Competition among three primate species at Way Canguk, Sumatra, Indonesia

A Dissertation Presented

by

Alice Anne Elder

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Doctor of Philosophy

in

Anthropology

(Physical Anthropology)

Stony Brook University

August 2013

Stony Brook University
The Graduate School

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Abstract of the Dissertation

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Interspecific competition is the most common form of interaction described for coexisting organisms. Because of shared resource requirements, each of two species faces fitness costs in the presence of the other. Such competition can be reduced when species diverge in niche use. If, however, sympatric species maintain ecological similarity, heterospecific aggression should be high and interspecific dominance relationships may structure access to preferred resources. Across animal species, body mass has often been found to equate to dominance, providing large-bodied species with priority of access. Large group size may also lead to a competitive advantage. Nevertheless, because dominant species cannot simultaneously occupy all resources in their home range, subordinate species may survive by using either lower-quality or unoccupied resources. Thus, subordinate groups avoid potentially dangerous encounters with dominant species; these encounters can directly reduce reproductive success in subordinate species and, in extreme cases, be fatal. As more studies become available it seems that interspecific aggression may have a much higher explanatory value for individual species' behavior than previously assumed for primate ecology. Likely because this topic requires data for multiple habituated, sympatric groups of different species, it has, however, rarely been investigated in the past.

This dissertation investigated coexistence in a community of three primate species living at Way Canguk, Bukit Barisan Seletan National Park, Sumatra: the ecologically-similar siamangs (*Symphalangus syndactylus*) and agile gibbons (*Hylobates agilis*) and the ecologically-dissimilar mitered langurs (*Presbytis melalophos*). Four major research topics were addressed: (1) in what ways do these sympatric species overlap and differ in dietary niche use, (2) what determines interspecific dominance and what are the costs of being a subordinate species, (3) how do alternative mechanisms - other than niche partitioning - promote species coexistence, and (4) how does interspecific competition impact sleeping strategies?

Because siamangs are about twice the mass of agile gibbons and mitered langurs, they are expected to be dominant over the other two species. Alternatively, if group size is a better determinant of dominance, then langurs should be dominant. Because large body size also increases locomotor costs, it was predicted that agile gibbons would travel faster and farther than siamangs, while siamangs would feed longer in larger, more-productive patches. Agile gibbons were furthermore expected to avoid encounters with siamangs, resulting in lower daily energy intake and higher energy expenditure than siamangs.

Following 9 months of preparatory work during which 1 mitered langur, 2 siamang, and 2 agile gibbon groups were habituated, systematic data were collected on 4 siamang, 2 agile gibbon, and 1 mitered langur groups from November 2008 through October 2009 with the support of 4 local assistants. During 3,298 contact hours, data were collected on food intake, availability, and nutritional composition (249 food items), as well as interspecific encounters, activity budgets, ranging, and sleeping site use (226 agile gibbon, 223 siamang, and 48 mitered langur nights). The dietary niche of each species was described based on 282 all-day follows (151 days for siamangs, 95 for agile gibbons, and 26 for mitered langurs). The context and outcome of all interspecific encounters (*n* = 289) were used to assess dominance ranks. Interspecific comparisons of hylobatids' foraging strategies were made based on 269 all-day follows (161 siamang days and 108 agile gibbon days) and 2,817 siamang and 1,161 agile gibbon feeding bouts.

As expected, observations of feeding behavior (Chapter 2) suggested that the potential for interspecific competition was much higher between siamangs and agile gibbons than between hylobatid species and mitered langurs. As simple-gutted species, both hylobatid species predominantly fed on ripe fruits and figs and about equally used young leaves and flowers to supplement their diets. In fact, dietary overlap at Way Canguk was high compared with other populations where siamangs and small-bodied gibbons occur in sympatry. Mitered langurs (colobines with complex digestive anatomy adapted to a fibrous diet), in contrast, spent the majority of feeding time on leaves and supplemented with unripe fruits and flowers.

Interspecific dominance relationships (Chapter 3) were mediated by body mass and possibly not group size. That is, siamangs were dominant over both agile gibbons and mitered langurs. The much heavier siamangs initiated and won almost all encounters with agile gibbons (98%) and mitered langurs (100%). However, encounters between ecologically-similar siamangs and agile gibbons were much more frequent and aggressive than between mitered langurs and either hylobatid species. Encounter locations were non-random, occurring more often in shared-food than non-food locations. Agile gibbons incurred energetic costs and, rarely even physical wounds as a result of lost encounters with siamangs. Perhaps as a tactic to evade detection and reduce harassment by siamangs, agile gibbons frequently became motionless and remained in dense vegetation when approached by siamangs (passive avoidance). Taken together, agile gibbons seem to be at a real disadvantage in the system and their persistence requires an alternative explanation to classical niche partitioning.

I examined two potential mechanisms of hylobatid coexistence (Chapter 4), under which dominant and subordinate species are expected to differ in foraging strategies within a heterogeneous habitat. Subordinate agile gibbons were hypothesized to either 1) be fugitive species (i.e., they more rapidly reach and consume foods than dominant siamangs) or 2) use different, lower-quality feeding patches as competition refuges. Results revealed that agile gibbons are not fugitives, but likely use competition refuges. In support of the second hypothesis, agile gibbons fed in less productive patches, for shorter bouts, and at lower intake rates than siamangs. Additionally, agile gibbons minimized their energy expenditure by spending a much higher percentage of time resting each day. Due to their use of lower-quality feeding patches and the risks inherent in encounters with siamangs (Chapter 3), agile gibbons may struggle to meet their energy requirements. If that is the case, then the use of competition refuges would not facilitate their persistence and, in fact, coexistence of siamangs and agile gibbons may not be locally stable.

In addition to being subordinate and (seemingly) at an energetic disadvantage, agile gibbons were found to use a sleeping strategy unexpected for arboreal primates (Chapter 5). Compared with sympatric mitered langurs and siamangs, agile gibbons used shorter, smaller and more densely-vegetated sleeping trees. These characteristics are opposite to what is usually preferred by primates (i.e., large, emergent trees with open crowns), and should increase

predation risks for agile gibbons. Agile gibbon’s use of suboptimal (i.e., vulnerable to predation), yet well-concealed sleeping trees suggests that the subordinate species puts a priority on avoidance of detection by dominant siamangs. This would be an extreme, as of yet described, reaction to interspecific competition.

Overall, this dissertation suggests that sympatry with siamangs at Way Canguk is very challenging for agile gibbons. A clear mechanism for their stable coexistence has yet to be identified. Thus, it is possible that this population may only persist through periodic re-population from a nearby source population.

Dedications

For my family in Texas –

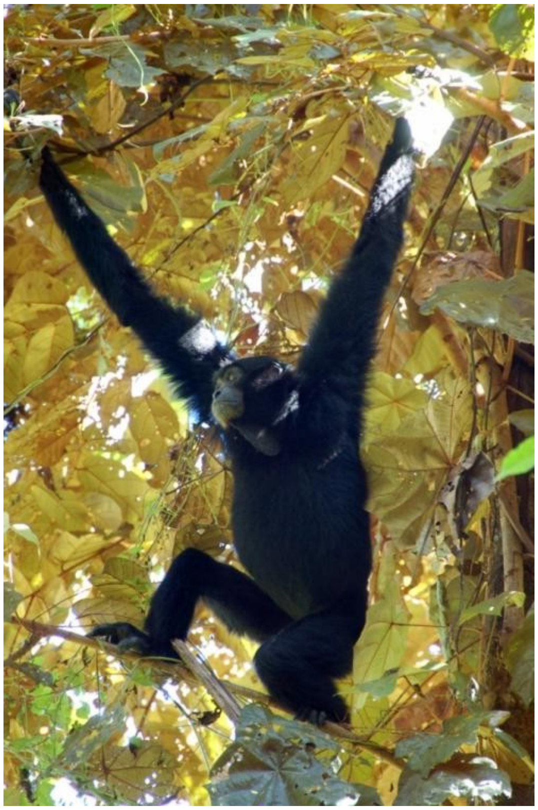
For my dad George for awakening the naturalist in me

For my mom Rose for teaching and supporting me in more ways than I can name

For my sisters Emily and Sara for sharing great adventures as children, for extending our family as adults, and for their constant friendship

For Katherine for being my third sister and my most indefatigable friend

Agile gibbons (*Hylobates agilis*): adult female and young infant from group 1



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Acknowledgments

Funding for this project was generously provided by the American Society of Primatologists, the Leakey Foundation, the National Science Foundation (DDIG BCS-0726089), and a Mildred and Herbert Weisinger Dissertation Fellowship from the Graduate School at Stony Brook University. The study was approved by Stony Brook University's IACUC (2006-2008-1491) and conformed to the laws and regulations in Indonesia and the United States. All research reported here was conducted in full compliance with the regulations of the Indonesian Ministry of Forestry (PHKA), Bukit Barisan Selatan National Park (TNBBS), and the Ministry of Research and Technology (RISTEK). I thank the RISTEK staff for granting and extending my permits as a foreign researcher. I thank the staffs of PHKA and TNBBS for granting permits to carry out research inside the national park and to collect and remove nutritional samples from TNBBS. I thank Dr. Wartika Rosa Farida and her staff at the Indonesian Institute of Sciences for their thorough and efficient work in analyzing my many, many nutritional samples.

I thank Carola Borries, John Fleagle, Charles Janson, Andreas Koenig, Susan Lappan, and Ryne Palombit for agreeing to form a truly formidable committee. With their unfathomable wealth of experience, knowledge, enthusiasm, common sense, and genius, they contributed immensely to making my doctoral project and this dissertation as good as possible. I most sincerely thank each of them for providing helpful comments and suggestions, as well as steadfast patience and guidance over the course of this project. I know that my research benefitted immensely from their involvement. I particularly thank Carola Borries for putting so much effort into her role as my advisor throughout my time at Stony Brook. I thank her for her unfailing organizational skills and attention to detail, her teatime meetings, and her belief in me as a scientist.

I especially thank all of the students of IDPAS, both past and present for helping to survive these 10 years (gulp) of graduate school. I never expected to find such a diverse, but welcoming group of people when I naively moved from Texas to New York. You made an incredibly stressful time not only bearable, but actually fun. For helping me to survive graduate school and make friends along the way, I thank: Andrea Baden, Mathew Banks, Mark Coleman, Wendy Erb, Kristin Ericson, David Fernandez, Chris Gilbert, Ari Grossman, Heather Hassel-Finnigan, James Herrera, Mitch Irwin, Rachel Jacobs, Eileen Larney, Jessica Lodwick, Amy Lu, Sara Martin, Kerry Ossi-Lupo, Biren Patel, Danielle Royer, Roberta Salmi, Clara Scarry, Mat Sisk, Elizabeth St Clair, Anne Su, Ian Wallace, Brandon Wheeler, and Jesse Young.

I appreciate Dr. Noviar Andayani for agreeing to be my research counterpart in Indonesia, for allowing me to work at Way Canguk, and for facilitating the research permit application and extension processes. I thank the staff of the Wildlife Conservation Society-Indonesia Program (WCS-IP) in Bogor and Kota Agung for their support, advice, and late night dinner runs. In particular, I thank Ibu Minda for helping me from afar to appease immigration in Lampung and the staff of TNBBS in Kota Agung when I was at my wits end.

I thank Meyner Nusalawo for his jokes, music, and friendship while in the forest, on the road, and when sharing great food in Kota Agung and Bandar Lampung. He is a great station manager and consummate mediator in times of stress. I thank Susan Lappan for first introducing me to the forest and the siamangs of TNBBS, and for helping me to navigate the Kafka-like experience that is the bureaucracy of Indonesia; I felt her echoed presence while drinking water through tiny straws in the offices of PHKA and falling in the mud (a lot) at Way Canguk. I extend special thanks to Luca Morino for his camaraderie, insightful discussions, humor, compassion, and impressive B.S.ing skills (though this we had in common) during our shared time in the forest. It would have been a much lonelier experience without him.

I am eternally grateful to my assistants in the field: Panut, Setiono, Ferry Wilantara, and Janji for their tireless work. There is absolutely no way I could have done this without them. They stayed in the trenches with me, even when habituation seemed impossible, the rain was torrential, and the nasi and mie were in short supply. They accepted me into their homes and families, and they never ceased to amaze me with their intelligence, humor, kindness, and individuality. Thank you guys and Go Team Owa!

Of course, I must also thank the non-human primates of Way Canguk for (eventually – agile gibbons you know who I am talking about) allowing us to observe your behavior. Thank you for putting up with us wet, bedraggled, and annoying humans all those years. I fervently hope that, by disseminating the findings of this research, more people will come to appreciate your worth.

I also thank my cats for serving as the non-human members of my support staff back home. Thank you Austin, Angel, and Johnny for keeping me company through literally countless late-night work sessions; you have been wonderful fluffy paper weights, great lap warmers, and very poor, but humorous typing assistants.

Finally, I would like to thank my family and friends ("the civilians") in and from Texas. To my dad: so yeah it took 10 years and you clearly won that bet. I wish you could have been here to witness the completion of my efforts and I know you would have been proud. Thank you for all of your love, emotional and monetary support, and unyielding, selfless belief in what I was pursuing. I thank my mom for being one of my best friends and role models; I could not think of a more kind, gentle, or loving person. Thank you for tolerating tedious discussions of ecological theory, my workaholic tendencies, and my (perhaps) overly-analytical view of the world. I am so appreciative of our relationship and all that you gave me, give me, and (undoubtedly) will give me down the road. I thank my sisters Emily and Sara, and my dear friend Katherine Goff for always being there and loving me when I needed you, and for the extended family members whom I gained from each of you. I thank my two brothers-in-law (Ryan and Dave) for loving and supporting me like a sister, and for helping to produce my three beautiful nieces: Erin, Keira, and Chloe. Thank you all for keeping me laughing and grounded.

Chapter 1

Species coexistence: an introduction to interspecific competition and niche divergence

INTERSPECIFIC COMPETITION AND LIMITATIONS ON COEXISTENCE

Interactions among organisms of different species may be beneficial (e.g., Gartlan and Struhsaker 1972; Cords 1984; Mitani 1991; Noë and Bshary 1997; Windfelder 2001; Smith et al. 2004), neutral (e.g., Ihobe 1997; de Resende et al. 2004) or adverse (e.g., Gause et al. 1934), depending on the costs and benefits of coexistence. However, interspecific competition, whereby each of two species suffers a reduction in fecundity, survivorship, or growth as a result of activities of the other species, is the most common form of ecological interaction reported for natural communities sampled across a wide range of organisms (reviewed in Connell 1983; Schoener 1983). In most cases, competing species are adversely affected due to use of the same limiting resource/s.

Traditionally, interspecific competition (like intraspecific competition) is divided into two main mechanisms: exploitative competition and interference competition (Park and Lloyd 1955). Exploitative competition is indirect, such that a resource is consumed or preemptively occupied and so cannot be used by individuals of another species (Schoener 1983). In contrast, interference competition is direct and operates when threat, harassment, or physical aggression benefits an individual's foraging, survival, or reproduction at the expense of an individual of another species (Schoener 1983). Both exploitation and interference may result in loss of energy or food. When most severe, interference may directly result in injury or even death (Park 1962). These mechanisms can be considered roughly synonymous with the ideas of scramble and contest competition (Nicholson 1957) that are more commonly used in primate behavioral literature (e.g., van Schaik 1989).

Since the writings of Darwin (1859), scientists have highlighted the importance of interspecific competition in determining community assembly (e.g., Hutchinson 1959; Fox 1987; Houle 1997; Ganzhorn 1999; Peres and Janson 1999) and resource use (Grinnell 1904; Volterra 1926; Lotka 1932; Gause et al. 1934; Hutchinson 1957). The simplest form of interspecific competition is represented by the competitive exclusion principle (e.g., Gause et al. 1934), which states that if two species live in the same geographic area and occupy the same ecological niche (i.e., are limited by the same resources), then one species will go locally extinct. The surviving population will be that which has a competitive or reproductive advantage, no matter how slight (Hardin 1960).

The competitive exclusion principle has been supported by laboratory studies, most notably in a series of classic experiments on three *Paramecium* species: While each species thrived in isolation, when placed into dyads of sympatry, either one species went extinct or both species survived by segregating the test tube vertically (Gause et al. 1934; Gause and Witt 1935). Furthermore, Tilman and colleagues (1981) found that one of two algae species put into sympatry died out when the concentration of limiting silicate remained below the level necessary for the excluded species' survival.

Field studies have provided additional support for the competitive exclusion principle: For example, differences in the distribution of two barnacle species were determined by interspecific competition rather than tidal conditions; one species limited the distribution of the other by physically excluding them from attachment sites (Connell 1961). Similarly, sympatric chipmunk species excluded each other depending on habitat structure, where one species had the advantage during agonistic encounters in sparse vegetation and the other fled these encounters and evaded contact aggression in denser tree stands (Brown 1971).

Nevertheless, multiple closely-related and/or ecologically-overlapping species often live together in natural assemblages (see examples below). This phenomenon is best understood by distinguishing between fundamental and realized niches. While the fundamental niche is the full range of environmental conditions under which an organism can exist, due to interactions with other organisms sharing a habitat, often a more narrow niche is realized (Hutchinson 1957). Thus, when sympatric species are able to diverge in ecology, the level of interspecific competition is reduced and exclusion is prevented (the character displacement model; Brown and Wilson 1956). At a certain level of niche overlap, coexistence of ecologically-similar species can be stable (the theory of limiting similarity; Abrams 1983). Thus, multiple species with broadly-similar ecologies may be able to occur in sympatry if shared niche space is sufficiently partitioned (Schoener 1975). Interspecific differences in morphology provide one mechanism to facilitate coexistence in these systems (Hutchinson 1959; Hutchinson and MacArthur 1959). In particular, ecologically-similar species are hypothesized to coexist if they differ in body mass by a factor of at least 1.5 (e.g., Bowers and Brown 1982; Ganzhorn 1999) or in linear traits (e.g., beak and cranial lengths) by a factor of at least 1.3 (e.g., Emmons 1980).

CLASSICAL NICHE PARTITIONING AND SPECIES COEXISTENCE IN PRIMATES

The ecological niche describes the multi-dimensional space of resources used by a species. In practice, a niche is typically divided into three main dimensions: dietary, spatial, and temporal (Schoener 1974). Classical niche partitioning refers to the differential use of these three components by competing species, independent of environmental fluctuations or resource heterogeneity (Chesson 2000). In cases of high ecological overlap between species, the niche is expected to be further subdivided into microhabitats. For example, sympatric species may differ in foraging location, feeding height, feeding time, and specific food types or parts eaten. Such partitioning is only an option if resources are available to be divided into microhabitats (Rusterholtz 1981). Niche partitioning leads to stable coexistence of two or more species, although one species may still be more successful than the other/s (e.g., higher birth rate or survivorship; Hairston 1980), with the strength of interspecific competition being inversely related to the level of niche segregation (Pacala and Roughgarden 1982).

Niche divergence has been shown to explain coexistence for the majority of systems studied (e.g., Pianka 1973; Schoener 1974). This mechanism for coexistence is particularly widespread across radiations of the primate order. Due to their ecological flexibility, extensive biogeographic distribution, and diverse dietary and locomotory adaptations (reviewed in Fleagle 2013), primate communities provide apt model systems within which to examine patterns of resource partitioning (Fleagle and Reed 1996; Ganzhorn 1997; 1999; Schreier et al. 2009). Sympatric primate species partition all three of the main dimensions of niche space, consuming different foods, dividing habitats structurally, and varying in activity patterns (discussed below). Multiple forms of niche partitioning may occur simultaneously in the same community (e.g., Terborgh 1983; Mitani 1991), and patterns of segregation often vary with changing ecological conditions (e.g., Gautier-Hion 1980).

Dietary niche partitioning

Dietary segregation of niche space takes a variety of forms, including differences in food species, parts, maturity, and nutritional quality, as well as dietary breadth (i.e., the number of different food items used, indicating degree of dietary specialization). For example, the diets of sympatric guenons (*Cercopithecus spp.*) differ in plant parts and species eaten (Mitani 1991), and types of invertebrate prey (Gautier-Hion 1980). Additionally, tantalus monkeys (*Cercopithecus aethiops tantalus*) eat a wider range of lower quality foods than sympatric patas monkeys (*Erythrocebus patas*; Nakagawa 2003). Sympatric macaques and langurs eat similar food species, but differed in the parts and maturity of foods consumed (Singh et al. 2011). Sympatric New World monkeys (*Saguinus, Saimiri*, *Cebus*, *Ateles*, and *Alouatta*) share preferred foods, but diverge in supplementary foods and dietary breadths (Terborgh 1983; Guillotin et al. 1994). Similarly, sympatric lemurids (*Varecia variegata* and *Eulemur fulvus albifrons*) differ in dietary breadth and feeding patch size (Vasey 2000).

Between-species differences in digestive anatomy and physiology may result in divergent dietary constraints. For example, differences in the digestive strategies of sympatric African cercopithecines and colobines (i.e., generalized anatomy vs. specialized fermentation – Lambert 1998; significantly longer mean gut retention times in colobines – Vogel et al. 2009b; Vogel, Janson, and van Schaik pers. comm.) contribute to differences in dietary flexibility. Cercopithecines more frequently switch resource types and have more diverse diets than sympatric colobines (Lambert 2002). Additionally, differences in gut morphology also likely contribute to divergence in dietary diversity and food chemistry between sympatric indriid lemurs (*Propithecus diadema* and *Indri indri*; Powzyk and Mowry 2003).

While some species partition niche space consistently over time, for others differentiation may become most evident at times of resource scarcity. As preferred foods become less available, dietary overlap decreases between sympatric African apes (Tutin et al. 1991), Asian apes (Vogel et al. 2009a), Old World monkeys (Wahungu 1998; Singh et al. 2011), New World monkeys (Terborgh 1983; 1986; Guillotin et al. 1994; Stevenson et al. 2000), and lemurs

(Overdorff 1993; Vasey 2000). Coexistence among these taxa may be possible if ecologically-similar species reduce direct competition by switching to different supplementary foods and/or diverging in dietary diversity.

