaction among primate species than between primates and other taxa in Borneo. Primates may be interacting more with nonprimates because of the low diversity of primates in comparison to other taxa.

Past competition may have resulted in sufficient niche differentiation among primates to enable coexistence whereas constraints on competition between primates and other taxa may have prevented further differentiation and thus led to significant checkerboard patterning. Alternatively, historical changes in habitat cover may have driven surviving species into previously unoccupied niches [*sensu* Crowley et al., 2012].

For invertebrate-eating species, checkerboard results were significant for all communities except for primates and squirrels. However, for fruit-eating species, checkerboard scores were not significant for primates, squirrels, bats, or nonvolant species. These results are consistent with the interpretation that invertebrate eating species show more evidence of checkerboard distributions than fruit eating species. In Bornean forests, interactions by species feeding on invertebrates may result in significant ecological patterning more often than interactions for fruit, particularly within taxonomic groups. Because of the extreme fluctuations in the availability of fruit in Bornean forests [Cannon et al., 2007], fruit-eating species may necessarily rely on other resources when fruit is scarce (e.g. orangutans [Knott, 1998]). Invertebrates may represent an important source of fallback foods, *sensu* Marshall and Wrangham [2007], and consequently function as limiting resources that negatively affect species coexistence. While our study does not address the specific invertebrate and fruit resources that species may be competing for, our results suggest that further investigation of overlap in fallback foods among Bornean vertebrates is warranted.

A handful of recent papers have investigated checkerboard distributions in communities relevant to Bornean vertebrates. A study of primate communities in the Sunda Shelf area found significantly high *C*-scores for observed primate communities when defined by all species or by folivorous species, but not by frugivorous species [Kamilar & Ledogar, 2011]. The authors suggested that the lack of significant difference in *C*-scores among frugivorous communities was a reflection of the generalist habits of these species [Kamilar & Ledogar, 2011]. Another recent study investigated checkerboard distributions of mammals on 240 small islands in Southeast Asia [Cardillo & Meijaard, 2010]. When all islands were considered, Cercopithecidae, Viverridae (civets), Pteropodidae (fruit bats), and Sciuridae (squirrels) had significantly higher *C*-scores than expected under the null model, but Cervidae (deer), Felidae (cats), and Emballonuridae (sheath-tailed bats) did not. While these studies have demonstrated significant co-occurrence patterns within individual families of Southeast Asian mammals, we build upon this growing body of research by considering competitive interactions among families and between mammals and birds.

Our study did not address the additional alternative hypothesis that historical environmental conditions may have caused current checkerboard distributions. In addition, the analyses undertaken in this study assume that species dispersal among sites is not limited. We suggest that future studies explore the role of historical habitats and dispersal ability in driving community composition. Lastly, we suggest that future work investigate potentially artificial effects of sampling effort and seasonality on co-occurrence patterns.

We found fixed guild structure in birds, primates, squirrels, and the nonvolant communities, which supports the test for guild proportionality in these communities. These results are consistent with the interpretation that competition within and between these taxonomic groups has resulted in proportional membership in foraging guilds across sites for squirrels, primates, and the two taxa combined, which differs from the results of the checkerboard analyses and highlights the potential influence of guild characterizations for driving patterns. We also note that guilds containing few species, as is the case with primates and squirrels, may be more likely to appear fixed due to the nature of the statistical test.

Although there is evidence in favor of Fox's assembly rule for communities of invertebrates [Rodriguez-Fernandez et al., 2006], salamanders [Adams, 2007], birds [de Silva & Medellin, 2002], small mammal communities in multiple regions [Fox & Kirkland, 1992; Kelt, 1999; Kelt et al., 1995; McCay et al., 2004], and in Malagasy lemur communities [Ganzhorn, 1997], we did not find support for the rule in any of the vertebrate communities examined. Fox's assembly rule assumes that the distribution of resources is homogeneous within and between sites and it is likely that this assumption is not met given that fruit production varies across habitat types [Marshall et al., 2009a; Wich et al., 2011]. An alternative explanation is that our foraging guild categorization was insufficient to detect competition because a lack of resolution in the dietary data prevented us from a more nuanced analysis. Lastly, we may have failed to find support for Fox's assembly rule because we lacked foraging guild data for some species. The absence of a subset of species may have been sufficient to preclude support of this very strictly defined rule.

Despite the overwhelming complexity and diversity of tropical rain forests, we found evidence of significant ecological structure in Bornean vertebrate communities of primates, birds, bats, and squirrels. This research addresses a gap in our understanding of primate communities; our results contribute to the understanding of the extent to which deterministic interactions within and between taxonomic groups may structure these communities. We suggest that as the field of primate community ecology progresses, it is important that primatologists

take into account the broader vertebrate communities in which primates occur and consider the role of biotic interactions within and between taxonomic groups in shaping primate communities. We have drawn attention to the importance of nonprimates as potential competitors of primates with this study, and we hope that more researchers will explicitly consider interspecific interactions between primates and other taxa. We believe that this is an important area of future research that warrants consideration across regions.

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