Spatial niche partitioning

In addition to partitioning niches through dietary differences, sympatric primate species may diverge in their use of spatial niches. Within Malagasy lemur communities, taxa may be divided into two main guilds (folivores and frugivores), and within each guild species are further segregated by structural differences in habitat use (Ganzhorn 1989). Sympatric mouse lemurs (*Microcebus murinus* and *M. ravelobensis*) do not diverge in activity cycle, daily torpor timing, torpor seasonality, reproductive seasonality, diet, social system, or body size. However, these very small-bodied primates differ in sleeping site ecology; while one species exclusively uses tree holes, the other uses a broad range of sites (Radespiel et al. 2003). Differences in habitat use are also found between coexisting cercopithecine monkeys, such that faster-moving patas monkeys prefer grasslands and tantalus monkeys prefer woodlands (Nakagawa 1999). Additionally, capuchins (*Cebus apella* and *C. albifrons*) foraged within different substrates than sympatric tamarins (*Saguinus imperator* and *S. fuscicollis*; Terborgh 1983). Vertical segregation of the shared habitat has also been demonstrated for sympatric guenons (Mitani 1991), macaques (Singh et al. 2011), and callitrichines (Heymann and Buchanan-Smith 2000).

Temporal niche partitioning

Although primates vary widely in activity patterns, including diurnal, nocturnal, crepuscular, and cathemeral species (reviewed in Fleagle 2013), this variation is almost exclusively restricted to strepsirhine taxa. Out of all haplorhine species, only owl monkeys (*Aotus spp*) and tarsiers (*Tarsius spp*) are known to show non-diurnal behavior (Wright 1989). Furthermore, many nocturnal primates are small-bodied insectivores, while sympatric diurnal species tend to be larger-bodied and to feed on fruits and leaves (Charles-Dominique 1975). Thus, temporal partitioning may rarely occur among primate species (Schreier et al. 2009). More generally, it has been suggested that temporal niche partitioning may be much less common than divergence in diet or space use across animal communities (Kronfeld-Schor and Dayan 2003; but see Charles-Dominique 1975). Alternatively, it is possible that the temporal axis of niche space is under-studied relative to the other two axes. Temporal partitioning may also occur on a finer scale than differences in diet and space, as was found for certain bats (Adams and Thibault 2006) and mice (Kronfeld-Schor and Dayan 1999). Very few examples of temporal niche partitioning have been suggested for primates. Based on a review of the modes of niche separation among potential primate competitors, differential timing of activity was restricted to Madagascar (i.e., purportedly to the exclusion of primate communities in Africa, Asia, and the Americas) and only occurred for 4 of 22 species-pairs sampled (Schreier et al. 2009). For example, mongoose lemurs (*Eulemur mongoz*) switch from a diurnal to nocturnal activity pattern during the dry season when feeding competition with sympatric *Eulemur fulvus* may be greatest (Tatersall and Sussman 1975). In addition, through nocturnal foraging, owl monkeys (*Aotus*) likely avoid direct competition with diurnal frugivorous species, such as sympatric *Callicebus*, *Saimiri*, *Cebus*, and *Ateles* monkeys (Terborgh 1983; Wright 1989).

ALTERNATIVE MECHANISMS OF COEXISTENCE

Niche partitioning is not always the main mechanism of coexistence, and in some communities species maintain sympatry despite high levels of ecological overlap. In these systems, coexisting species can use the same set of resources, but must either be limited by different resources (Tilman 1987) or be limited in different ways by the same variably-abundant resource (e.g., Stewart and Levin 1973). Access to patchy resources may be structured by interspecific dominance relationships (Morse 1974; Schoener 1983). Dominant species gain priority of access to resources through harassment of or aggression against individuals of the competing species (i.e., interference competition; Morse 1974; Schoener 1983). Subordinate species can persist, therefore, only by using resources of the same species and/or quality that are overlooked or not preferred by the dominant species (Horn and MacArthur 1972; Levin 1974; Slatkin 1974).

Interspecific dominance

The outcomes of behavioral interactions (i.e., interspecific encounters) may be used to infer ecological relationships among coexisting species (e.g., Dickman 1991; Robinson and Terborgh 1995; Martin and Martin 2001). These interactions are mediated by an inequality in resource holding potential (Morse 1974), where those species with greater fighting abilities gain priority of access to resources (Maynard Smith and Parker 1976). Resource holding potential correlates positively with body mass for the majority of animal communities (reviewed in Morse 1974; Abrams 1983; Connell 1983; Terborgh 1983; French and Smith 2005). Although large body mass requires absolutely more energy to maintain (Kleiber 1932), it also often enables the larger species to win encounters (Maynard Smith 1982). Lighter species may, however, still win interspecific encounters if they outnumber the heavier species and use cooperative resource defense (Fisler 1977; Wrangham 1980; Terborgh 1983; Fuller and Kat 1990). Despite potentially having greater resource holding potential, larger groups do not necessarily have higher per capita energy gain than species living in smaller groups. As group size increases, individual foraging efficiency increases, but only up to the point at which foraging costs (i.e., within-group scramble competition; van Schaik 1989; Sterck et al. 1997) outweigh this benefit (Janson 1988).

Communities where closely-related species stably coexist are expected to be rare and such species are expected to exhibit high levels of interspecific aggression (Houle 1997; Peiman and Robinson 2010). In these systems subordinate species should develop strategies to avoid encounters with dominant species, particularly if the outcomes of such interactions are predictable and uni-directional (Maynard Smith 1982). Selective pressure, therefore, may encourage the use of unoccupied and/or concealed feeding patches (e.g., Durant 1998; 2000) and resting sites (Navarrete and Castilla 1990; Souza-Alves et al. 2011).

Fugitive species

Hutchinson (1951) proposed an alternative model for the coexistence of ecologically-similar species, whereby the subordinate may be able to coexist with a dominant species by more rapidly invading new patches as "fugitives." Although the fugitive model was developed to understand extinction and colonization by sessile organisms, it may be extended to explore competition between mobile organisms over renewable food patches, where there is a tradeoff between dominance and foraging efficiency (e.g., Houle et al. 2006). Even if one species always wins encounters, a group of this species cannot occupy all food patches at once. Thus, subordinate fugitives may survive by fleeing from direct competition and more rapidly reaching and exploiting renewed food patches than dominants. In such systems both species use the same, exact patches, but subordinate species access them first and consume as much as possible before being displaced. This mechanism has been described for spiders (Marshall et al. 2000), parasitic mites (Downes 1991), and cercopithecine monkeys (Waser and Case 1981; but see Janson 1992).

Competition refuges

Alternatively, subordinate species may avoid direct interactions with dominant species by seeking out competition refuges. Developed as an extension of predator-prey theory's predator refuges (i.e., areas with reduced predation pressure; Hassell and May 1973), this mechanism posits that: if subordinate species use resources of the same type or species but of lower-quality as competition refuges, then they may avoid encounters with dominant species that are more likely to occur at preferred, high-quality patches (Durant 1998). Competition refuges, therefore, include resources that are smaller or less productive (dung beetles - Horgan 2005), more dispersed (tamarin monkeys – Terborgh 1983; Terborgh and Stern 1987; African carnivorans - Durant 1998; gerbils - Abramsky et al. 2001), or less protected (intertidal crabs - Navarrete and Castilla 1990; hermit crabs - Turra and Denadai 2004).

COMPETITION BETWEEN SYMPATRIC HYLOBATIDS

Communities of hylobatids (siamangs and other gibbons) are good model systems for studying mechanisms of interspecific competition because species coexist while using very similar ecological niches. Sympatric hylobatids have been found to use the same part of the canopy (Raemaekers 1977; MacKinnon and MacKinnon 1980) and eat the same food species, sizes and parts (Raemaekers 1979; Palombit 1997). Although it has been suggested that siamangs are more folivorous than other hylobatids, an analysis of variation in diet across the family revealed that siamangs and smaller-bodied gibbons (i.e., species of *Nomascus*, *Hylobates*, and *Hoolock* gibbons) did not significantly differ in the percentage of time spent eating leaves, fruit, flowers or insects (Elder 2009). This held true for sympatric as well as allopatric species. Dietary variation in hylobatids is significantly correlated with mean annual rainfall (a proxy for resource availability), but not with body mass.

Because siamangs are about twice the body mass of *Hylobates* gibbons (mean female masses=10.7 kg vs. 5.7 kg; Smith and Jungers 1997), they are expected to have a competitive advantage over these sympatric gibbon species (Raemaekers 1978). With longer mandibles (Hylander 1985), higher chewing rates (Raemaekers 1979) and crested molars (Kay 1984), siamangs may deplete food patches more rapidly than smaller *Hylobates* gibbons. However, locomotor costs should be higher in siamangs due to their larger mass and shorter stride (Fleagle 1976; Raemaekers 1979; Fleagle 1980).

Although siamangs are expected to be dominant over *Hylobates* gibbons (Raemaekers 1978), sympatric hylobatid populations date from at least the late Pleistocene (Jablonski and Chaplin 2009). In fact, siamangs are occur with *Hylobates* gibbons across their distribution, including *H. lar* in Malaysia and northern Sumatra and *H. agilis* in central and southern Sumatra (review in Chatterjee 2009). Furthermore, interspecific territoriality does not occur between siamangs and *Hylobates* gibbons (Raemaekers 1978; Elder pers. obs.). In light of the ecological similarity between sympatric hylobatids, other mechanisms of coexistence should be in place.

RESEARCH OBJECTIVES

In this dissertation I aim to explore mechanisms and consequences of coexistence among three Sumatran primate species: the ecologically-similar siamangs (*Symphalangus syndactylus*) and agile gibbons (*Hylobates agilis*), and the ecologically-dissimilar mitered langurs (*Presbytis* *melalophos*). Mitered langurs are similar in body size to agile gibbons (female body mass = 5.8; 6.5 kg respectively; Smith and Jungers 1997), but have specialized digestive anatomy, allowing them to subsist on more fibrous, lower-quality foods (Kay and Davies 1994; Lambert 1998). Due to a low level of direct competition with hylobatids, langurs are expected to access resources throughout hylobatid home ranges (Raemaekers 1978). However, the large group size of langurs may provide a competitive advantage over agile gibbons and siamangs, allowing them to have priority of access to food patches. Therefore, langurs are incorporated in the study because they 1) are expected to be the next most important primate competitors after hylobatids for each gibbon species (where more frugivorous macaque species (MacKinnon and MacKinnon 1980) - *Macaca nemestrina* and *M. fascicularis* - rarely enter the study groups' home ranges), 2) serve as a control to assess the effects of body mass and group size on between-species dominance interactions and 3) will serve as a control to distinguish interactions with closely-related species from those between distantly-related species.

Four major research topics are addressed: **(1) dietary niches*:*** to what extent do the diets of each pair of primate species overlap and in what ways do they differ **(2) interspecific dominance**: a) what are the effects of ecological similarity, body mass, and group size on interspecific dominance relationships and heterospecific aggression and b) what are the energetic costs of being a subordinate species, **(3) alternative mechanisms promoting coexistence for hylobatids**: are subordinates a) fugitive species or b) do they use competition refuges, and c) is this truly a stable system, and **(4) the influence of predation avoidance and interspecific competition on sleeping strategies**: a) are differences in interspecific dominance reflected in each species' sleeping strategy, b) rather than avoiding predation, do subordinate species try to evade detection by and harassment from dominant species?

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Chapter 2

Dietary niches of three sympatric primate species: exploring the potential for feeding competition

INTRODUCTION

An ecological niche is the multi-dimensional space of resources available to and used by a species (Schoener 1974). While the fundamental niche is the full range of environmental conditions under which an organism can exist, due to interactions with other organisms sharing a habitat, often a more narrow niche is realized (Hutchinson 1957). Closely-related species of the same ecotype are expected to diverge in niche use when living in sympatry to reduce direct competition (Brown and Wilson 1956) and avoid competitive exclusion (Gause et al. 1934). Coexistence of ecologically-similar species should become stable at some threshold of niche overlap (Abrams 1983), thereby allowing multiple species with broadly-similar ecologies to occur in sympatry once shared niche space is sufficiently divided (e.g., Schoener 1975). Species coexistence is often facilitated by interspecific differences in morphology (e.g., body mass; Hutchinson and MacArthur 1959; Bowers and Brown 1982) and/or physiology (e.g., digestive strategies; Chivers and Hladik 1980; Lambert 2002). Despite coexistence, however, levels of niche overlap may be used to evaluate the potential for interspecific competition within a system (e.g., Pacala and Roughgarden 1982). Furthermore, even under stable coexistence, one species may be more successful than the other (Hairston 1980).

Resource partitioning refers to the differential use of niche space, whereby sympatric organisms diverge in their use of resources across dietary, spatial, and temporal dimensions (Schoener 1974). Niche partitioning seems to be a pervasive mechanism of coexistence across animal systems (Schoener 1974; Schoener 1982), including sympatric primates from all major radiations of the order (Ganzhorn 1999). Due to their ecological flexibility and wide variety of dietary adaptations (reviewed in Fleagle 2013), primate communities provide interesting systems for which to examine patterns of resource partitioning (Ganzhorn 1989; Fleagle and Reed 1996; Ganzhorn 1997). Sympatric primate species have been reported to partition niche space along all three dimensions of niche space (reviewed in Chapter 1; Schreier et al. 2009), as well as to exhibit multiple forms of partitioning within the same community (e.g., Mitani 1991). This includes interspecific differences in primates' food species (Gautier-Hion 1980; Terborgh 1983; Mitani 1991; Guillotin et al. 1994), parts (Mitani 1991; Singh et al. 2011), maturity (Singh et al. 2011), and nutritional quality (Nakagawa 2003; Powzyk and Mowry 2003), as well as dietary breadth (i.e., the total number of different food items used, indicating the degree of dietary specialization; Mitani 1991; Guillotin et al. 1994; Vasey 2000; Lambert 2002; Nakagawa 2003). In addition to dietary partitioning of their niches, sympatric primate species also divide habitats structurally (e.g., Eudey 1981; Terborgh 1983; Ganzhorn 1989; Heymann and Buchanan-Smith 2000; Radespiel et al. 2003) and (more rarely) temporally (Terborgh 1983; Wright 1989).

Here I aim to evaluate the potential for feeding competition among sympatric siamangs (*Symphalangus syndactylus*), agile gibbons (*Hylobates agilis*), and mitered langurs (*Presbytis melalophos*) by describing 1) each species' dietary breadth and 2) the degree of dietary overlap between each pair of species. My primary goal is to provide basic characterizations of each species' diet as a way to describe the competitive climate in the study system.

Available data suggest that dietary overlap should be high between siamangs and agile gibbons. Siamangs coexist with *Hylobates* gibbons (*H. lar* in Malaysia and northern Sumatra; *H. agilis* in central and southern Sumatra) throughout their distribution range (Chatterjee 2009).

Despite their long-term sympatry (Jablonski and Chaplin 2009), ecological overlap remains high between siamangs and *Hylobates* gibbons. They use the same level of the canopy (Raemaekers 1977; MacKinnon and MacKinnon 1980) and eat similar species and sizes of ripe, pulpy fruits (Raemaekers 1977; 1979; Raemaekers 1984; Palombit 1997; Chivers 2001). Although it has been suggested that siamangs are more folivorous than other hylobatids (e.g., Raemaekers 1984), dietary variation within the family is better correlated with proxies of resource availability than with body mass (Elder 2009). Furthermore, across locations and species, hylobatids' population densities are limited by the availability of figs (Marshall 2004; Marshall and Leighton 2006). As resources that occur in large, asynchronously-fruiting patches (Raemaekers 1978; Raemaekers et al. 1980), figs likely serve as important supplementary foods (Marshall 2004; Vogel et al. 2009; Harrison and Marshall 2011) and, in some populations, may even be preferred over nutritionally superior fruits (Palombit 1997). Thus, figs differ from other fruits in both their availability and relative value to frugivore consumers (Conklin and Wrangham 1994; Kinnaird and O'Brien 2005), and should be treated separately from non-fig fruits in comparisons of dietary niches.

Even though siamangs and *Hylobates* gibbons have broadly-overlapping ecologies, a disparity in their body masses results in differences in energetic constraints. Siamangs are close to twice the body mass of sympatric white-handed (*Hylobates lar*), as well as agile gibbons (female mean masses=10.7 vs. 5.3 and 5.8 kg respectively; Smith and Jungers 1997). Larger-bodied animals expend less energy and require less food per unit of body mass, yet require absolutely more food than smaller-bodied organisms (Kleiber 1932). Because body size has significant effects on primate locomotion, foraging, and energetics, hylobatids may differ in dietary breadth or composition in relation to body mass (Raemaekers 1984). Niche breadth has been hypothesized to influence the size of an organism's geographical range (Brown 1984), such that larger species often require more space to meet their higher (absolute) energetic needs (McNab 1963). As a key component of this hypothesis, a positive correlation is expected between body mass and niche breadth because heavier organisms should encounter and exploit a wider range of resource types within their larger home ranges (Ottaviani et al. 2006; Costa et al 2008). Alternatively, differences in dietary breadth may reflect metabolic consequences of body mass; due to their lower metabolic rate (Kleiber 1932), heavier species may be less constrained by the size and quality of food items and, therefore have more diverse diets (i.e., wider dietary breadth; reviewed in Brown 1995). Due to either of these potential mechanisms, siamangs are expected to have wider dietary breadths than sympatric agile gibbons. Furthermore, siamangs have longer mandibles (Hylander 1985), higher absolute ingestion rates (Chapter 4; Raemaekers 1979), relatively heavier guts (Aiello and Wheeler 1995), and higher-crested molars (Kay 1984) than *Hylobates* gibbons. Thus, siamangs may be more efficient than these smaller gibbon species at processing fibrous food items, and therefore be better able to gain nutrients from certain food types (e.g., young and mature leaves). In particular, hylobatids have been found to diverge in the type of foods selected to supplement their fig-dominated diets; while siamangs consumed more leaves, smaller-bodied, white-handed gibbons spent more feeding time on ripe fruits and/or insects (Raemaekers 1979; Raemaekers 1984; Palombit 1997).

Mitered langurs are only slightly heavier than agile gibbons (langur females=6.5 kg; Smith and Jungers 1997), but have specialized digestive anatomy. Like all colobine monkeys, mitered langurs are foregut fermenters; sacculated stomachs containing anaerobic cellulytic bacteria allow them to subsist on more fibrous, lower-quality foods (e.g., leaves and seeds containing high levels of secondary compounds), yet result in long gut-retention times (Vogel, Janson, and van Schaik pers. comm.) and limit their ingestion of acidic foods, such as ripe fruits

(Waterman 1984; Davies et al. 1988; Lambert 1998). As anatomically-specialized folivores, colobines typically have less diverse diets (i.e., narrow dietary breadths) relative to sympatric species with generalized digestive anatomy (e.g., African ceropithecines; Lambert 2002). Thus, the physiological strategies of colobines differ from those of comparatively simple-gutted, largely-frugivorous hylobatids (Chivers and Hladik 1980), and mitered langurs are expected to diverge in diet from siamangs and agile gibbons across all niche parameters. Mitered langurs thereby serve as a good control to evaluate levels of niche overlap and the potential for feeding competition between sympatric hylobatids.

Based on the hypothesis that the degree of similarity in digestive anatomy and physiology influences the similarity of sympatric organisms' dietary niches, it is predicted that 1) dietary overlap will be higher between agile gibbons and siamangs than between each hylobatid and mitered langurs, and that 2) dietary breadth will be more narrow in mitered langurs than in either hylobatid. Addtionally, if niche breadth increases with body mass, then siamangs are expected to have wider dietary breadths than agile gibbons. Taken together, the two hypotheses concerning niche breadth suggest that diets should increase in width from mitered langurs to agile gibbons to siamangs.

MATERIALS AND METHODS

Study site

This study was conducted at Way Canguk Research Area (5° 39' S, 104° 24' E, 50 m a.s.l.) in Bukit Barisan Selatan National Park (BBS), Sumatra, Indonesia. Way Canguk comprises 900 ha of primary lowland rain forest within a large protected area (3,568 km^2), and is run by the Indonesian Ministry of Forestry and the Wildlife Conservation Society Indonesia

Program (WCS-IP). The study area, bisected by the Canguk River, is crossed by 105 km of trails at 200 m intervals (O'Brien et al. 2004). In addition to siamangs, agile gibbons, and mitered langurs, three other diurnal primate species (long-tailed macaques - *Macaca fascicularis*, pig-tailed macaques - *M. nemestrina*, and silvered langurs - *Trachypithecus cristatus*) occur at BBS. These species, however, have low densities and predominantly range outside of the study area (WCS IP unpub. data).

Data collection

Data on dietary niches were collected from November 2008 through October 2009 during all-day follows of one mitered langur (*P.m.*), four siamang (*S.s.*) and two agile gibbon (*H.a.*) groups. A total of 282 all-day follows were completed, including 151 siamang days (1,437 contact hours), 95 agile gibbon days (934 contact hours), and 36 mitered langur days (379 contact hours). Each group was followed by teams of 2-3 observers for a minimum of three consecutive days per month. Focal individuals included all adult siamangs (8 males and 4 females) and agile gibbons (2 males and 2 females), and a subset of adult mitered langur individuals (5 females and 1 adult male) from a one-male group. Instantaneous focal sampling was used for one-hour protocols and one-minute intervals (Martin and Bateson 1993) to record the individual’s general activity state. Whenever an individual was feeding, the food name, type (i.e., fruit, fig, flower, leaf, shoot, pith, or insect), part (i.e., skin, pulp, seed, bud, petal, lamina, stem, or whole), and maturity (i.e., ripe or unripe fruits and figs; young or mature leaves) was recorded. Seeds were recorded as food items only when specifically selected, masticated, and ingested (i.e., pre-dispersal seed predation; Janzen 1971). In instances when seeds were swallowed whole and defecated intact, they were not included as food items. Focal individuals were rotated hourly so that each individual was sampled evenly across the active period. Daily mean percentages of feeding time spent on each food type and individual item (i.e., unique part/maturity/type/food species) were calculated for each group using focal follows of adult individuals. These daily group means were then averaged for each month, and then monthly group means were averaged across conspecific groups to arrive at mean monthly values per primate species.

Feeding observations were compiled across instantaneous focal data to complete the list of food items used (Appendix 1). Whenever possible, primate foods were identified in the field and assigned to family, genus, and species levels following prior identifications made by WCS-IP. Scale photographs were taken and descriptions recorded for samples of all food items, so that these preliminary identifications could be later validated against those provided by Slik (2009) and The Plant List (2010). It is likely that results for the total number of different items eaten by each species will be influenced by the number of observation days and the availability of different food items per home range. In this study, the number of all-day follows is disproportionately low for mitered langurs compared with siamangs and agile gibbons. Thus, the results presented may not give a complete picture of each species' dietary diversity and should be interpreted with this limitation in mind.

Data analyses

Dietary breadth. Two measures of niche breadth were calculated to assess each primate species' level of dietary specialization. Firstly, gross dietary breadths were defined as the total number of different food items used per primate species. Because the number of focal groups varied among primate species (i.e., *S.s.*=4, *H.a.*=2, *P.m.*=1), dietary breadths were averaged separately across groups of siamangs and agile gibbons. These mean per group dietary breadths were then used in interspecific comparisons of absolute dietary breadth.

Secondly, Levins' (1968) measure of niche breadth, the reciprocal of the Simpson's diversity index (1949), was used to quantify the distribution of each primate species' diet within a set of 28 mutually-exclusive food categories. Each of these categories comprised a distinct food part of a given maturity per food type (e.g., pulp of ripe fruits). Levins' niche breadth (B) is calculated as: $B = 1/\sum p_j^{\ 2}$, where p_j = the proportion of items in the diet from food category j. This measure was selected to assess niche breadth because it does not focus on variation in the abundance of resources (i.e., does not disproportionately emphasize rare or abundant resources). Furthermore, Levins' measure can be standardized to a 0-1 scale if corrected for a finite number of resources and then divided by the total number of resource states (here the number of food categories). That is, Levins' standardized niche breadth (B_A) is found by the following formula: $B_A = (B - 1)/(n - 1)$, where n = the total number of possible resource states (Hurlbert 1978). Values close to 0 indicate dietary specialization (i.e., a narrow niche), while values close to 1 indicate a dietary generalization (i.e., a wide niche; Colwell and Futuyama 1971). Operationally, a species is considered to have a wide niche breadth when $B_A \geq 0.5$ (Krebs 1999).

Dietary overlap. Absolute dietary overlap was first calculated for each pair of primate species by dividing the total number of food items shared between species by the total number of different food items eaten per species. Thus, for every species-pair, two separate values of overlap were calculated (i.e., one from each species' perspective). In addition, Morisita's simplified index (Horn 1966) for niche overlap was calculated to evaluate overlap in the proportions of feeding time spent on foods across the same 28 categories used to assess niche breadth. Morisita's index (C_H) was chosen because it has the least bias out of all overlap measures for small and/or uneven sample sizes (Smith and Zaret 1982). Dietary overlap between species x and y, therefore, is calculated as: $C_H = 2\sum p_{ix}p_{iy}/(\sum p_{ix}^2+\sum p_{iy}^2)$, where p_{ix} = proportion of feeding time spent on food category i by species x and p_{iy} = proportion of feeding time spent on food category i by species y. Monthly C_H values were calculated for each species-pair from the mean (averaged across conspecific focal groups) proportions of feeding time per food category per primate species. Overall levels of Morisita's dietary overlap were then determined by averaging across monthly C_H measures for each pair of primate species.

Top food items. Each month, those food items comprising the top 75% of daily feeding time for each focal group were recorded as "top food items". Feeding time on each top food item was averaged across focal days and groups to arrive at monthly values for feeding time per item per primate species. Overlap between each pair of species in the use of these top food items was then calculated each month as the sum of feeding times spent on each shared top food item (i.e., those identified as top food items for both species).

RESULTS

Dietary compositions

Similarity in overall dietary composition was greater between siamangs (*S.s.*) and agile gibbons (*H.a.*) than between mitered langurs (*P.m.*) and either hylobatid species (Fig. 2.1). Based on species' means across the 12-month study period, siamangs and agile gibbons spent the largest perecentage of their feeding time on ripe fruits (*S.s.*=39%; *H.a.*=49%), followed by leaves/shoots (*S.s.*=24%; *H.a.*=20%) and figs (*S.s.*=27%; *H.a.*=18%). Furthermore, hylobatids very rarely consumed unripe fruits (*S.s.*=1%; *H.a.*=2%) and never ate pith. In contrast to siamangs and agile gibbons, mitered langurs spent much less feeding time on ripe fruits (18%) and figs (7%), much more time eating unripe fruits (16%), and nearly twice as much time consuming leaves and shoots (47%). While insects comprised a very small percentage of feeding time across species, agile gibbons spent slightly more time eating insects (1%) than either siamangs or mitered langurs (<1% each). All three primate species, however, spent about equal and relatively large percentages of feeding time consuming flowers (*S.s.*=9%, *H.a.*=10%, *P.m.*=12%; Fig. 2.1). Flowers accounted for 9% (*n*=26) of siamangs', 9% (*n*=15) of agile gibbons', and 12% (*n*=19) of mitered langurs' total food items (Appendix 1). Of these flowers, 10 eaten by siamangs, 4 eaten by agile gibbons, and 6 eaten by mitered langurs contributed to the top 75% of daily feeding time (Table 2.1).

Dietary diversity and gross dietary breadth

During this study, 387 different food items (i.e., unique food parts per maturity per type per species) were recorded (Appendix 1). Of these, 204 items were eaten exclusively by only one primate species: 99 by siamangs, 20 by agile gibbons, and 85 by mitered langurs (Table 2.2). There were 37 items that were consumed by all three species, while the number of shared food items varied among species-pairs. By far the most items were shared only by siamangs and agile gibbons (111 items; 29% of all items). In contrast, there were 32 items eaten only by mitered langurs and siamangs, and 2 items were exclusively shared between agile gibbons and mitered langurs (Table 2.2).

Siamangs consumed a total of 278 different food items from 47 families, 74 genera, and 224 species (Table 2.3; Fig. 2.2). Compared with siamangs, agile gibbons and mitered langurs had lower dietary diversity (Table 2.3); they fed on items from fewer total families (39 each), genera (*H.a.*=60; *P.m.*=73), and species (*H.a.*=150; *P.m.*=125), and each ate a much smaller total number of food items (*H.a.*=169 and *P.m.*=157 items respectively). However, the apparent divergence among species in absolute dietary breadth (Fig. 2.2) was influenced by differences in the number of groups sampled for each primate species. Of siamangs' 278 total food items, only 84 were used by all four groups studied. Similarly, only 72 of agile gibbons' 169 total food items were consumed by both groups. On average, each siamang group consumed 138 different food items, while each agile gibbon group ate a mean of 121 different food items (Table 2.3). Per group dietary diversity, therefore, was largest for mitered langurs, followed by siamangs, and then agile gibbons.

Levins' dietary breadth and the importance of food categories

Despite interspecific differences in absolute dietary breadths, overall values of both gross and standardized Levins' dietary breadths were remarkably similar across primate species (Table 2.4). Siamangs, agile gibbons, and mitered langurs all had narrow diets ($B_A = 0.19$, 0.19, and 0.17 respectively); dietary breadths fell well below the cutoff indicative of generalized diets (i.e., $B_A > 0.5$). Thus, each species consumed foods from a relatively small number of different categories. As single values, however, Levins' measures of dietary breadth do not reveal whether primate species concentrated on the same food categories.

By more closely examining percentage utilizations (Table 2.4), it is evident that hylobatids, in fact, diverged from mitered langurs in the distribution of food items across categories. The majority of both siamangs' and agile gibbons' food items consisted of ripe fruit pulp, whole ripe figs, and whole young leaves (Table 2.4; combined: *S.s.*= 63%; *H.a.*=61%). Ripe fruit skin and pulp (*S.s.*=8%; *H.a.*=11%), as well as whole ripe fruits (*S.s.*=7%; *H.a.*=8%) made the next largest contribution to each hylobatid's diet. Compared with siamangs, a lower percentage of agile gibbon foods were leaves (Combined: 34% vs. 13%), and agile gibbons were observed to eat only one type of mature leaves (Table 2.4). In contrast with each hylobatid's diet, that of mitered langurs was disproportionately focused on whole young leaves (38% of total items) and more evenly distributed across a larger number of supplementary food categories (Table 2.4). Furthermore, only mitered langurs ate mature pith and mature leaf stems, and mitered langurs preyed on a far-wider range of fruit seeds than siamangs or agile gibbons (combined: 15% vs 0.4% and 0.6% respectively).

Absolute dietary overlap

Patterns of absolute dietary overlap closely followed phylogenetic relationships and general similarity in dietary compositions (Fig. 2.3). Absolute dietary overlap (148 total food items) was highest between siamangs and agile gibbons (53% and 88% of total diets respectively), lower between siamangs and mitered langurs (69 total items; 25% and 44% of total diets respectively), and lowest between agile gibbons and mitered langurs (39 total items; 23% and 25% of total diets respectively).

Indices of dietary overlap

Like results for absolute dietary overlap, similarity in the proportions of feeding time spent on 28 distinct food categories (detailed in Table 2.4) mirrored the degree of phylogenetic distance between species. Overall, Morisita's indices of dietary overlap (Table 2.5) were higher between hylobatid species ($\bar{x}$ =0.80) than between mitered langurs and either siamangs ($\bar{x}$ =0.42) or agile gibbons ($\bar{x}$ =0.32). Furthermore, overlap in the use of food categories was consistently high across months between siamangs and agile gibbons (C_H: SD=0.10; min=0.57; max=0.96), while *S.s.*-*P.m.* overlap values (C_H: SD=0.18; min=0.05; max=0.65) varied more widely across months and only exceeded minimum *S.s.*-*H.a.* overlap for 2 of 12 months (Table 2.5; Fig. 2.4).

Agile gibbons and mitered langurs diverged farthest in diet. Indices for *H.a.-P.m.* overlap (C_H: SD=0.18; min=0.02; max=0.60) rarely reached comparably-high levels and were very low for some months (Table 2.5; Fig. 2.4).

Overlap in use of top food items

The high degree of ecological similarity between hylobatid species was most apparent for interspecific comparisons in the use of shared top food items (Appendix 2). On average, siamangs spent 54% of feeding time and agile gibbons spent 78% of feeding time on the same, shared top food items each month (Table 2.6). Across months, the degree of overlap in feeding time on shared top items remained high (Table 2.6; >50%: *S.s*=8/12 months; *H.a.*=12/12 months). Additionally, the majority of agile gibbon's top food items were shared with siamangs ($\bar{x}$ =7/9 monthly). Siamangs, however, typically used a larger number of top food items than agile gibbons each month, such that shared items comprised a smaller percentage of siamang's total items ($\bar{x}$ =7/17 monthly). Thus, overlap in the use of shared top foods was higher from the perspective of agile gibbons than from that of siamangs.

Comparatively, overlap in the use of top food items was much lower between mitered langurs and each hylobatid (Table 2.7; Appendix 2). Average percentages of feeding time spent on shared top items were lowest for mitered langur's use of *H.a.-P.m.* items ($\bar{x}$ =4%), approximately equal for siamang's and agile gibbon's use of *S.s.-P.m.* ($\bar{x}$ =6%) and *H.a.-P.m.* ($\bar{x}$ =5%) items, and highest for mitered langurs use of *S.s.-P.m.* items ($\bar{x}$ =10%; Table 2.7). Furthermore, mitered langurs tended to share a very low proportion of their top food items ($\bar{x}$ = <1 of 8 items) with either hylobatid species.

DISCUSSION

Patterns of dietary niche overlap and divergence

Consistent with the hypothesis that the degree of similarity in digestive anatomy and physiology should influence the similarity of sympatric species' dietary niches (Lambert 2002), the overall dietary profiles of siamangs and agile gibbons were far more similar than either hylobatid's diet was to that of mitered langurs. While simple-gutted siamangs and agile gibbons spent the majority of feeding time on ripe fruits and figs, langurs emphasized the consumption of leaves, unripe fruits, and seeds. These trends are very similar to those found for the same species in Malaysia (MacKinnon and MacKinnon 1980) and for Asian colobines in general (reviewed in Bennet and Davies 1994).

Contrary to predictions, dietary breadths were similarly narrow across primate species. Mitered langurs were expected to have the most narrow diets as a consequence of their digestive specialization as forestomach fermenters (e.g., Lambert 2002). However, results suggest that hylobatids were equally specialized, but selected a distinctly different set of food items. While the colobine is specialized for slowly digesting fibrous foods (i.e., leaves, unripe fruit, and seeds) that contain challenging secondary metabolites (reviewed in Lambert 1998), hylobatids are specialized for rapidly harvesting and digesting sugary, acidic foods (i.e., ripe fruit pulp and figs; Gittins and Raemaekers 1980; reviewed in Elder 2009). Langurs are unable to ingest most hylobatid foods because they would interfere with the alkaline environment required for normal digestion and fermentation (Lambert 1998), while hylobatids lack the specialized anatomy and physiology necessary to access energy trapped in structural carbohydrates (Chivers and Hladik 1980).

In addition to being similar to langurs in their level of specialization, hylobatid species were indistinguishable from each other based on dietary breadth. Although it was expected that the greater body mass of siamangs relative to agile gibbons would covey increased dietary breadth, this was not supported. The predicted relationship between body mass and dietary breadth was based on two possible mechanisms: body mass increases with either 1) home range size (and thereby the range of resources types encountered) or 2) dietary flexibility (reviewed in Brown 1995). The first of these mechanisms apparently does not apply to hylobatids (Chivers 1984); Malaysian siamangs have smaller home ranges than sympatric white-handed gibbons (*H. lar*; Raemaekers 1984), and siamangs and agile gibbons at Way Canguk have equal-sized home ranges (Chapter 3). Thus, home ranges occupied by siamangs must contain resources of adequate abundance and/or quality (e.g., large, super-productive figs) to support their metabolic requirements. The second mechanism (increased dietary breadth in heavier species) may also be rejected for siamangs if they are anatomically restricted from using foods in certain categories. That is, from a hylobatid's perspective, many langur foods (e.g., pith, leaf stems, leaves high in secondary metabolites, and seeds) simply may not be edible. However, siamangs and agile gibbons could still differ in the diversity of food items used within typical hylobatid food categories. Results for per group dietary diversity (the total number of different food items used) indicate that, in fact, siamangs did tend to use a wider range of items than agile gibbons (138 vs. 121 total items). A very similar pattern was observed for sympatric siamangs and white-handed gibbons at Kuala Lompat, Malaysia (112 vs. 99 total items; MacKinnon and MacKinnon 1980).

Dietary niches found for siamangs and agile gibbons at Way Canguk are comparable to feeding behavior reported for sympatric hylobatids in Malaysia (Raemaekers 1979; Gittins and Raemaekers 1980) and northern Sumatra (Palombit 1997). Across these populations, hylobatids are predominantly frugivorous and maximize their feeding time on preferred figs (Palombit 1997; Kinnaird and O'Brien 2005). The level of frugivory seems to depend on resource availability, where siamangs and *Hylobates* gibbons increase their use of figs with the density of individual plants. Figs play a key role in determining the reproductive output of hylobatids (Marshall and Leighton 2006) and are sources of reliable, easily digested energy for frugivores consumers (Kinnaird and O'Brien 2005). Thus, the patterns found for siamangs and agile gibbons at Way Canguk provide further support for the relationship between figs and hylobatids. However, in contrast with Malaysian and northern Sumatran populations, sympatric hylobatid species at Way Canguk differed very little in how they supplemented their fruit-dominated diets. It was hypothesized that differences in body mass between siamangs and *Hylobates* gibbons result in divergent foraging strategies (Raemaekers 1979). Larger-bodied siamangs were expected to be limited by their slower, more expensive locomotion, but to be more efficient at masticating fibrous foods; smaller-bodied, faster-travelling gibbons, in contrast, would be able to more easily access rare, high energy fruit patches (Raemaekers 1984). Thus, siamangs were predicted to eat more leaves, while *Hylobates* gibbons should supplement by increasing consumption of ripe, non-fig fruits. Dietary divergence between siamangs and white-handed gibbons was found to meet these predictions at both Kuala Lompat, Malaysia (Raemaekers 1984) and Ketambe, Sumatra (Palombit 1997). At Ketambe, in addition to supplementing with young leaves or ripe fruits, both siamangs and white-handed gibbons spent about a quarter of their feeding time eating and/or foraging for insects (Palombit 1997). At Way Canguk, however, such partitioning in dietary niches was less evident. Agile gibbons spent more feeding time on ripe fruits, but leaf consumption was only slightly higher in siamangs than agile gibbons. Furthermore, insectivory was rare for both species, while flower consumption at Way Canguk was higher than has been reported for other sites (Elder 2009). Siamangs at Way Canguk have been previously described to spend unusually high proportions of feeding time on flowers (Lappan 2009). Results of this study suggest that both mitered langurs and agile gibbons spend equally high amounts of feeding time on these food items. Perhaps, flowers take the place of figs at Way Canguk as potential fallback foods (Marshall et al. 2009); like figs, flowers may be available across seasons and in highly-productive patches (reviewed in Lappan 2009). This hypothesis is further supported by the fact that fig densities are lower at Way Canguk (Kinnaird and O'Brien 2005) than at Kuala Lompat (Raemaekers et al. 1980) or Ketambe (Palombit 1997). Thus, hylobatids at Way Canguk may counteract the relative rarity of figs, by supplementing with flowers. It should be noted, however, that flowers differ nutritionally from figs (flowers are higher in protein and fiber; McConkey et al. 2003; Simmen et al. 2007) and, therefore, should pose divergent challenges to primates consumers. At Way Canguk, flowers consumed by primates tended to contain slightly more gross energy ($\bar{x}$ =3.92 vs. 3.79 kcal/g dry matter; *n*=32; *n*=42) and much more protein ($\bar{x}$ =16% vs. 6% of dry matter; *n*=19; *n*=37) than figs eaten (Table 2.1; Elder unpubl. data).

The potential for interspecific competition

Due to the large degree of divergence between the diets of mitered langurs and each hylobatid species, it is unlikely that interspecific feeding competition plays an important role in the behavioral ecology of the colobine species. Ecological similarity between sympatric siamangs and smaller, agile gibbons, on the other hand, is expected to have important implications for the nature and intensity of hylobatid interspecific encounters. Even taking into account the limitations in this study, there is a high potential for interspecific feeding competition in hylobatids. The limited degree of niche partitioning between siamangs and agile gibbons should increase the importance of interspecific competition at Way Canguk. Due to the comparably low densities of figs in this population, preferred fig patches may be economically monopolizable (van Schaik 1989; Sterck et al. 1997); that is, the benefits of defending these patches should increase as fig density decreases. Increased contest competition between hylobatid species could result either directly from low fig density and/or indirectly from a shift toward increased effort to defend specific fig patches. Additionally, in light of the high level of dietary overlap between siamangs and agile gibbons, stable coexistence at Way Canguk may necessitate subtle differences in foraging strategies.

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Table 2.1 Types and nutritional quality of flowers contributing to top 75% of daily feeding time for siamangs (*S.s.*), agile gibbons (*H.a.*), and mitered langurs (*P.m.*)

Family	**Genus**	**Species**	**kcal/g dry**	**% protein**	**Top foods for**
? (liana Petai)			3.61	----	*S.s.*
Achariaceae	*Hydnocarpus*	*gracilis*	3.79	22	*S.s.*; *H.a.*
Annonaceae	*Mitrepora*	*polypirena*	3.86	29	*S.s.*; *H.a.*
Annonaceae	*Stelacocarpus*	*burahol*	4.01	12	*S.s.*
Annonaceae	?	?	3.78	----	*S.s.*; *H.a.*
Cannabaceae	*Celtis*	*nigrescens*	3.55	17	*S.s.*; *P.m.*
Convolvulaceae	*Merremia*	*peltata*	3.70	9	*P.m.*
Dilleniaceae	*Dillenia*	*excelsa*	3.59	9	*S.s.*; *H.a.*; *P.m.*
Menispermaceae	*Anamirta*	*cocculus*	4.00	14	*S.s.*
Moraceae	*Antiaris*	*toxicaria*	4.01	----	*S.s.*
Olacaceae	*Strombosia*	*javanicum*	----	----	*P.m.*
Rubiaceae	*Anthocephalus*	*chinensis*	4.24	13	*P.m.*
Sterculiaceae	*Pterospermum*	*javanicum*	3.71	10	*S.s.*; *P.m.*

Table 2.2 Distribution and diversity of food items across primate species (387 items total, see Appendix 1)

Consumed by	N families	N genera	N species	N items	% total food items
Siamangs (*S.s.*) only	26	40	85	99	25.65
Agile gibbons (*H.a.*) only	13	16	20	20	5.18
Mitered langurs (*P.m.*) only	30	54	77	85	22.02
S.s.-H.a.	28	42	105	111	28.76
S.s.-P.m.	14	22	29	32	8.29
H.a.-P.m.	2	2	2	2	0.52
S.s.-H.a.-P.m.	15	22	35	37	9.59

Table 2.3 Diversity of primate diets and mean numbers of food items eaten per focal group

Species	N families	N genera	N species	N items	Mean N items/group	N focal groups
Siamangs	47	74	224	278	138	4
Agile gibbons	39	60	150	169	121	2
Mitered langurs	39	73	125	157	157	1

Table 2.4 Percentage utilization of 28 food categories and Levins' dietary breadths of each primate species

Food category	Siamangs		Agile gibbons		Mitered langurs	
	N items	% items	N items	% items	N items	% items
Ripe figs – whole	48	17.3	38	22.5	10	6.4
Unripe figs – skins	0	0.0	0	0.0	2	1.3
Unripe figs - whole	0	0.0	0	0.0	2	1.3
Flowers – buds	2	0.7	1	0.6	2	1.3
Flowers – petals	6	2.2	4	2.4	5	3.2
Flowers – whole	18	6.5	10	5.9	12	7.6
Ripe fruits – Arillus	0	0.0	1	0.6	0	0.0
Ripe fruits – pulp	52	18.7	45	26.6	11	7.0
Ripe fruits – seeds	0	0.0	0	0.0	6	3.8
Ripe fruits – skins	2	0.7	1	0.6	1	0.6
Ripe fruits – skins/pulp	23	8.3	19	11.2	2	1.3
Ripe fruits – whole	20	7.2	14	8.3	9	5.7
Semi-ripe fruits – pulp	0	0.0	0	0.0	1	0.6
Semi-ripe fruits – seeds/pulp	0	0.0	0	0.0	1	0.6
Unripe fruits – pulp	1	0.4	1	0.6	0	0.0
Unripe fruits – seeds/pulp	0	0.0	0	0.0	3	1.9
Unripe fruits – seeds	1	0.4	1	0.6	14	8.9
Unripe fruits – skins/pulp	0	0.0	0	0.0	1	0.6
Unripe fruits – whole	2	0.7	2	1.2	2	1.3
Epiphyte leaves	2	0.7	1	0.6	1	0.6
Mature leaves – laminae	4	1.4	0	0.0	0	0.0
Mature leaves – stems	0	0	0	0.0	3	1.9
Mature leaves – whole	13	4.7	1	0.6	7	4.5
Young leaves – whole	76	27.3	20	11.8	59	37.6
Petioles – whole	0	0.0	1	0.6	0	0.0
Mature pith	0	0.0	0	0.0	1	0.6
Young shoots	4	1.4	2	1.2	1	0.6
Insects	4	1.4	7	4.1	1	0.6
Total	278	100.0	169	100.0	157	100.0
Levin's DB (*B*)	6.28		6.20		5.76	
Levin's standardized DB (B_A)	**0.19**		**0.19**		**0.17**	

Table 2.5 Monthly and overall indices of dietary overlap between each pair of primate species, where *S.s.*= siamangs, *H.a.*= agile gibbons, *P.m.*= mitered langurs

	Morisita's simplified index (C_H)		
Month	***S.s.-H.a.***	***S.s.-P.m.***	***H.a.-P.m.***
Nov 08	0.73	0.65	0.32
Dec 08	0.82	0.34	0.29
Jan 09	0.78	0.05	0.12
Feb 09	0.96	0.50	0.49
Mar 09	0.74	0.32	0.02
Apr 09	0.87	0.46	0.14
May 09	0.81	0.57	0.37
Jun 09	0.82	0.63	0.52
Jul 09	0.80	0.41	0.60
Aug 09	0.87	0.37	0.33
Sep 09	0.87	0.19	0.18
Oct 09	0.57	0.51	0.41
Mean	**0.80**	**0.42**	**0.32**
SD	**0.10**	**0.18**	**0.18**

Table 2.6 Monthly overlap between siamangs (*S.s.*) and agile gibbons (*H.a.*) in the use of top food items (total number shared and mean percentage of daily feeding time)

	N top items		**N shared top items**	**% feeding time shared items**	
Month	***S.s.***	***H.a.***		***S.s.***	***H.a.***
Nov 08	19	8	6	30.05	58.67
Dec 08	11	6	4	43.62	70.08
Jan 09	20	5	4	52.89	63.46
Feb 09	20	13	11	65.99	92.49
Mar 09	25	7	5	42.71	70.65
Apr 09	15	9	8	68.78	80.23
May 09	13	7	7	65.00	89.74
Jun 09	23	11	9	52.28	72.13
Jul 09	21	12	11	46.58	89.70
Aug 09	10	8	7	66.57	87.99
Sep 09	13	10	8	55.02	86.25
Oct 09	19	12	9	61.53	81.17
Mean	**17.42**	**9.00**	**7.42**	**54.25**	**78.55**
SD	**4.87**	**2.59**	**2.39**	**11.93**	**11.28**

Table 2.7 Monthly overlap between each hylobatid species (*S.s.*=siamangs; *H.a.*=agile gibbons) and mitered langurs (*P.m.*) in the use of top food items

	N top items	**N shared top items**		**% feeding time shared items**			
Month	***P.m.***	***S.s-P.m.***	***H.a.-P.m.***	***S.s.-P.m.***		***H.a.-P.m.***	
				S.s.	***P.m.***	***H.a***	***P.m.***
Nov 08	6	0	0	0.00	0.00	0.00	0.00
Dec 08	3	1	0	5.62	9.50	0.00	0.00
Jan 09	3	0	0	0.00	0.00	0.00	0.00
Feb 09	10	0	0	0.00	0.00	0.00	0.00
Mar 09	10	0	0	0.00	0.00	0.00	0.00
Apr 09	10	2	1	27.35	38.71	24.44	5.15
May 09	6	2	1	5.84	6.26	7.08	3.26
Jun 09	13	1	1	3.72	5.30	1.57	5.30
Jul 09	15	1	1	1.97	4.06	6.57	4.06
Aug 09	8	1	1	5.17	14.48	11.79	14.48
Sep 09	6	2	1	16.98	38.05	11.79	9.97
Oct 09	6	1	0	2.21	6.07	0.00	0.00
Mean	**8.00**	**0.92**	**0.50**	**5.74**	**10.20**	**5.27**	**3.52**
SD	**3.72**	**0.79**	**0.52**	**8.29**	**13.88**	**7.61**	**4.69**

Fig. 2.1 Dietary compositions of siamangs, agile gibbons, and mitered langurs based on mean percentages of feeding time across 12 months

Fig. 2.1

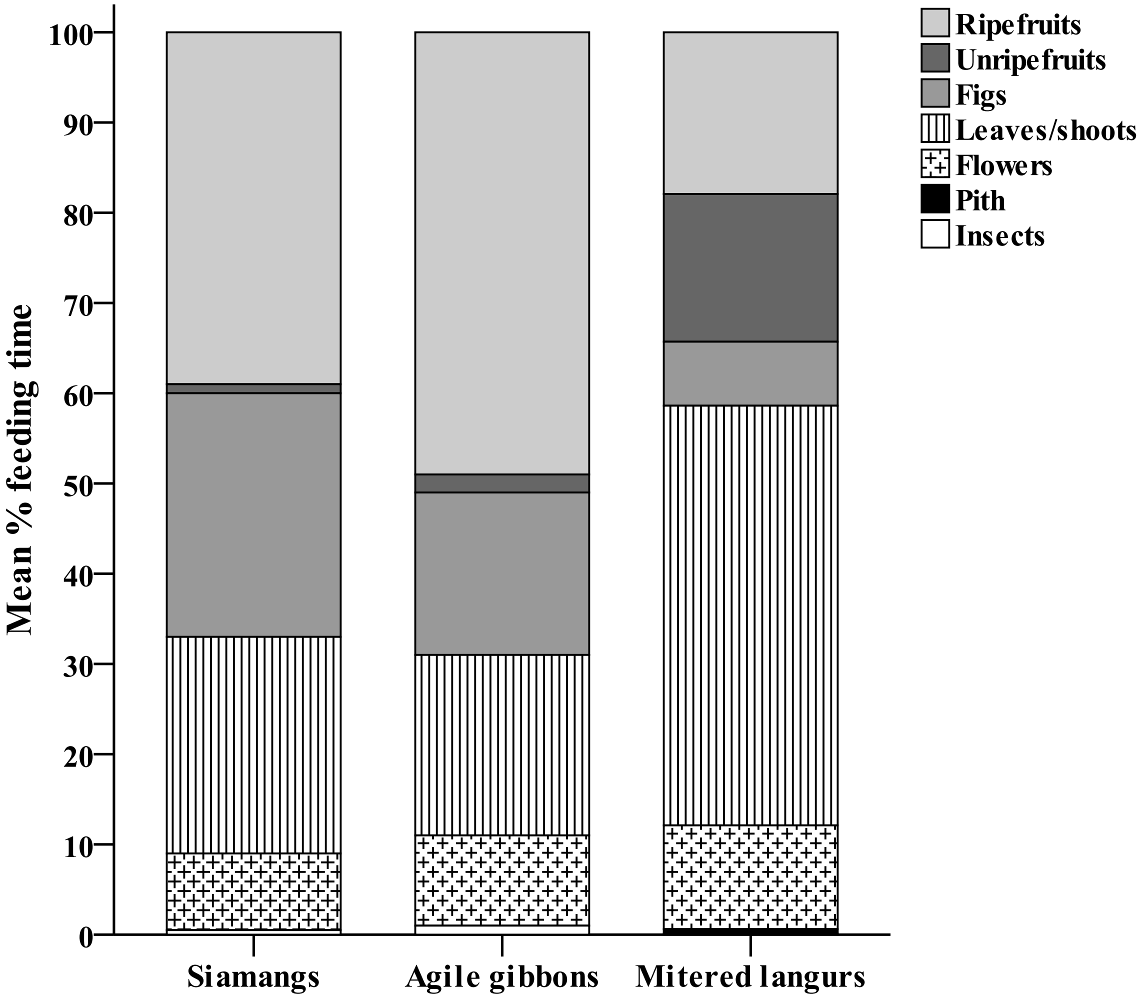

Mean % feeding time
0
10
20
30
40
50
60
70
80
90
100
Siamangs
Agile gibbons
Mitered langurs
Ripefruits
Unripefruits
Figs
Leaves/shoots
Flowers
Pith
Insects

Fig. 2.2 Total recorded diets of siamangs, agile gibbons, and mitered langurs categorized by the numbers of different food families, genera, species, and items consumed

Fig. 2.2

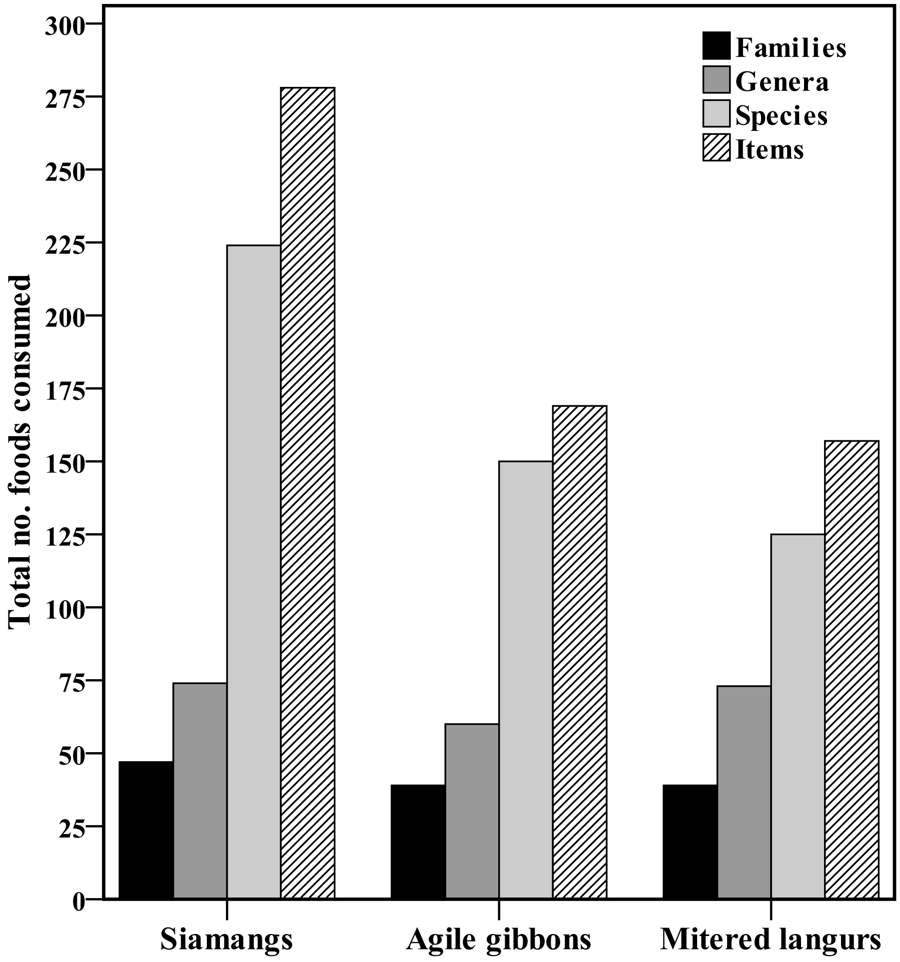

Total no. foods consumed
0
25
50
75
100
125
150
175
200
225
250
275
300
Families
Genera
Species
Items
Siamangs
Agile gibbons
Mitered langurs

Fig. 2.3 Total number of different food items used by each primate species, total number of shared food items, and absolute percentages of dietary overlap between each species-pair

Fig. 2.3

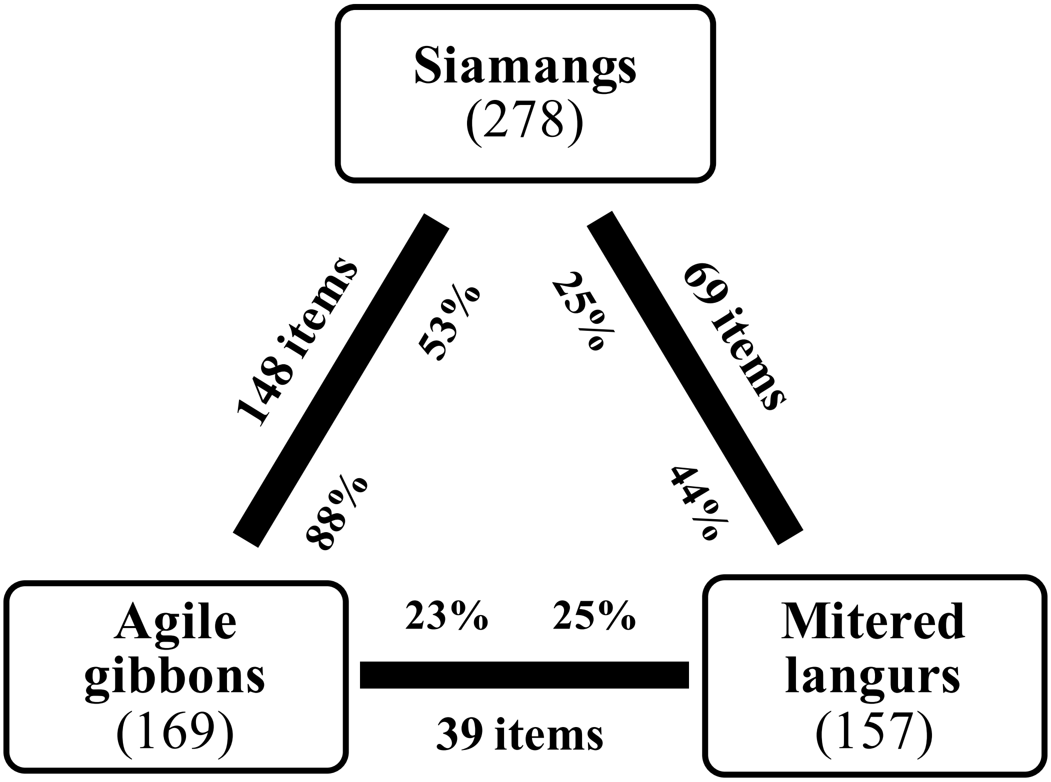
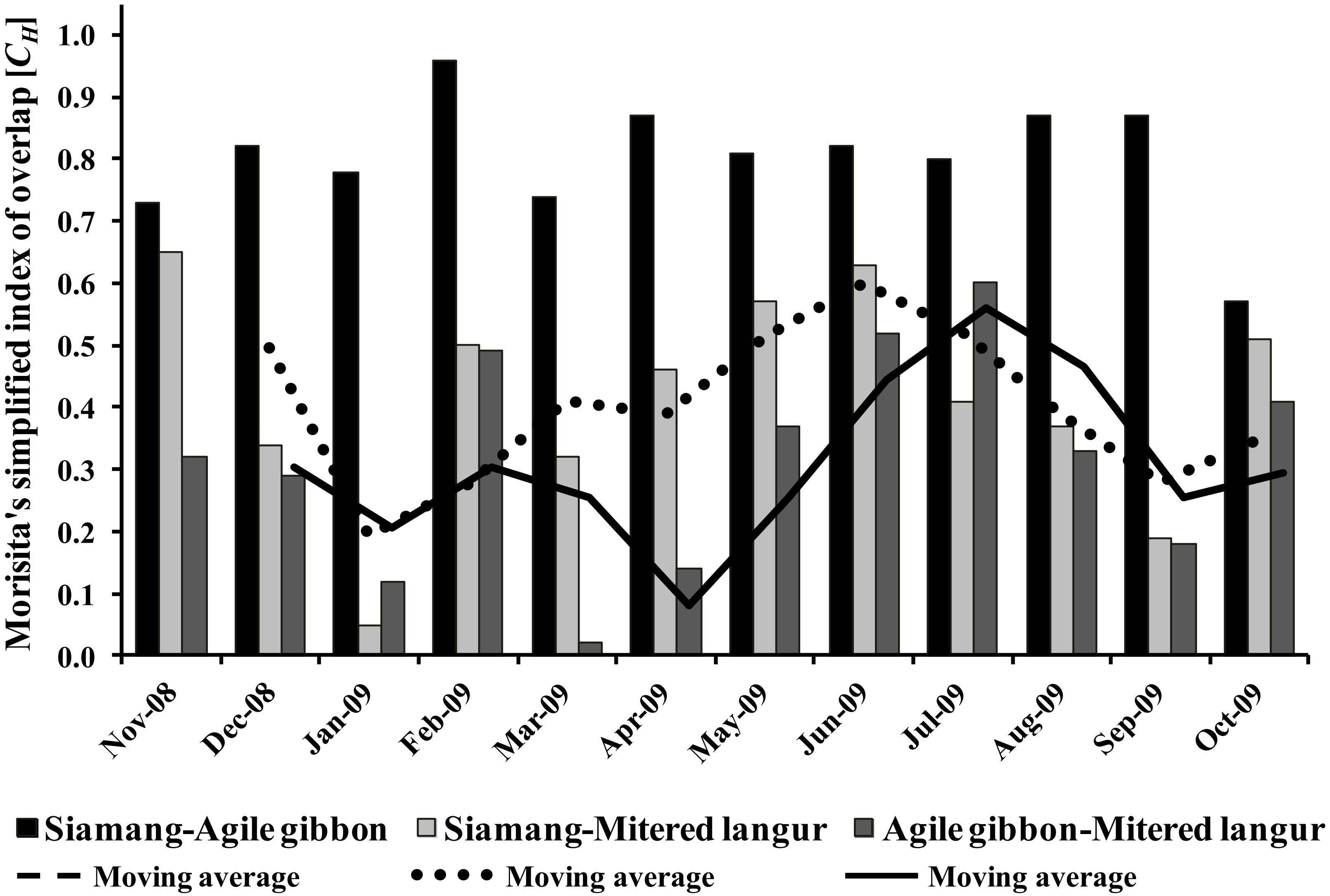

Siamangs
(278)
148 items
53%
88%
25%
69 items
44%
Agile
gibbons
(169)
23%
25%
39 items
Mitered
langurs
(157)

Fig. 2.4 Monthly values and trendlines (two-period moving averages) for Morisita’s simplified indices of dietary overlap between each species-pair

Fig. 2.4


Morisita's simplified index of overlap [C_H]
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Nov-08
Dec-08
Jan-09
Feb-09
Mar-09
Apr-09
May-09
Jun-09
Jul-09
Aug-09
Sep-09
Oct-09
Siamang-Agile gibbon
Siamang-Mitered langur
Agile gibbon-Mitered langur
Moving average
Moving average
Moving average

Chapter 3
Interspecific dominance and energetic costs of coexistence in three sympatric primate species

ABSTRACT

Competition between ecologically similar species is often characterized by interspecific dominance relationships, where inequalities in resource holding potential (RHP) structure access to patchy resources. Dominant species use interference (i.e., harassment or aggression versus competitors) to gain priority of access to resources, while subordinate species avoid encounters with dominant species by using unoccupied patches. I explored the nature and consequences of interactions among three sympatric primate species: the ecologically similar siamangs (*Symphalangus syndactylus*) and agile gibbons (*Hylobates agilis*), and the ecologically dissimilar mitered langurs (*Presbytis melalophos*) at Way Canguk, Sumatra. I investigated the influences of ecological similarity and two measures of RHP (body mass and group size) on interspecific encounters. I also assessed whether encounter locations and rates were the result of feeding competition, and estimated the energetic costs of lost encounters (as a proxy for fitness costs). Due to differences in body mass, siamangs were predicted to dominate agile gibbons and mitered langurs. Alternatively, if group size equated to RHP, mitered langurs would be the dominant species. Because heterospecific aggression (HA) should increase with ecological similarity, siamang-agile gibbon encounters were expected to be more aggressive than siamang-mitered langur and agile gibbon-mitered langur encounters. Additionally, encounter rates were predicted to be higher at food sources than non-food locations and to increase with decreasing food availability. Lost encounters were expected to result in increased energy expenditure and/or

decreased energy intake. Data were collected from March 2008 to October 2009 on the context (i.e., time, location, and who encountered whom), duration, and outcome of interspecific encounters (N = 289) among seven siamang, three agile gibbon, and five mitered langur groups. During 404 all-day follows of one mitered langur, three agile gibbon, and four siamang focal groups, data were collected on food intake, availability, and nutritional composition, as well as ranging to assess energy costs of lost encounters.

As predicted, HA increased with the degree of ecological similarity between species. For agile gibbons and mitered langurs (but not siamangs), encounter rates were much higher between heterospecifics than between conspecifics. Interspecific dominance rank was related to body mass, but not to group size; siamangs were dominant over agile gibbons and mitered langurs, and agile gibbons were dominant over mitered langurs. Interspecific encounters occurred at shared-food locations more often than expected by chance and encounter locations were significantly associated with the species identities of the primate involved. However, the rates of agonistic encounters did not increase with decreasing food availability. Agile gibbons, but not mitered langurs, were found to incur energetic costs and, more rarely, physical wounds as a result of encounters with siamangs. Furthermore, when displaced from a feeding source by siamangs, agile gibbons shifted to foods that were energetically inferior to the patch from which they were evicted. However, there were no significant differences in agile gibbon's energy expenditure or intake between days with and without lost encounters. While this may indicate compensatory mechanisms and agile gibbons continue to subsist in sympatry with siamangs, their low infant survival and birth rates suggest possible long-term costs of interspecific competition.

INTRODUCTION

Whenever more than one species occupies the same ecological niche and geographic area, either all but one species will be excluded (Gause et al. 1934; Abrams 1983) or species will diverge in some dimension of niche use, thereby reducing interspecific resource competition (e.g., Brown and Wilson 1956). Across systems (e.g., Pianka 1973; Schoener 1974), there is abundant evidence for niche partitioning (i.e., ecological differences independent of environmental fluctuations; Chesson 2000). If, however, sympatric species maintain high ecological similarity, coexistence requires different mechanisms. Access to individual, patchy resources may be structured via interspecific dominance relationships (Morse 1974; Schoener 1983). In avian (Alatalo and Moreno 1987; Martin and Martin 2001), rodent (Heller 1971), and ungulate systems (Berger 1985), the outcomes of interspecific encounters have been used to assess between-species dominance. When dominant species overlap with subordinate species, the latter may coexist only by using resources overlooked or not preferred by the dominant species (Horn and MacArthur 1972; Levin 1974; Slatkin 1974).

Interference competition operates when harassment or aggression benefits an individual's foraging, survival, or reproduction at the expense of another individual (Park 1962). These costs can include loss of energy or food, injury, or death (Schoener 1983). Because energy gain and use may critically influence survival and reproduction, the energetic costs of encounters are often used as proxies for fitness consequences of coexistence (review in Leonard and Ulijaszek 2002). In baboons, reductions in energy intake have been found to reduce milk yield, and in turn decrease infant growth (Roberts et al. 1985). Interference competition between species may also negatively impact birth rates in subordinate species if available energy is overly restricted (e.g., Watts and Holekamp 2009). Furthermore, because the maintenance of a healthy immune system has high energetic costs (Lochmiller and Deerenberg 2000), individuals with insufficient energy intake may experience higher mortality due to disease. In cases of the most intense interspecific aggression, encounters themselves can be fatal. This is most apparent in carnivore communities (Durant 2000; Tannerfledt et al. 2002; Berger 2007), where individuals of dominant species occasionally prey upon subordinate competitors. As more studies become available, interspecific dominance (as a consequence of heterospecific aggression - HA) is emerging as a primary influence on a variety of behaviors, including feeding ecology (review in Peiman and Robinson 2010) and sleeping strategies (e.g., Chapter 5).

Interspecific dominance is suggested to reflect an inequality in Resource Holding Potential (RHP; Morse 1974), where those species with greater perceived fighting abilities gain priority of access to resources (Maynard Smith and Parker 1976). RHP has been found to correlate positively with body mass in the majority of animal systems (Connell 1983), including crustaceans (Navarrete and Castilla 1990), fish (Blann and Healey 2006), birds (e.g., Gorton 1972; Robinson and Terborgh 1995; Martin and Martin 2001; Shelley et al. 2004), marsupials (Dickman 1991), rodents (Gliwicz 1981; Lemen and Freeman 1986), primates (Peres 1996; Houle et al. 2006), and carnivorans (Durant 1998; Tannerfledt et al. 2002; Berger 2007). However, greater body mass also leads to higher absolute energetic requirements (Kleiber 1932). In addition to body mass, group size may influence RHP through communal defense of resources (Fisler 1977). For example, large packs of African wild dogs are able to defend kills against smaller groups of hyenas or lions, despite greater individual body mass of both latter species (Fuller and Kat 1990).

It has been demonstrated across communities that HA increases with the degree of ecological overlap between species (Peiman and Robinson 2010). Based on the resource overlap hypothesis (Brown and Wilson 1956), species that depend on the same resources should fight most frequently for access to a contested patch (e.g., Jenssen *et al.* 1984). In contrast, for species with low ecological overlap, there is little to gain from HA compared to its costs, and hence, HA should be rare or of low intensity (Fisler 1977; Berger 1985; French and Smith 2005). Thus, HA could have a greater influence on long-term resource gain (and in turn fitness) when used against an ecologically similar species than when used against a dissimilar species.

Primate researchers have described interspecific contests over food (Terborgh 1983), discussed the effect of interspecific competition on population densities (Waser and Case 1981; but see Janson 1992), and more recently focused on the importance of aggressive interactions in regulating access to resources in South American monkeys (Stevenson et al. 2000), African monkeys (French and Smith 2005; Houle et al. 2006), and Malagasy lemurs (Thoren et al. 2011). Expanding on previous primate studies, here I investigate the nature and consequences of behavioral interactions among three Asian primate species. Specifically, I assess the effects of ecological similarity, body mass, and group size on interspecific dominance relationships and HA. Furthermore, I aim to estimate the energetic costs of lost interspecific encounters as a proxy for the costs of coexistence.

I selected the primate community at Way Canguk, Sumatra as my model system because it includes two ecologically similar hylobatid species, the siamang (*Symphalangus syndactylus*) and the agile gibbon (*Hylobates agilis*), as well as the ecologically dissimilar mitered langur (*Presbytis melalophos*). Communities where closely related species stably coexist are expected to be rare and such species should exhibit high levels of interspecific aggression (Houle 1997). Siamangs are of particular interest in this regard because they are symatric with *Hylobates* gibbons (*H. lar* in Malaysia and northern Sumatra; *H. agilis* in central and southern Sumatra) across their distribution (review in Chatterjee 2009), and these genera have occupied the same habitats since at least the Late Pleistocene (Jablonski and Chaplin 2009). Sympatric siamangs and *Hylobates* gibbons are both ripe fruit specialists (review in Palombit 1997; Elder 2009), use figs, young leaves, and flowers as fallback resources (Marshall 2004; Lappan 2009; Harrison and Marshall 2011), and use the same level of the canopy (Raemaekers 1977; MacKinnon and MacKinnon 1980). On average, 54% of siamang feeding time was spent eating foods also consumed by agile gibbons, and 78% of agile gibbon feeding time was spent on foods shared with siamangs at Way Canguk (Chapter 2). Similarly, pairs of siamang groups spent between 45% and 52% of their feeding time on the same foods (unpubl. data). Furthermore, although interspecific territoriality mitigates competition within several non-primate communities (Heller 1971; Murray 1971; Harrison et al. 1989), as well as between hybridizing *Hylobates* gibbons (Suwanvecho and Brockelman 2012), neither interbreeding nor territoriality occurs between siamangs and *Hylobates* gibbons (Raemaekers 1978; Elder pers. obs.).

In the study system, mitered langurs serve as a control. In contrast to hylobatids, their diet consists primarily of unripe fruits, seeds, and young leaves, and is much more fibrous (Appendix 1; MacKinnon and MacKinnon 1980; Davies et al. 1988). Furthermore, the three species differ in body mass and group size. Siamangs are the heaviest species (adult female=10.7 kg), weighing about twice as much as agile gibbons and mitered langurs (adult female=5.8 and 6.5 kg respectively; Smith and Jungers 1997). At Way Canguk, group size is largest in mitered langurs (mean=15.0), followed by siamangs (mean=5.5), and then agile gibbons (mean=3.0; unpubl. data).

Research hypotheses and predictions

I address three main sets of hypotheses, each of which focuses on a different aspect of interspecific encounters. These include the 1) outcomes, 2) characteristics, and 3) costs of encounters.

Encounter outcomes. H1: Interspecific dominance reflects an inequality in RHP. If dominance equates to body mass, siamangs should be dominant over the other two species, displacing heterospecific groups regardless of the number of individuals encountered. If, however, group size provides a competitive advantage beyond that afforded by body mass, then in the study system mitered langurs would be predicted to rank first, followed by siamangs, and then agile gibbons.

Encounter characteristics. H2: Subordinate species should minimize the risks of encounters with dominant species. Thus, interspecific encounters are expected to be 1) more frequently initiated by dominant species and 2) terminated by subordinate species. Additionally, if subordinate species use tactics to avoid dominant species, then 3) their encounters should occur less often than expected by chance. H3: If HA increases with ecological similarity, then siamang-agile gibbon encounters should be more aggressive than those between mitered langurs and either hylobatid. H4: If the benefit/cost ratios of winning an encounter is similar for both members of a species-pair with high ecological overlap (Parker and Rubenstein 1981), then siamang-agile gibbon encounters should have longer durations than hylobatid-mitered langur encounters. In addition, H5: if encounter characteristics are the result of feeding competition, then 1) encounters should predominately occur at locations where food used by both species is available and 2), assuming that both species concentrate on dwindling supplies of the same resources, the rate of agonistic encounters should increase as food availability decreases (and competition increases).

Encounter costs. H6: Assuming that encounters with ecologically similar, but dominant species are costly for subordinate species, lost interspecific encounters are predicted to result in 1) increased energy expenditure and 2) decreased energy intake per encounter and/or per encounter day.

MATERIALS AND METHODS

Study site

Data were collected at Way Canguk research area (5° 39' S, 104° 24' E, 50 m a.s.l.), which lies within Bukit Barisan Selatan National Park, Sumatra, Indonesia. Established in 1997, Way Canguk is managed by the Indonesian Ministry of Forestry and the Wildlife Conservation Society Indonesia Program (WCS IP). The study site includes 900 ha of primary lowland rain forest within a 3,568 km^2 protected area, and is crossed by 105 km of trails at 200 m intervals (O'Brien *et al.* 2004). During the study period, mean annual temperature was 28^{o} C and mean annual rainfall was 3,354 (range= 2,492-4,549 mm), with a very wet period (>200 mm/month) from September to April and a less wet period (<100 mm/month) from May to August (WCS IP unpubl. data, 2007-2009). Siamangs, agile gibbons, and mitered langurs are the most common primate species at Way Canguk. In addition to the three study species, the diurnal primate community includes long-tailed macaques (*Macaca fascicularis*), pig-tailed macaques (*M. nemestrina*) and silvered langurs (*Trachypithecus cristatus*). These species occur at very low densities and/or predominantly range outside of the study area (WCS IP unpubl. data).

Data collection

From March 2008 through October 2009, teams of two observers conducted a total of 404 all-day follows of one of eight focal groups, including one mitered langur (*P.m.*1), three agile gibbon (*H.*a. 1*,* 2*,* and 3), and four siamang groups (*S.s.* A*,* E*,* J, and M; Fig. 1). Encounters were observed among these focal groups, along with seven additional neighboring groups (three siamang and four mitered langur groups). Non-focal groups involved in encounters, although not always fully habituated, were accustomed to the presence of human observers.

Activity budgets. Instantaneous focal sampling for one-hour protocols with one-minute intervals (Martin and Bateson 1993) was used to record general activity states for focal individuals. Focal individuals were rotated hourly so that each individual was sampled evenly across the active period. The sample consisted of 22 adult individuals, including twelve siamangs (8 males and 4 females), four agile gibbons (2 males and 2 females), and six mitered langurs (1 male and 5 females). While the social structure of agile gibbon groups was monogamous, all siamang groups were polyandrous (1 adult female and 2 adult males) and mitered langurs were polygynous (1 adult male and multiple adult females). Mean annual activity budgets were calculated separately for each species from group means of focal individuals' mean activity budgets.

Group spread. Group spread, defined as the maximum straight-line distance between any two group members, was assessed during scans of all group members conducted every 10-minutes (Martin and Bateson 1993). Group spread was estimated visually when all individuals were visible from the same location. When group members were more widely-dispersed, an effort was made to separately follow each individual, and group spread was calculated as the farthest Euclidean distance between sets of coordinates that were recorded at individuals' locations during group scans.

Interspecific encounters. Intergroup encounters were conspicuous events that could be documented via all-occurrence sampling (Altmann 1974), and were recorded as soon as two groups were within 50 m of each other (Oates 1977; Bennett 1986). At Way Canguk home range overlap was high among the three species (Table 3.1; $\bar{x}$ =58% of a group's total home range was shared with each of the other species), while home ranges were small (Fig 3.1; Table 3.1; siamangs: $\bar{x}$ =23 ha, σ=6.78, n=4; agile gibbons: $\bar{x}$ =24 ha, σ=1.73, n=3; mitered langurs: $\bar{x}$ =17 ha, n=1). Thus, interspecific encounters were anticipated to be frequent events. Interspecific dominance was determined from the outcome of these encounters, such that the dominant group ("the winner") displaced the subordinate ("the loser") from its location (i.e., the individual tree occupied at the start of the encounter) through either a chase or approach-retreat (e.g., Fashing 2001). The group identities, individuals present within 50 m, time, duration, and location of each encounter were recorded. The geographic location of an encounter was recorded as a set of coordinates relative to Way Canguk's trail system that represented the location of the group being approached at the start of the encounter. Whenever possible, it was noted which group initiated (first travelled to within 50 m) and which terminated (first travelled farther than 50 m) each encounter. Encounters were assigned to five mutually-exclusive types, four of which followed Bartlett (2003): 1) *agonistic* encounters included displacements, chases or contact aggression; during 2) *vocal disputes*, one or both groups sang duets, trios, or long calls without chases or contact aggression; 3) *affiliative* encounters exclusively included interspecific play, and in 4) *neutral* encounters none of the aforementioned behaviors were observed. Additionally, 5) *passive avoidance* was defined as when, upon being approached, individuals of one group ceased activities, monitored individuals from another group, and remained motionless in concealed locations. The attention of the approaching group was not directed toward the individuals avoiding the interaction. When behaviors diagnostic of more than one type of encounter occurred during a single encounter, that encounter was classified according to the most aggressive behavior observed (e.g., a vocal dispute followed by chasing = agonistic encounter). Agonistic encounters were assigned to four classes based on the intensity of aggression: 1) *approach* and displace, 2) *threaten* and diplace via aggressive vocalizations, 3) *chase* (pursuits of displaced individuals beyond the encounter location), and 4) *escalated aggression* (aggressive physical contact, including biting and grappling – individuals interlocked in intense grabbing, slapping, and wrestling).

Energetic costs of lost interspecific encounters. Of all agonistic encounters observed, 50 occurred at patches where food known to be used by both groups was available. This subset of encounters was used to determine changes in energy expenditure and energy intake for the losing groups. Location data were recorded as xy coordinates following the trail system at Way Canguk 1) at 10 minute intervals at the center of focal groups, 2) at all feeding patches, and at the initiation and cessation of chases. To evaluate whether encounter costs were large enough to be biologically meaningful, energy expenditure directly attributable to lost interspecific encounters (i.e., chase distance) was gauged against known travel costs of increasing group size (following Janson and Goldsmith 1995). This comparison was selected because the costs of group size have been established to have significant per capita energy costs.

Nutritional contents were determined for all food items consumed during all-day follows, allowing for direct comparisons of items in contested patches with those in patches used after a lost encounter. Following each contact period (3-4 days per focal group), fresh samples were collected and weighed, then dried in a gas-powered oven at low heat (40° C), reweighed and packed airtight. For each food item (i.e., part of the same maturity per species), fresh and dry weights were repeated across a minimum of 20 individual samples per food item to calculate mean masses per item. Analyses of gross energy (kcal/g dry mass) were conducted at the Indonesian Institute of Sciences by Dr. Wartika Rosa Farida and her staff.

Feeding bout lengths were defined operationally as the total number of minutes an individual fed continuously, irrespective of the boundaries of focal sessions. Pauses in feeding greater than 10 minutes were treated as indicating the initiation of a separate bout. During all-day follows of adult individuals, the lengths of every feeding bout were recorded by a separate observer via all-occurrence sampling (Martin and Bateson 1993). Observers recorded ingestion rates by opportunistically counting the number of food items ingested per minute for each food item. Ingestion rates were assessed only when individuals were fully visible, enabling accurate counts of the exact numbers of fruits, flowers, leaves, shoots, or invertebrates picked, fully masticated, and swallowed per minute. Multiple ingestion rates were assessed for every food item, and mean adult ingestion rates were calculated. Combining this information with the energy content data for each item, energy intake per feeding bout was estimated (bout length x ingestion rate x dry item mass x kcal/g dry mass; Koenig et al. 1997). Total daily intake was then estimated from the sum of all feeding bouts. To assess lost energy intake per encounter, it was assumed that losing groups would have continued to feed in the contested patch as long as they typically fed on the item when no encounter occurred. Thus, lost feeding time was estimated as the mean undisturbed bout (same food items and individual patch) minus the duration of the bout prior to displacement (Janson 1985). These lost minutes were then multiplied by the rate of caloric intake of the contested food item (i.e., ingestion rate x dry item mass x kcal/g dry mass).

Food availability. Since 1997, WCS staff have continuously monitored 2,106 trees in 100 10 x 50 m phenological plots to estimate food availabilities (Kinnaird and O'Brien 2005). Each month these trees were assessed for the presence of ripe fruit and young leaves. Additionally, fruit crop sizes were visually estimated on Leighton's (1993) exponential scale and total monthly fruit production (a reliable estimate for fruit biomass at Way Canguk; Kinnaird and O'Brien 2005) was then calculated as the sum of these scores across the entire community.

Data analyses

A chi-square test of independence (Siegel and Castellan 1988) was used to determine whether the type of interspecific encounter differed across species-pairs. Chi-square tests for goodness of fit (Siegel and Castellan 1988) were used for each species-pair to assess which species more often 1) initiated or 2) terminated encounters. In these comparisons, the observed distribution was tested against an even distribution for each species. A one-way ANOVA and Tukey post-hoc tests (Sokal and Rohlf 1995) were used to determine if the duration of interspecific encounters (log transformed) differed among species pairs.

Hutchinson and Waser's (2007) updated ideal gas model ($f=[8pv(d+s)/\pi]c$) was used to predict interspecific encounter rates for pairs of neighboring groups, where p=local group density, v=velocity (m per day), d=detection distance (here 50 m), and s=mean group spread. A correction factor ($c=o^2/h_1h_2$) was used to account for partial home range overlap, where o=overlap area, h_1=home range of group 1, and h_2=home range of group 2 (Leu *et al.* 2010). Home range sizes and overlaps were estimated from 95% adaptive kernel analyses using Biotas 2.0 Alpha (2012). To test whether observed encounter rates differed from these predictions, 95% confidence limits were generated from variation across months in mean daily encounter rates (described in Hutchinson and Waser 2007).

To evaluate whether encounter characteristics are the result of feeding competition, the relationships between 1) encounter species and location and 2) encounter type and location were tested (Chi-square test of association with Cramer's coefficient; Siegel and Castellan 1988). Encounters were assigned to three location categories: non-food, shared food (at least one group in patch with items available known to be eaten by both study species), and non-shared food (at least one group in patch with food available and known to be eaten by only one study species). Wilcoxon signed-ranks tests (Siegel and Castellan 1988) were used for each species-pair to compare monthly expected and observed numbers of encounters at shared food locations. To control for seasonality, these comparisons were made monthly. Expected numbers of encounters at shared food locations were estimated per pair of groups as the total number of encounters observed each month multiplied by the monthly fraction of overlapping home ranges containing shared food locations (i.e., *n* 50x50 m quadrants with shared food/total *n* quadrants). Only quadrants within areas of interspecific home range overlap were included in these calculations, and a shared food quadrant was defined as any containing at least one shared food patch that was actively producing shared food items in a given month. For example, if the total area of interspecific overlap between two groups comprised 60 quadrants and during one month 15 of these quadrants contained at least one food patch, then this monthly fraction would be calculated as: 15/60 = 0.25. If, during the month, these groups encountered each other 10 times, then the expected number of encounters at shared food locations would be: 10x0.25=2.5. Additionally, Spearman’s rank order correlation analyses (Siegel and Castellan 1988) were used to examine the relationship between agonistic encounter rates and monthly food availability (total fruit production and N trees with ripe fruit and young leaves).

All focal groups of siamangs had two adult males, while agile gibbons lived in one-male groups. Thus, even though second adult males sometimes travel independently from other group members (Elder, pers. obs.), siamangs often have an advantage in group size as well as body mass over agile gibbons. To disentangle the effects of these two factors on RHP, a Jonckheere test for ordered alternatives and Kendall's tau-b (Siegel and Castellan 1988) were used to evaluate whether the intensity of HA that siamangs directed at agile gibbons increased with the number of agile gibbons relative to siamangs present per encounter. Encounter group size was defined as the total number of individuals per group within 50 m of an encounter (i.e., the geographic location at the start of an encounter); this excluded all infants and small juveniles (2-4 years old; Lappan 2005), as individuals in these age classes are unlikely to participate in encounters.

A paired t-test (Sokal and Rohlf 1995) was used to determine if contested food items and alternative food items (i.e., those items consumed immediately after displacements from feeding patches) differed in caloric content.

To estimate the cumulative daily costs of lost encounters, Mann-Whitney U-tests (Siegel and Castellan 1988) were used to compare 1) per capita daily energy intake and 2) daily path lengths between days with lost encounters and non-encounter days for groups of subordinate species. To control for the effect of food availability on energy intake and expenditure, these comparisons were made separately for months with low and high ripe fruit availabilities. Based on optimal foraging theory (Charnov 1976): during periods of decline in the availability of preferred resources, organisms initially maintain feeding behavior and activity budgets. However, when the availability of these foods drops below the critical level at which they can be exploited profitably, individuals must meet energy requirements by changing foraging tactics (van Schaik et al. 1993; Hemingway and Bynum 2005). Therefore, known behavioral responses to food scarcity (including dietary switching to fallback foods, increased dietary breadth, and increased feeding time; rev. in Hemingway and Bynum 2005) were used to identify a cutoff between low and higher ripe fruit availabilities at 5.2 fruiting trees per ha. When ripe fruit availabilities fell below this cutoff, primates at Way Canguk substantially increased (i.e., increases > mean+SD of each behavioral parameter across the study period) time spent feeding on non-fruit foods (e.g., leaves, figs, or flowers), feeding time overall, and/or the total number of different food items eaten monthly. Due to limitations in the data set available at the time of analysis, estimates of ripe fruit availabilities included all species of ripe fruit available within phenological transects (rather than only those known to be eaten by the primate species in question). During the study period (Mar. 2008-Oct. 2009), fruit availabilities were low in March 2008, September-November 2008, and May-July 2009. Statistical tests were conducted using SPSS Statistics 17.0 at an alpha level of 0.05.

RESULTS

Interspecific encounters

Over the study period, 80 siamang-mitered langur, 161 siamang-agile gibbon, and 48 mitered langur-agile gibbon encounters were observed; interspecific encounter rates were 0.61, 0.45, and 0.33 encounters per group per day respectively. In comparison, siamang-siamang encounters were observed at a rate of 0.33 encounters per day, while both langur-langur (0.13 encounters/day) and agile gibbon-agile gibbon (0.05 encounters/day) encounters were much less frequent.

Encounter types. Encounter types were not equally frequent for either siamang-mitered langur (Chi-square test: χ^2=79.42, df=4, p<0.001) or mitered langur-agile gibbon interactions (Chi-square test: χ^2=62.83, df=3, p<0.001). The majorities (Fig. 3.2; Table 3.2) of these encounters were neutral (59% and 73% respectively) and few were agonistic (6% and 2% respectively). Although passive avoidance was infrequent for encounters between mitered langurs and either hylobatid (Fig. 3.2; Table 3.2), in all cases mitered langurs were the avoiding groups. In addition, siamangs and mitered langurs were observed to engage in interspecific play (10% of encounters) and co-feeding (i.e., simultaneous use of feeding patches). Juvenile siamangs played with both juvenile and adult mitered langurs; these interactions included tail pulling and play chases. Juvenile mitered langurs reciprocated play, while adults tolerated these activities. In contrast, affiliative behavior was never observed between siamangs and agile gibbons or agile gibbons and mitered langurs. The paucity of juvenile agile gibbons in focal groups (n=1), however, may have limited the opportunity for play between these species.

Interactions between siamangs and agile gibbons were not evenly distributed among encounter types (Chi-square test: χ^2=38.61, df=3, p<0.001). Compared with hylobatid-mitered langur encounters, encounters between siamangs and agile gibbons were about equally often vocal disputes (21% each vs. 19% respectively), but much less often neutral (9%; Fig. 3.2; Table 3.2). Most siamang-agile gibbon encounters were either passive avoidance (29%) or agonistic (43%; Fig. 3.2; Table 3.2); both types were very rare in encounters for the other species-pairs. In all cases siamangs were the aggressors, causing agile gibbons to retreat through approaches alone (n=22), and threatening (n= 20 encounters), chasing (n= 24 encounters) and biting agile gibbons (n= 3 encounters). Agile gibbons, in contrast, were the avoiding groups in all instances, and spent a total of 8.28 hours out of 1,809 observation hours in passive avoidance encounters with siamangs. Dividing active time into two-hour blocks, avoidance encounters were observed about equally often in the early (30%) and late morning (37%), but less often in the afternoon (13%) and evening (23%).

Encounter outcomes and interspecific dominance

Of the 161 total times that siamangs and agile gibbons were within 50 m of each other, 47 (29%) were passive avoidance. Excluding these, a winner could be determined for 75% (86 of 114) of siamang-agile gibbon encounters. In contrast, the outcome was decided for only 9% of all siamang-mitered langur and 6% of all mitered langur-agile gibbon encounters. Based on the outcome of decided interspecific encounters, siamangs were dominant over agile gibbons and consistently displaced mitered langurs, winning 98% (*n*=85) and 100% (*n*=7) of encounters respectively. Agile gibbons displaced mitered langurs for 100% (*n*=3) of the decided encounters.

The frequency of aggressive encounters and the intensity of aggression observed between siamangs and agile gibbons were much higher than that between the other species (Fig. 3.2). During the entire study period contact aggression was observed in four instances between siamangs and agile gibbons, including aggressive grappling on two occasions, attempted biting of an adult female agile gibbon by a siamang male, and a bite wound inflicted to the back of an adult male agile gibbon by a siamang male. Such contact aggression was never observed between the other species.

Encounter characteristics

Minimizing risks of encounters. The species differed in who initiated and terminated interspecific encounters (Table 3.3). Siamangs more frequently initiated siamang-mitered langur encounters (Chi-square test: χ^2=5.39, df=1, p<0.05), but neither species was more likely to terminate encounters (Chi-square test: χ^2=1.37, df=1, p=0.24). Siamang-agile gibbon encounters were significantly more often initiated by siamangs (Chi-square test: χ^2=71.26, df=1, p<0.001), but terminated by agile gibbons (Chi-square test: χ^2=12.09, df=1, p<0.001). Agile gibbons more often initiated encounters with mitered langurs (Chi-square test: χ^2=4.46, df=1, p<0.05); however, neither species was significantly more likely to terminate encounters (Chi-square test: χ^2=1.82, df=1, p=0.18).

Siamang-agile gibbon encounter rates observed for three of four group-pairs did not significantly differ from encounter rates predicted from an ideal gas model (Table 3.4). For one group-pair (*S.s.*M-*H.a.*1), however, their encounter rate ($0.08 \leq x \leq 0.33$) was significantly lower than expected by chance (0.59 encounters/day). While encounters between one pair of siamang and mitered langur groups (*S.s.*E-*P.m.*3) were more frequent than predicted ($0.25 \leq x \leq 0.58$ vs 0.13 encounters/day), a second group-pair (*S.s.*M-*P.m.*1) met as expected by chance (Table 3.4). Predicted rates of mitered langur-agile gibbon encounters fell within observed confidence limits for both group-pairs analyzed. Overall, therefore, both siamang-agile gibbon and mitered langur-agile gibbon encounters tended to occur as expected under an assumption of random movement (3/4 and 2/2 group-pairs respectively), but results for siamang-mitered langur encounters were less consistent.

Based on the operational definition used here, during passive avoidance encounters, only the avoiding groups detected (i.e., directed their attention towards) approaching groups. This type of encounter was particularly frequent between siamangs and agile gibbons. While these one-way interactions were still encounters, they may reflect attempts to reduce the rate of agonistic interactions. In a separate set of analyses, therefore, passive avoidance encounters were excluded from calculations of observed siamang-agile gibbon encounter rates. Encounter rates for two of four group-pairs tested (SJ-G3 and SM-G1) significantly differed from rates predicted from an ideal gas model (Table 3.4). For each of these, interspecific encounters were observed less frequently than expected by chance ($0.27 \leq x \leq 0.42$ vs. 0.46 encounters/day and $0.12 \leq x \leq 0.22$ vs. 0.59 encounters/day respectively). For the remaining group-pairs, expected encounter rates still fell within observed confidence limits (Table 3.4).

Intensity of heterospecific aggression. Siamangs won encounters over mitered langurs and agile gibbons, independent of encounter group size. Although total encounter group sizes could not always be determined for mitered langurs, in most cases (42/50) there were more mitered langurs present than siamangs. Siamangs won all but one encounter with agile gibbons, despite variation in encounter group sizes. However, the intensity of HA by siamangs during successful displacements of agile gibbons varied depending on the number of agile gibbons relative to siamangs present at an encounter (Fig. 3.3). A significant, positive association (Kendall's T_B=0.22) was found between relative encounter group size and HA intensity (Jonckheere's test: J=854, z=1.957, p<0.05). When siamangs had a numerical advantage over agile gibbons, HA was less intense and consisted of approach and displace behavior on the part of the siamang more often than threatening or chasing agile gibbons (Fig. 3.3). When there were equal numbers of siamangs and agile gibbons, siamangs most often chased agile gibbons and less frequently displaced groups through lower intensity HA. Siamangs directed the most intense HA at agile gibbons when at a numerical disadvantage; all observations of escalated aggression occurred when more agile gibbons than siamangs were present at encounters. For 40% of instances when siamangs escalated HA to long-distance chases and contact aggression, encounters were between agile gibbon pairs and single adult male siamangs. These second adult males were subordinate in their group (Morino 2011; 2012) and frequently travelled independently from other group members (pers. obs.).

Encounter duration. The duration of interspecific encounters significantly differed across species pairs (1-way ANOVA: $F(2,204)=21.93$, 2-tailed $p<0.001$; $\bar{x}=37.81$ min; $\sigma=91.41$ min). Encounters between siamangs and mitered langurs ($\bar{x}=93$ min; $\sigma=175$ min; $n=47$) were significantly longer than both mitered langur-agile gibbon ($\bar{x}=33$ min; $\sigma=42$ min; $n=37$; Tukey post hoc test: $p<0.05$) and siamang-agile gibbon encounters ($\bar{x}=18$ min; $\sigma=24$ min; $n=123$; Tukey post hoc test: $p<0.001$). Additionally, mitered langur-agile gibbon encounters were significantly longer than siamang-agile gibbon encounters (Tukey post-hoc test: $p<0.05$).

Feeding competition. A moderate (Cramer's $V=0.23$) and significant association was found between the location of encounters and the species-pair involved (Chi-square test: $\chi^2=30.25$, df=4, $p<0.001$). For all three species-pairs, encounters occurred least often (2-14% of encounters) at non-shared food locations (Fig. 3.4). The distribution of encounters between non-food and shared food locations, however, varied among species-pairs. The majority (50%) of siamang-mitered langur encounters occurred at shared food locations, while encounters at non-food locations accounted for 36% of the observations. Both siamang-agile gibbon and mitered langur-agile gibbon encounters occurred most frequently at non-food locations (62% and 75% respectively) and less often at shared food locations (36% and 19% respectively).

Although absolutely more siamang-agile gibbon and mitered langur-agile gibbon encounters occurred at non-food locations than at other locations, these comparisons did not account for fluctuations in the availability of food locations. In fact, a significantly greater number of both siamang-mitered langur and siamang-agile gibbon encounters occurred at shared food locations than expected from the monthly availability of these locations across overlapping home ranges (Table 3.5; Wilcoxon signed-ranks tests: z=-3.33, p<0.01; z=-2.05, p<0.05 respectively). Mitered langur-agile gibbon encounters, in contrast, were observed at shared food locations as expected by chance (Table 5; Wilcoxon signed-ranks test: z=-0.11, p>0.05).

The relationships between encounter type and location were not significant for either siamang-mitered langur (Chi-square test: χ^2=5.01, df=8, p=0.757) or siamang-agile gibbon encounters (Fig. 3.5; Chi-square test: χ^2=1.42, df=6, p=0.964). For mitered langur-agile gibbon encounters, however, agonistic and avoidance encounters, while infrequent, all occurred at shared food locations (Chi-square test: χ^2=20.38, df=6, p=0.002; Cramer's V=0.47; Fig. 3.5). Vocal encounters were more evenly-distributed across location types, while neutral encounters predominantly (88%) occurred at non-food locations (Fig. 3.5).

Food availability did not significantly influence rates of HA per day, including HA between species with the greatest ecological similarity (i.e., siamangs and agile gibbons). Across species-pairs, no significant relationships were found between the rates of agonistic encounters and total fruit production, ripe fruit availability or young leaf availability (Table 3.6; Spearman's rank correlations: all p>0.05).

Energetic costs of interspecific encounters

Of the 50 agonistic encounters observed in a feeding context, 42 were between siamangs and agile gibbons and 8 involved mitered langurs. Both siamang (n=5) and agile gibbon displacements of mitered langurs (n=3) were brief, allowing individuals to remain in the patch and resume feeding. Although mitered langurs and hylobatids consumed the same food types (i.e., figs, fruits, or leaves) during each of these interactions, their food items typically differed in maturity (n= 6/8 encounters). Mitered langurs ate semi-ripe figs and fruits, while hylobatids consumed ripe figs and fruits. Thus, the energetic costs of these displacements seem to be negligible for mitered langurs. In contrast, displaced agile gibbons were never observed to return during the same day to feeding patches occupied by siamangs. Thus, agile gibbons likely incurred energetic costs as a result of these lost encounters.

Costs per lost encounter. All necessary data were available for 32 of the 42 siamang-agile gibbon encounters at shared food locations. After being displaced, agile gibbons were chased 100 meters (σ= 63 m) on average. Across agile gibbon groups, this extra energy expenditure directly attributable to lost encounters accounted for 9 to 11% of the mean daily path lengths on non-encounter days. Furthermore, agile gibbons' alternative food items (i.e., those items next consumed after a lost encounter) were significantly lower in caloric content ($\bar{x}$ =2.61 kcal/g; σ=1.75 kcal/g) than contested items ($\bar{x}$ =3.78 kcal/g; σ=0.87 kcal/g; Paired t-test: t=3.55, p=0.002). Subsequent food items varied in type. For 54% of cases agile gibbons shifted from ripe fruits or figs of one species to ripe fruit or figs of another, while they shifted less often from ripe fruits or figs to young leaves (23%) or flowers (9%) and rarely shifted from flowers to ripe fruit (9%) or between different species of young leaves (5%). Lost feeding time was assessed by comparing durations of feeding bouts prior to displacements and mean undisturbed bouts in the same exact patches. On average, 14 min (σ=9 min) of feeding time in contested patches were lost due to displacements. This translates into a mean per capita cost of 99.38 kcal (σ= 93.86 kcal) per lost encounter for agile gibbons. The reduction in energy intake due to the average lost encounter accounted for 12.66% (σ=14.87%) of total per capita intake on encounter days.

Cumulative daily costs. Because the two agile gibbon groups significantly differed in both daily path lengths (Table 3.7; $F(1,133)=15.40$, $p<0.001$; $\bar{x}$ =1112 m vs. 887 m; σ=355 m vs. 294 m) and daily per capita energy intake (Table 3.7; $F(1,131)=16.51$, $p<0.001$; $\bar{x}$ =547 kcal vs.

754 kcal; σ=223 kcal vs. 277 kcal), groups were analyzed separately for cumulative daily costs of encounters. There was no significant difference in daily path lengths between lost encounter and non-encounter days for individuals from either agile gibbon group (Mann-Whitney U-tests; Table 3.7). This result was the same for months with low and higher ripe fruit availability. Furthermore, per capita daily energy intake for agile gibbons from both groups did not differ between lost encounter and non-encounter days, regardless of ripe fruit availability (Mann-Whitney U-tests; Table 3.7).

DISCUSSION

Determinants of interspecific dominance

It was hypothesized (Table 3.8) that either body mass or group size would equate to RHP and, therefore, determine rank between species, regardless of ecological similarity. As predicted, siamangs (the heaviest species in the system) were dominant over smaller-bodied agile gibbons and won decided encounters with mitered langurs. Group size alone was not found to influence interspecific dominance rank. Siamangs displaced mitered langurs and agile gibbons independent of encounter group sizes, including instances when the smaller-bodied competitors had a numerical advantage over siamangs. Additionally, despite larger group size and similar body mass, mitered langurs lost most agonistic encounters with agile gibbons. Thus, interspecific rank was likely better determined by body mass than group size. This trend is consistent with those found for the majority of animal systems (Schoener 1983; Persson 1985), including other primate communities (e.g., Houle et al. 2006). However, it must be noted that the small sample size available for decided encounters between mitered langurs and each hylobatid species warrants some caution with this result. Additionally, despite the fact that siamangs won interspecific encounters even when siamang individuals present were outnumbered by agile gibbon individuals, siamangs always had the larger total group sizes. It is possible that agile gibbons assess the strength of siamang groups based on past knowledge of total group size, rather than encounter group size. Taken together, these limitations imply that the influence of group size on RHP cannot be entirely dismissed, and additional studies of interspecific encounters in populations where siamangs and *Hylobates* gibbons have the same group sizes would clarify the individual roles of body mass and group size in determining RHP. On the other hand, the apparent dominance of agile gibbons over mitered langurs is inconsistent with both predictions for RHP. White-bearded gibbons (*Hylobates albibarbis*) were also observed to successfully displace red langurs (*Presbytis rubicunda*; Marshall et al. 2009), and Kloss's gibbons (*Hylobates klossii*) dominated Mentawai langurs (*Presbytis potenziani*; Tilson and Tenaza 1982). This may indicate a determinant of RHP beyond body mass and group size, such as agility or canine size. Alternatively, ecologically dissimilar species (e.g., agile gibbons and mitered langurs) may differ in how they assess the relative value of a given resource and, in turn, may not be equally willing or able to engage in HA (Peiman and Robinson 2010). For example, capuchin monkeys (*Cebus capucinus*) aggressively displaced larger, more folivorous howler monkeys (*Alouatta palliata*) from fruit resources (Rose *et al.* 2003; but see Terborgh 1983).

Minimizing risks of interspecific encounters

Groups of subordinate species were expected to minimize the risk of encountering groups of dominant species. This should be particularly true for species that mainly have agonistic encounters. As predicted (Table 3.8), for species that rarely engaged in HA (i.e., siamang-mitered langur and mitered langur-agile gibbon), both species were equally likely to terminate encounters. Agile gibbons, in contrast, were significantly more likely to terminate encounters and significantly less likely to initiate encounters with dominant siamang groups. Similarly, Malaysian siamangs at Krau Game Reserve initiated most agonistic encounters with lar gibbons (Raemaekers 1978). However, these siamangs were less successful at displacing lar gibbon groups from feeding patches than siamangs at Way Canguk (Malaysian siamangs won 35% vs. 98% of decided encounters in this study). Furthermore, unlike results reported here, agonistic encounters were limited to direct feeding competition and co-feeding was observed between siamangs and lar gibbons in large, non-fruit patches (Raemaekers 1978). Differences in the intensity of HA between Sumatran and Malaysian hylobatids may reflect variation between locations in resource availability and population densities. Compared with Krau Game Reserve, the forest at Way Canguk was found to be more productive and less seasonal, and to have higher siamang but lower agile gibbon population densities (O'Brien et al. 2004; Kinnaird and O'Brien 2005). Due to greater energetic constraints, Malaysian siamangs may have, therefore, used HA against lar gibbons only when most profitable (i.e., in defense of preferred, monopolizable food resources). In contrast, the use of HA against agile gibbons should have lower relative energy costs for siamangs at Way Canguk. Alternatively, aggression could be a function of the density of competitors, such that higher siamang population densities at Way Canguk lead to higher costs of hylobatid coexistence. Thus, the benefit of aggressively displacing agile gibbons may be greater for siamangs at Way Canguk than in other populations.

Despite the high frequency of avoidance encounters between siamangs and agile gibbons, encounter rates for the majority of these groups did not differ from rates predicted by chance. Excluding passive avoidance encounters, however, siamang-agile gibbon encounters did occur less often than expected for half of the group-pairs examined. Likely due to hylobatids’ high home range overlap and siamang's high population density, agile gibbons did not avoid interspecific encounters frequently enough to reduce encounter rates below chance.

Ecological similarity and heterospecific aggression

In the study system, although in most cases encounter rates did not deviate from chance, HA was influenced by the degree of ecological similarity between species. As predicted (Table 3.8), encounters between species with high ecological overlap (siamangs and agile gibbons) were predominantly decided, often agonistic, and never affiliative. In contrast, those between more divergent species (mitered langurs and either hylobatid) were rarely decided, largely neutral and, in the case of siamang-mitered langur encounters, occasionally affiliative. Similar to siamang-agile gibbon encounters at Way Canguk, siamangs at Ketambe in Malaysia escalated the majority of encounters with lar gibbons, and rarely escalated encounters with ecologically dissimilar species such as leaf monkeys (Raemaekers 1978). Siamangs also seemed to be dominant over lar gibbons in northern Sumatra; however, on very rare occasions interspecific play was observed between juvenile individuals at Ketambe (Palombit, pers. comm.). Results here lend additional support to the resource overlap hypothesis (Peiman and Robinson 2010), in which the rate of HA has been found to positively correlate with ecological similarity across animal communities.

An individual should escalate aggression only if there is a chance to gain some fitness benefit (Maynard Smith and Parker 1976). Hylobatids (including populations at Way Canguk) have been found to prefer the flesh of acidic, pulpy fruits and ripe figs over alternative food items (Ungar 1995; Appendix 1) and to overlap broadly in diet when in sympatry (Elder 2009; unpubl. data). In addition to dietary similarity, hylobatid densities (across sites and species) are limited by the availability of figs (Marshall 2004; Marshall and Leighton 2006). Siamang and agile gibbon populations at Way Canguk, therefore, may be limited by similar food resources. In contrast, mitered langurs avoid acidic foods and instead prefer unripe fruits, seeds, and leaves (Davies et al. 1988). Thus, low rates of HA were expected during mitered langur-hylobatid encounters. This is supported by observations of prolonged, non-agonistic encounters between siamangs and mitered langurs. Even encounters at shared feeding patches may not increase HA if competition is mitigated by fine-scale differentiation in feeding ecology (e.g., Mitani 1991). For example, mitered langurs were observed to consume semi-ripe figs, while siamangs selected riper figs from the same patches at Way Canguk. In Africa (e.g., Wachter et al. 1997) and South America (review in Terborgh 1990), associations between ecologically dissimilar species have been found to provide more benefits (e.g., reduced predation risk; play opportunities for immature individuals) than costs (e.g., feeding competition). Associations between siamangs and mitered langurs may provide similar benefits; however, observed encounter rates did not consistently differ from chance. Thus, the high frequency of siamang-mitered langur encounters may reflect high population densities and home range overlap between these species (O'Brien et al. 2004; WCS unpubl. data).

Ecological similarity and encounter duration

Contrary to expectations (Table 3.8), the species with the greatest ecological overlap (siamangs and agile gibbons) had shorter encounters than ecologically-divergent species (siamang-mitered langur and mitered langur-agile gibbon). As an alternative mechanism to ecological overlap, similarity in competitive ability may promote prolonged, escalation of aggression (Parker 1974). When opponents diverge in competitive ability, their encounters should have more predictable outcomes and shorter durations. Large asymmetries in the perceived risk of encounters, as well as competitive ability were apparent between siamangs and gibbons, despite their ecological similarity. Therefore, it could not be assumed that the benefits/costs ratios of encounters were similar for these species and, instead, the inherent costs of prolonged encounters must be taken into account (Parker and Rubenstein 1981). Although HA between hylobatids was less intense than in carnivore communities (e.g., Durant 2000), observations of grappling and biting suggest that these interactions can be dangerous. Agile gibbons, therefore, should avoid prolonged encounters with siamangs, where the risk of injury likely increases with the duration of an encounter. Support for this hypothesis was evident from the effect of encounter group size on the intensity of HA: Escalation of aggression was much higher during siamang-agile gibbon encounters when the the two species were more evenly matched.

Encounter characteristics and feeding competition

As predicted (Table 3.8), the locations of interspecific encounters were a result of direct feeding competition. Although the majority of encounters were at non-food locations, siamang-mitered langur and siamang-agile gibbon encounters occurred at shared-food locations more often than expected by chance. Contra predictions (Table 3.8), however, the intensity of HA was not a result of direct feeding competition. The majority of agonistic encounters, including those between species with the most resource overlap, occurred at non-food locations. Likewise, no significant relationships were found between food availabilities and the rates of agonistic encounters across species-pairs. In contrast, agonistic encounters among sympatric South American primates almost exclusively occurred in feeding contexts and rates of HA varied with fluctuations in fruit abundance (Stevenson et al. 2000). The assumption that both hylobatids concentrate on decreasing supplies of the same resources may not apply. Results could instead suggest that, (despite broad ecological overlap) when the availability of preferred food drops below a certain level, siamangs and agile gibbons diverge more in diet. As a consequence of this divergence, HA may not increase. Alternatively, findings here may suggest that seasonality at Way Canguk is not pronounced enough to affect rates of HA, resulting in relatively abundant food throughout the year. Although ripe fruit production is seasonal, fig production at Way Canguk is almost constant and dominates overall fruit production (Kinnaird and O'Brien 2005). Figs at Way Canguk, however, may still be a shared limiting resource for sympatric hylobatid species because in each home range only about 4 individual plants (1 fig per 6 ha) produce fruit monthly (Kinnaird and O’Brien 2005). Thus, siamangs have the opportunity to monopolize these patches to the exclusion of subordinate agile gibbons. Figs are important fallback foods for hylobatids, providing a reliable food source during times of ripe fruit scarcity and seemingly limiting hylobatid biomass across Asia (Marshall 2004; Marshall and Leighton 2006). Home range overlap is high among siamang, mitered langur, and agile gibbon groups, while home ranges are comparatively small (Fig. 3.1). Chance meetings, therefore, may occur throughout the day. In addition, because HA was observed between siamangs and agile gibbons across location types, competition between these species may not be limited to contests over food. Furthermore, regardless of encounter location, siamangs may influence agile gibbons’ foraging decisions. For example, siamangs may displace agile gibbons far from the initial encounter location and gain exclusive access to a feeding patch that agile gibbons may have used had the encounter not occurred. Therefore, HA may be spatially separate from a food resource, yet still effectively disrupt the subordinate species’ foraging decisions. Given their intense competition and lack of interspecific territoriality, agile gibbons may coexist with siamangs by using either marginal or overlooked resources (Horn and MacArthur 1972; Slatkin 1974).

Energetic costs of coexistence

Following lost encounters with siamangs, agile gibbons incurred energetic costs, including increased energy expenditure and decreased energy intake. Travel costs directly attributed to displacements of agile gibbons from feeding patches exceeded those associated with increasing group size in a closely-related species. Agile gibbons at Way Canguk were chased 100 m on average, while lar gibbons increased daily travel by 73 m for each additional group member (Savini et al. 2008; Savini, pers comm). Once displaced, agile gibbons consumed food items with lower caloric content and estimates of per capita energy losses account for almost 13% of daily caloric intake per encounter lost. To put this in perspective, this estimated cost approaches that calculated for subordinate capuchins under intense within-group contest competition; dominant individuals had 20.5% greater daily energy intake than the lowest-ranked individuals, a cost associated with decreased offspring survival (Janson 1985). The energetic cost per lost encounter estimated here, as well as the high rate of siamang-agile gibbon encounters relative to agile gibbon-agile gibbon encounters, leads me to suggest that interspecific competition has a significant impact on individual agile gibbon fitness at Way Canguk (see also below).

Encounters with dominant species, however, did not result in significant cumulative daily energy costs. Whether or not agile gibbons lost an encounter with siamangs and during months with both low and higher ripe fruit availability, there were no differences in daily path lengths or per capita daily energy intake. On encounter days, agile gibbons may compensate for lost energy by altering their foraging strategies. Additionally, agile gibbons may still undergo costs of competition on non-encounter days if they avoid resources where encounters with siamangs are likely to occur. Even if their energy intake and expenditure do not vary between lost encounter and non-encounter days, it is unclear from these analyses whether agile gibbons are meeting optimal energy requirements. To meet maintenance energy requirements in captive *Nomascus concolor* gibbons, it was recommended that about 850 kcal should be consumed daily (Gomis *et al.* 2006). Average daily energy intake for the somewhat smaller, but much-more active agile gibbons at Way Canguk, in contrast, was estimated at only 599 kcal. Even if energy recommendations are over-estimated, this may suggest that intake for wild agile gibbons in this population may regularly be below optimum. Alternatively, due to potential chance effects when measuring energy intake on a daily scale, the discrepancy between estimated requirements and intakes may reflect background noise. Furthermore, estimates of energy requirements generated from captive individuals may not be appropriate for studies of wild populations (e.g., Janson 1988).

The cumulative effects of daily interactions among competing species often have important long-term fitness consequences. In dung beetle (Horgan 2005), crab (Navarrete and Castilla 1990), and carnivore (Durant 1998) communities, individuals of subordinate species that minimized the chance of encounters with dominant species by relying on lower-quality resources also experienced lower reproductive success and/or increased mortality. At Way Canguk, O’Brien *et al* (2004) found that agile gibbons live at a much lower population density than siamangs and long-term demographic data suggest that agile gibbons at Way Canguk have lower birth rates and higher infant and juvenile mortality than siamangs (O'Brien and Kinnaird 2011). Based on the energetic costs and risks of interspecific encounters, these demographic differences may be attributable to competition with siamangs. If the agile gibbon population at Way Canguk is indeed in decline, then it may represent a “sink” (Pulliam 1988), whereby immature individuals fail to reach maturity and the area is re-populated by adult individuals immigrating from nearby source populations. Presumably, agile gibbons would be better adapted to conditions in source habitats. Therefore, this possibility would also suggest that, rather than differing in diet, siamangs and agile gibbons may coexist through larger-scale habitat divergence. In particular, a significant relationship has been reported between elevation and population density in Sumatran hylobatids (O'Brien *et al.* 2004); peak abundances were at mid elevations for agile gibbons and low elevations for siamangs, while both species were scarce at high elevations where preferred foods are rare.

Game theory and species coexistence

Game theoretical models can be used to analyze aggression during interspecific encounters. The sequential assessment game predicts a continuous increase in the intensity of agonistic encounters as asymmetry in fighting ability decreases (Enquist *et al.* 1990). In support of this model, a significant, positive trend was found between the intensity of HA siamangs directed at gibbons and relative encounter group size. Even though RHP best equated to body mass, this result indicates that competing species perceive encounters differently depending on the number of individuals present and, accordingly, vary their responses with changes in the direction of numerical advantage. Agile gibbons could be more willing to escalate encounters with siamangs when at a numerical advantage and/or siamangs may escalate these encounters when at a numerical disadvantage to ensure displacement of agile gibbons. HA was least intense when siamangs outnumbered agile gibbons and most intense when siamangs were at a numerical disadvantage. In 40% of the most intense encounters, the subordinate adult male siamang of a group behaved aggressively against a pair of agile gibbons. In these instances the opponents (i.e., 1 siamang vs. 2 agile gibbons) may be more evenly matched, and therefore siamangs are more likely to escalate HA. By engaging in riskier or energetically expensive interactions, subordinate siamang males may indirectly increase fitness for breeding individuals in their group (Gaston 1978). These benefits may, in part, explain why secondary males are tolerated in siamang groups.

If the cost of an interaction is greater than the value of the contested resource, subordinate individuals should retreat from dominant opponents rather than escalating fights (Maynard Smith and Parker 1976). Based on observations, agile gibbons use a strategy that fits this prediction for asymmetric contests. Agile gibbons' responses to competitors did not change with encounter group size. Instead, agile gibbons most frequent reaction was to flee from approaching siamangs. In primates, injuries as a consequence of HA are extremely rare. Nevertheless, agile gibbons were at risk of serious injury during the most intense encounters with siamangs. The perceived risk of escalating HA against siamangs, therefore, is likely greater than any potential payoff. Agile gibbons' reactions could reflect both unequal body size and prior knowledge of siamang group size and composition, regardless of the number of individuals present during an encounter. Moreover, agile gibbons were never observed to form coalitions against siamangs during agonistic encounters. This contrasts with carnivore communities, where subordinate species use cooperative defense to displace individual large-bodied competitors (Fuller and Kat 1990). If the outcome of encounters are predictable and uni-directional (as reported here), then game theoretical models also predict that subordinate species should favor strategies to avoid dominant species (Maynard Smith 1982). Accordingly, agile gibbons often reacted to approaching siamang groups by freezing in dense vegetation until siamangs travelled out of sight. It is possible that typical resting behavior could have been mistaken for avoidance behavior. However, the distribution of observations across the active period and the low frequency of avoidance encounters during the afternoon (when peak temperatures make resting more likely) suggest this was not the case. Nevertheless, due to the possible autocorrelation of activity and spatial data, the chance occurrence of agile gibbon activities at locations with dense (i.e., concealed) vegetation cannot be ruled out and, therefore, these incidents may only be ascribed to avoidance with this limitation in mind. Through the use of passive avoidance, gibbons may reduce detection by siamangs and limit the frequency of agonistic encounters.

CONCLUSIONS

This study suggests that HA is associated with the degree of ecological similarity between the species in the study system and that the locations of interspecific encounters are primarily the result of feeding competition. Interspecific encounters tended to occur no more frequently than expected by chance; however, when these encounters did happen, they occurred non-randomly and more often in shared-food locations. Furthermore, interspecific dominance relationships, as mediated by body mass (but possibly not group size), seem to structure access to resources within the primate community at Way Canguk. Dominance relationships between siamangs and agile gibbons meet the predictions of game theoretical models, with siamangs asserting their superior RHP through aggression and agile gibbons relying on a combination of flight and avoidance. Without the opportunity to compare siamang populations allopatric from and sympatric with competing *Hylobates* gibbons, it is not possible to assess whether HA is truly adaptive in hylobatid communities (Peiman and Robinson 2010). It can be surmised, however, that siamangs successfully won access to contested resources and gained an energetic advantage over their agile gibbon competitors. For agile gibbons, daily lost energy intake may translate into cumulative fitness costs of coexistence. Thus, it is suggested that HA is a beneficial component of siamang’s interference strategy. To identify interference as the mechanism of coexistence, however, a tradeoff between interspecific dominance and foraging efficiency must also be established (Ziv *et al.* 1993). This second component will be the subject of subsequent analyses of hylobatid ecology. If agile gibbons are not found to be more-efficient foragers than siamangs, then sympatry between these hylobatids must persist through alternative mechanisms and despite intense HA.

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Table 3.1 Estimated home range sizes and interspecific home range overlap

Group	**Home range size [ha]**	**% Home range overlap**							
		***H.a.* 1**	***H.a.* 2**	***H.a.* 3**	***S.s.* A**	***S.s.* E**	***S.s.* J**	***S.s.* M**	***P.m.* 1**
***H.a.* 1**	22	---	0%	0%	0%	0%	0%	80%	59%
***H.a.* 2**	25	0%	---	1%	28%	57%	3%	0%	0%
***H.a.* 3**	25	0%	1%	---	0%	0.9%	76%	0%	0%
***S.s.* A**	30	0%	34%	0%	---	12%	2%	0%	0%
***S.s.* E**	27	0%	61%	1%	11%	---	6%	0%	0%
***S.s.* J**	20	0%	2%	61%	3%	5%	---	0%	0%
***S.s.* M**	15	55%	0%	0%	0%	0%	0%	---	64%
***P.m.* 1**	17	44%	0%	0%	0%	0%	0%	68%	---

H.a.=agile gibbons, *S.s.*=siamangs *P.m.*=mitered langurs

Table 3.2 Total numbers of interspecific encounters by species-pairs and encounter types

Species	**Agonistic**	**Vocal dispute**	**Passive avoidance**	**Neutral**	**Affiliative**	**TOTAL**
S.s. – P.m.	5	17	3	47	8	80
S.s. – H.a.	69	31	47	14	0	161
P.m. – H.a.	1	10	2	35	0	48

S.s.=siamangs, *H.a.*=agile gibbons, *P.m.*=mitered langurs

Table 3.3 Frequencies of interspecific encounters initiated and terminated by each species

Encounter species	**Initiated by**				**Terminated by**			
	n	*S.s.*	*P.m.*	*H.a.*	*n*	*S.s.*	*P.m.*	*H.a.*
S.s. – P.m.	67	0.64*	0.36	----	59	0.58	0.42	---
S.s. – H.a.	146	0.85***	----	0.15	139	0.35	---	0.65**
P.m. – H.a.	44	---	0.34	0.66*	27	---	0.37	0.63

S.s.=siamangs, *H.a.*=agile gibbons, *P.m.*=mitered langurs; Chi-square tests: *$p<0.05$, **$p<0.01$, ***$p<0.001$

Table 3.4 Observed interspecific encounter rates and 95% confidence limits (CL) compared with encounter rates predicted from an ideal gas model

Groups	*n* Encounters	Observed $\overline{x}$ rate[†]	95% CL	Predicted rate	Significant difference?
All encounter types					
S.s. E – *H.a.* 2	69	0.51	$0.31 \leq x \leq 0.71$	0.32	No
S.s. J – *H.a.* 3	64	0.51	$0.30 \leq x \leq 0.71$	0.46	No
S.s. A – *H.a.* 2	5	0.06	$-0.04 \leq x \leq 0.16$	0.08	No
S.s. M – *H.a.* 1	10	0.20	$0.08 \leq x \leq 0.33$	0.59	**Yes (lower)**
S.s. E – *P.m.* 3	19	0.41	$0.25 \leq x \leq 0.58$	0.13	**Yes (higher)**
S.s. M – *P.m.* 1	34	0.61	$0.39 \leq x \leq 0.83$	0.70	No
P.m. 3 – *H.a.* 2	29	0.27	$0.11 \leq x \leq 0.44$	0.13	No
P.m. 1 – *H.a.* 1	6	0.33	$0.16 \leq x \leq 0.49$	0.42	No
Siamang-agile gibbon encounters excluding passive avoidance					
S.s. E – *H.a.* 2	53	0.37	$0.22 \leq x \leq 0.51$	0.32	No
S.s. J – *H.a.* 3	44	0.34	$0.27 \leq x \leq 0.42$	0.46	**Yes (lower)**
S.s. A – *H.a.* 2	4	0.05	$-0.02 \leq x \leq 0.13$	0.08	No
S.s. M – *H.a.* 1	8	0.17	$0.12 \leq x \leq 0.22$	0.59	**Yes (lower)**

[†] Mean no. encounters per day from monthly means; *S.s.*=siamangs, *H.a.*=agile gibbons, *P.m.*=mitered langurs

Table 3.5 Observed and expected mean monthly percentages of interspecific encounters at shared food locations

Group-pair	**Observed % encounters**	**Expected % encounters**
S.s. M – *H.a.* 1	30.5	15.1
S.s. E – *H.a.* 2	22.2	21.4
S.s. A – *H.a.* 2	50.0	4.9
S.s. J – *H.a.* 3	39.3	20.6
S.s. M – *P.m.* 1	44.7	15.4
P.m. 1 – *H.a.* 1	25.0	6.2

S.s.=siamangs, *H.a.*=agile gibbons, *P.m.*=mitered langurs

Table 3.6 Monthly correlations (N=20) between the rate of agonistic encounters and food availabilities

	Spearman's rank correlations $r_s(P)$					
Rate of agonistic encounters*	Total fruit production	*p* value	Ripe fruits	*p* value	Young leaves	*p* value
Siamangs – mitered langurs	-0.12	0.67	0.10	0.74	-0.16	0.58
Siamangs – agile gibbons	-0.32	0.17	0.10	0.68	-0.10	0.69
Mitered langurs – agile gibbons	-0.10	0.73	-0.31	0.28	-0.38	0.18

*Encounter rate=*n* agonistic encounters/*n* observation days; total fruit production=∑monthly fruit crop scores; ripe fruits=*n* trees with ripe fruits; young leaves=*n* trees with young leaves in phenological plots (WCS unpubl. data)

Table 3.7 Cumulative daily energetic costs of encounters between siamangs and agile gibbons (*H.a.*)

		Daily energy intake [kcal]						Daily path length [m]					
		Mean		SD		*U*	*p* value	Mean		SD		*U*	*p* value
***H.a.* grp**	**Ripe fruit availability**	**Lost enc**	**Non enc**	**Lost enc**	**Non enc**	**---**	**---**	**Lost enc**	**Non enc**	**Lost enc**	**Non enc**	**---**	**---**
2	Low	574.43	630.55	273.53	314.72	55.00	0.61	849.57	924.28	107.73	393.37	35.00	0.34
2	Higher	466.54	490.84	242.57	278.43	203.00	0.90	1489.59	1279.10	627.24	553.42	203.00	0.24
3	Low	941.84	837.24	279.50	363.34	24.00	1.00	633.38	1044.40	329.33	521.49	19.00	0.06
3	Higher	779.37	638.59	349.43	323.19	94.00	0.40	1008.00	797.12	361.16	326.91	54.00	0.23

Mann-Whitney U-tests between lost encounter (Lost enc) and non-encounter (Non enc) days

Table 3.8 Summary of predictions and results

Hypotheses:	**Predictions:**	**Results:**
Set 1: Encounter outcome		
H1. Interspecific dominance based on:		
a. Body mass	Ranks: *S.s* > *P.m.* & *H.a.*	**Yes**
b. Group size	*P.m.* > *S.s.* > *H.a.*	No
Set 2: Encounter characteristics		
H2. Subordinates minimize risks of encounters with dominants.	Encounters: Dominants initiate	**Yes**
	Subordinates terminate	**Yes**
	Occur less often vs. chance	No
H3. HA increases with ecological similarity.	HA: *S.s.-H.a.* encounters > *S.s.-P.m.* encounters	**Yes**
	and > *P.m.-H.a.* encounters	**Yes**
H4. Encounter duration increases with ecological similarity.	Duration: *S.s.-H.a.* > *P.m.-H.a.* & *S.s.-P.m.*	No

Hypotheses:	**Predictions:**	**Results:**
H5. Encounter characteristics are the result of feeding competition.		
a. Locations	Encounters predominantly at shared food locations	*S.s. – P.m.*: **Yes**
		S.s. – H.a.: **Yes**
		P.m. – H.a.: No
	Agonistic encounters predominantly at shared food locations	*S.s. – P.m.*: No
		S.s. – H.a.: No
		P.m. – H.a.: **Yes**
b. Rates	Agonistic encounter rate increases, as food availability decreases	No
Set 3: Encounter costs		
H6. Encounters with ecologically similar, dominant species are costly.	Per lost encounter: increased energy expenditure	**Yes**
	decreased energy intake	**Yes**
	Cumulative daily energy: increased energy expenditure	No
	decreased energy intake	No

HA=heterospecific aggression, *S.s.*=siamangs, *H.a.*=agile gibbons, *P.m.*=mitered langurs

Fig. 3.1 95% adaptive kernel home ranges and home range overlap for focal groups of mitered langurs (*P.m.*), siamangs (*S.s.*), and agile gibbons (*H.a.*); additional groups live in the study area but are not depicted here

Fig. 3.1

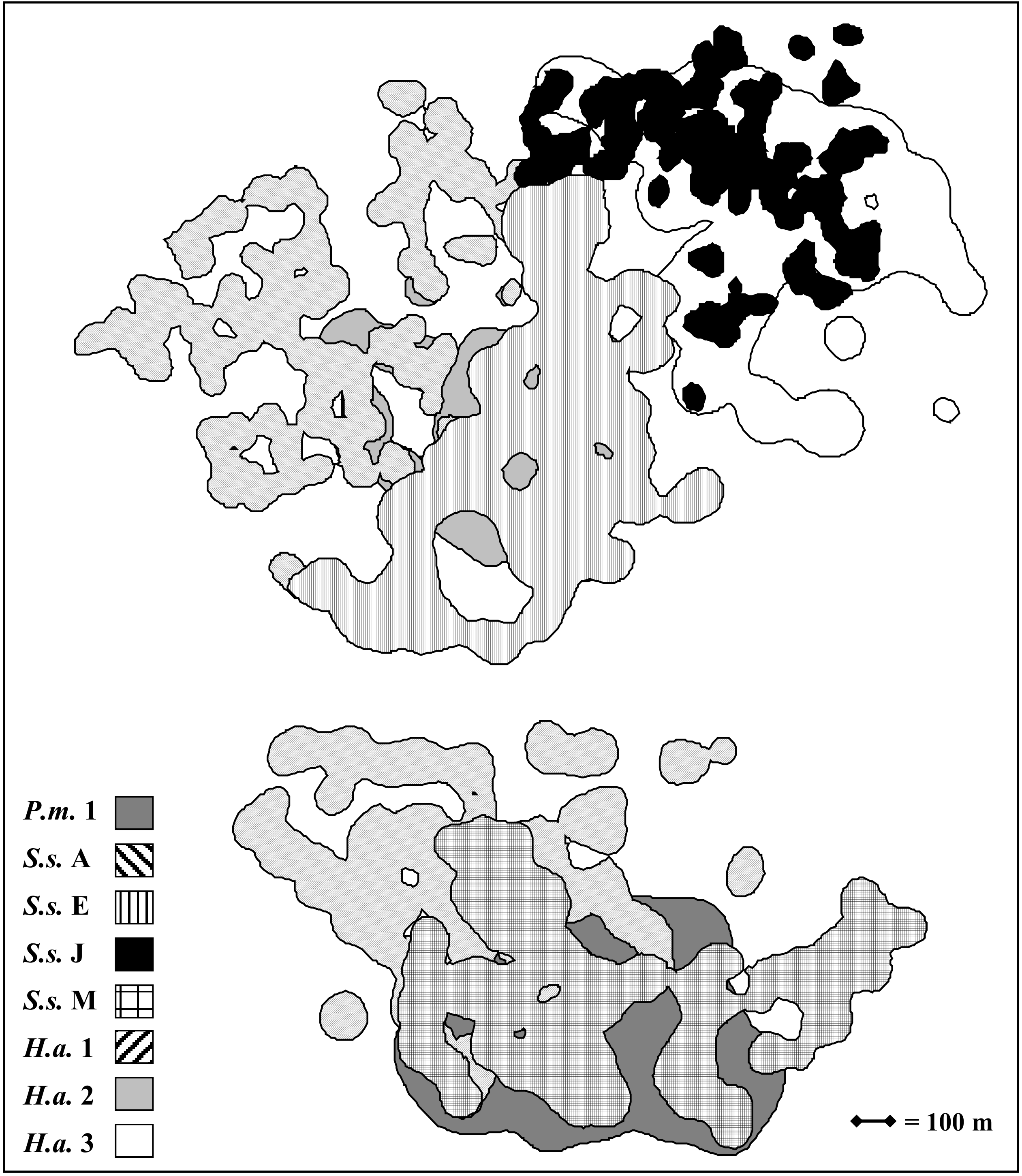


Fig. 3.2 Interspecific encounters; encounter types were not equally frequent across species-pairs; Chi-square tests of independence; ***= $p<0.001$; *S.s.*=siamangs, *H.a.*=agile gibbons, *P.m.*=mitered langurs

Fig. 3.2

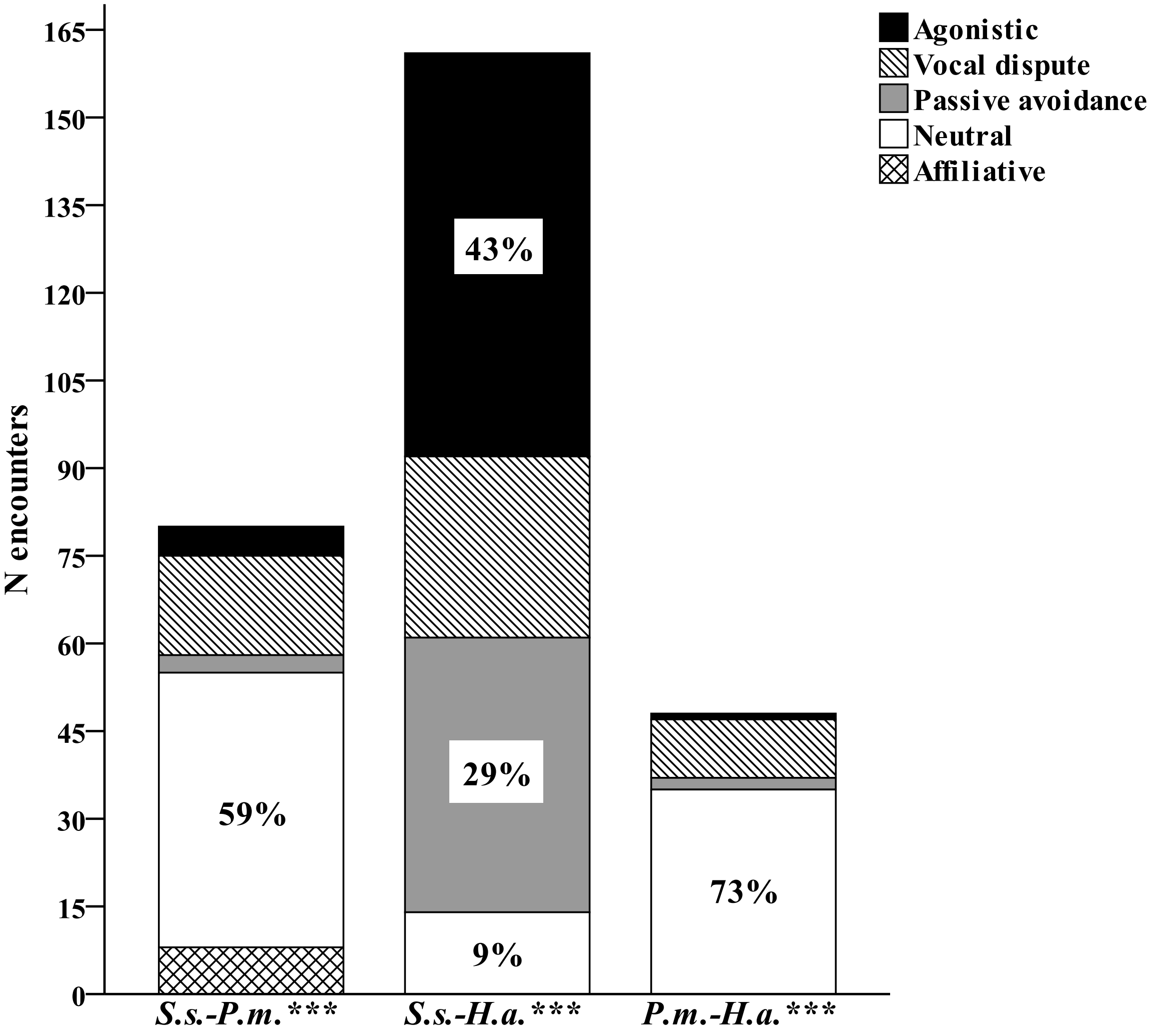
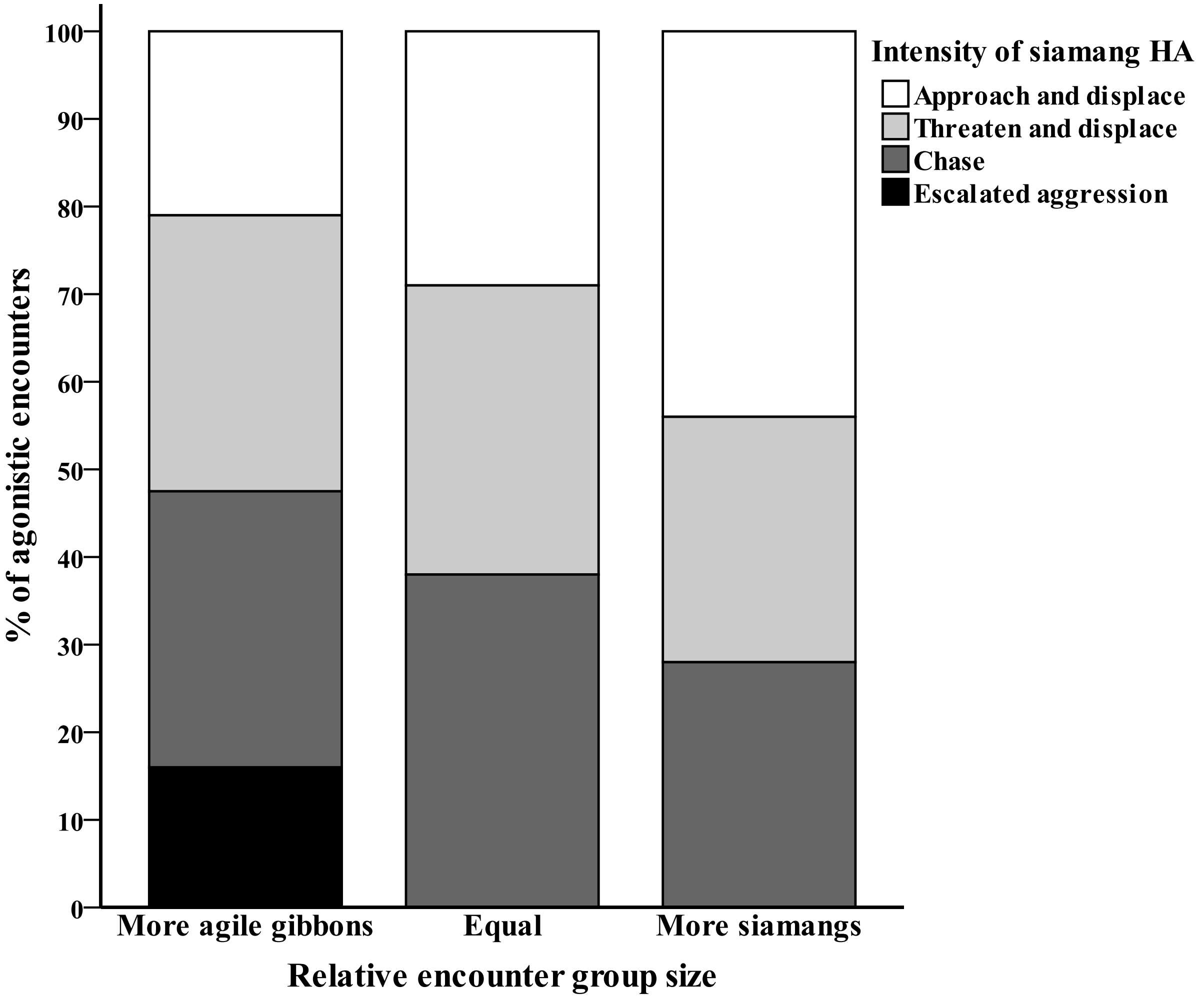

N encounters
0
15
30
45
60
75
90
105
120
135
150
165
Agonistic
Vocal dispute
Passive avoidance
Neutral
Affiliative
43%
29%
9%
59%
73%
*S.s.-P.m.****
*S.s.-H.a.****
*P.m.-H.a.****

Fig. 3.3 Intensity of HA (heterospecific aggression) siamangs directed at agile gibbons during agonistic encounters for three categories of relative encounter group size

Fig. 3.3



% of agonistic encounters
100
90
80
70
60
50
40
30
20
10
0
Intensity of siamang HA
Approach and displace
Threaten and displace
Chase
Escalated aggression
More agile gibbons
Equal
More siamangs
Relative encounter group size

Fig. 3.4 Location of interspecific encounters by species-pairs; *S.s.*=siamangs, *H.a.*=agile gibbons, *P.m.*=mitered langurs

Fig. 3.4

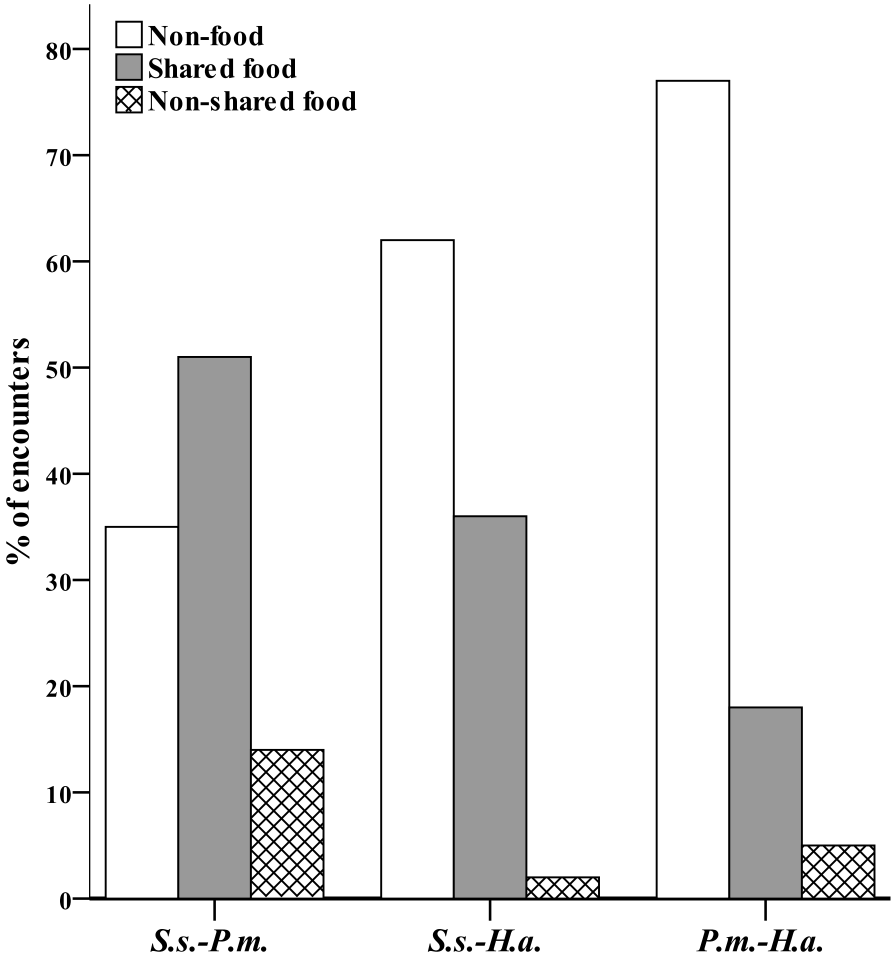
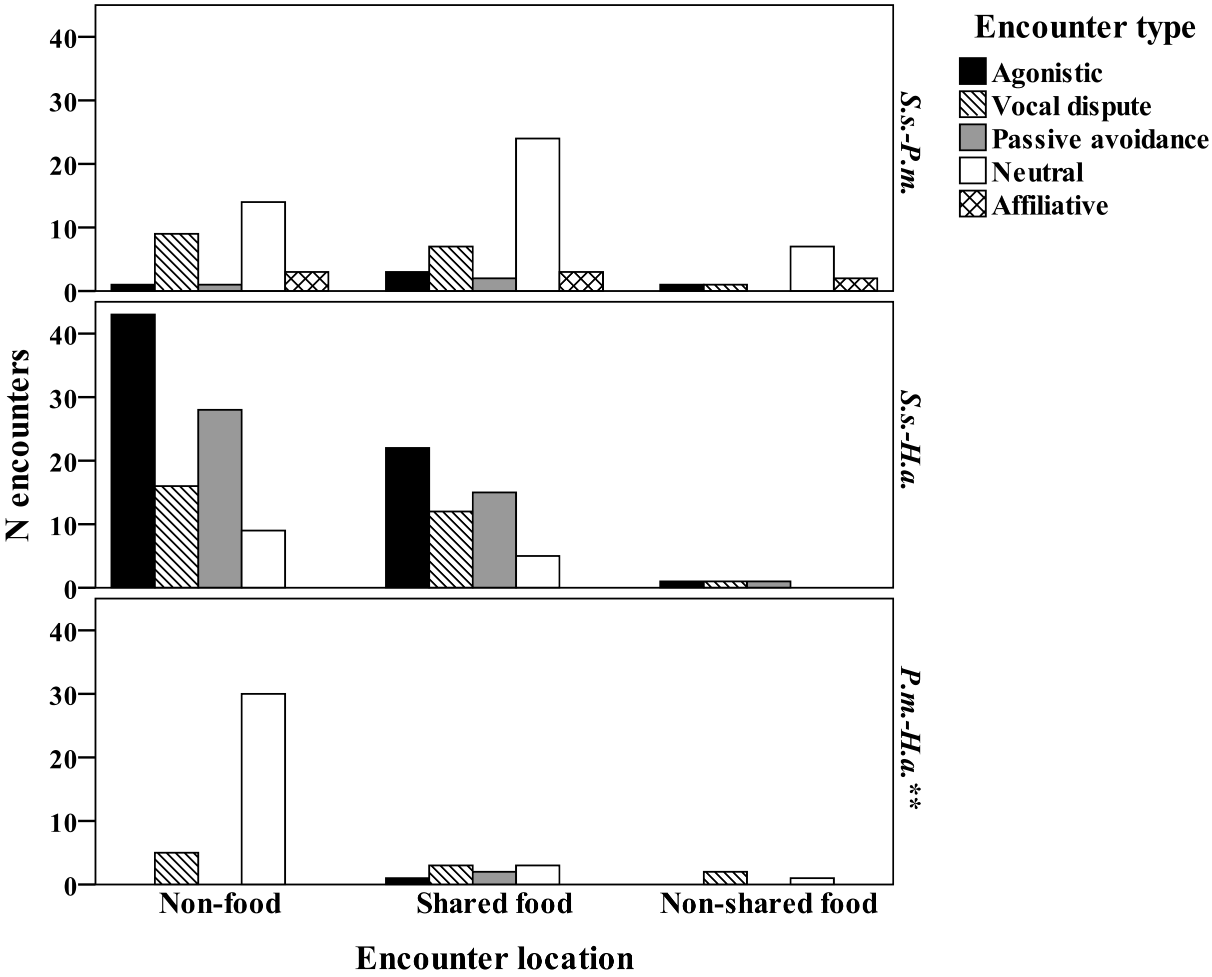

Non-food
Shared food
Non-shared food
% of encounters
80
70
60
50
40
30
20
10
0
S.s.-P.m.
S.s.-H.a.
P.m.-H.a.

Fig. 3.5 Encounter types by location per species-pairs; Chi-square tests of association; **= $p<0.01$; S.s.=siamangs, H.a.=agile gibbons, P.m.=mitered langurs

Fig. 3.5



Encounter type
Agonistic
Vocal dispute
Passive avoidance
Neutral
Affiliative
N encounters
0
10
20
30
40
S.s.-P.m.
S.s.-H.a.
P.m.-H.a.**
Non-food
Shared food
Non-shared food
Encounter location

Chapter 4
Fugitives or competition refuges? Mechanisms of coexistence in two hylobatid species

ABSTRACT

Competition between ecologically-similar species may be reduced through a tradeoff between dominance and efficiency accessing heterogeneously-distributed resources. Although dominant species can monopolize any given patch, subordinate species may still access unoccupied patches. It has been hypothesized that subordinate species may persist either 1) as fugitives by more rapidly utilizing renewed patches or 2) by relying on competition refuges (i.e., lower-quality resources of the same type or species). Either strategy may promote coexistence, but will increase travel costs or decrease energy intake or both for subordinates, depending on their foraging strategy. I investigated these mechanisms in sympatric siamangs (*Symphalangus syndactylus*, 4 groups) and agile gibbons (*Hylobates agilis*, 2 groups) living at Way Canguk, Sumatra. In this system, siamangs have been found to dominate agile gibbons in encounters that are aggressive and energetically costly. Data were collected from September 2008 to October 2009 on feeding patch characteristics and use (*n*=3,978 feeding bouts; *n*=269 all-day follows) and activity budgets (*n*=2,486 focal hours). The location, size and yield of all patches, as well as feeding bout durations were recorded, and activity budgets were calculated.

Results suggested that agile gibbons are not fugitive species, but instead use competition refuges in the system at Way Canguk. Contra fugitive predictions, agile gibbons 1) did not feed earlier in the morning than siamangs (Chi-square: $p>0.05$), and 2) fed in larger, but less productive patches, 3) for shorter durations, and 4) used fewer patches daily than siamangs

(Nested ANOVA: $p<0.05$). Additionally, 5) agile gibbons did not spend a higher percentage of time traveling than siamangs (Nested ANOVA: $p>0.05$). In support of the competition refuge hypothesis, agile gibbons fed: 1) in lower quality patches (fewer feeding minutes, lower productivity), 2) at lower intakes and 3) for shorter bout durations, and spent a higher percentage of time resting than siamangs (Nested ANOVAs: $p<0.05$). Along with minimizing energy expenditure, agile gibbons high inactivity is likely shaped by avoidance of dominant siamangs. Considerations of alternative mechanisms of coexistence suggest that, in addition to divergent foraging strategies, sympatry of siamangs and agile gibbons may be locally unstable and may persist due to differences between species in larger-scale habitat adaptations (e.g., source-sink population dynamics).

INTRODUCTION

In systems where dominance relationships are asymmetrical and interactions between ecologically-similar species are aggressive (e.g., Tannerfledt et al. 2002; Berger 2007; Watts and Holekamp 2009), subordinate species may persist through adaptive foraging strategies (Morse 1974; Schoener 1983). These strategies allow individuals of subordinate species to meet energy requirements, while minimizing the likelihood of risky encounters with dominant species. In heterogeneous habitats, individuals of dominant species gain priority of access to resources, but cannot occupy all patches at any one time. Thus, individuals of subordinate species still have opportunities to access unoccupied, high-quality resources and/or may switch to lower-quality resources, so that coexistence is maintained by dividing individual resources spatio-temporally (Horn and MacArthur 1972; Levin 1974; Slatkin 1974). Two possible mechanisms have been proposed for coexistence in these types of systems; subordinate species 1) are fugitive species or 2) use competition refuges. Unlike traditional niche partitioning, coexistence under each of these mechanisms requires patches of varying successional stages, as well as tradeoffs between competitive ability and movements to available patches (e.g., efficiency accessing feeding patches; Roxburgh et al. 2004).

Although developed (Hutchinson 1951) and predominantly employed to understand extinction and colonization of habitats by sessile organisms (e.g., marine invertebrates - Dayton 1973; terrestrial plants - Marino 1991; Turnbull et al. 1999), the fugitive species hypothesis may be extended to competition over renewable food patches among mobile species. Even if they always lose encounters with dominants, fugitive species may survive by more rapidly reaching and exploiting renewed food patches than dominant species. In such systems, both species use the exact same patches, but subordinate species access these resources first and consume as much as possible before being displaced by the dominant species. For example, competitively inferior species of spiders (Marshall et al. 2000) and parasitic mites (Downes 1991) were found to persist with dominant species through more efficient exploitation of unoccupied patches of prey and hosts respectively. Furthermore, subordinate redtail monkeys reached and exploited fruiting trees earlier in the morning than dominant blue monkeys and mangabeys (Waser and Case 1981). Mobile fugitives are expected to have higher energy expenditure than dominant competitors (i.e., spend a higher proportion of time traveling). If fugitive species are unable to compensate for these costs, then their foraging strategy should result in a lower energy balance compared to their dominant competitors.

Alternatively, rather than being fugitives, subordinate species may use competition refuges. To explain persistence of predator-prey systems, Hassell and May (1973) proposed that prey species seek out predator refuges (i.e., areas with reduced predation pressure). In the context of interspecific competition, subordinate species may use lower-quality resources as competition refuges and, thereby, avoid encounters with dominant species that are more likely to occur at higher-quality patches (discussed in Durant 1998). By subsisting in competition refuges, competitively-inferior species may survive by increasing inactivity to minimize energy expenditure, as well as to avoid detection by and encounters with groups of the dominant species. Compared with dominant competitors, individuals dependent on competition refuges should, therefore, spend a higher proportion of time resting. Competition refuges are expected to be lower quality resources than those used by dominant species, including resources that are 1) smaller or less productive (e.g., tamarin monkeys – Terborgh and Stern 1987; dung beetles - Horgan 2005), 2) more dispersed (e.g., tamarin monkeys – Terborgh 1983; Terborgh and Stern 1987; cheetahs - Durant 1998; gerbils - Abramsky et al. 2001; dung beetles - Horgan 2005), and 3) less protected (e.g., intertidal crabs - Navarrete and Castilla 1990). It is sufficient if resources fit at least one of these categories to function as competition refuges. In such systems, morphological and physiological constraints may prevent dominant species from accessing certain resources. For example, larger-bodied species may be less adept at accessing food items located on small branches (e.g., Fleagle and Mittermeier 1980). While reliance on competition refuges may reduce encounter rates, it may lead to reduced birth rates and/or increased mortality if the subordinate species cannot achieve a neutral or positive energy balance (Navarrete and Castilla 1990; Durant 1998).

Here I investigate these mechanisms of coexistence for two ecologically-similar hylobatid species, the siamang (*Symphalangus syndactylus*) and the agile gibbon (*Hylobates agilis*), living at Way Canguk, Sumatra. Interspecific territoriality does not occur between siamangs and *Hylobates* gibbons (Raemaekers 1978; pers obs), and these species overlap broadly across spatial and dietary niches: both use upper levels of the canopy (Raemaekers 1977;

MacKinnon and MacKinnon 1980), prefer the flesh of acidic, pulpy fruits and ripe figs (Gittins and Raemaekers 1980; Ungar 1995; Palombit 1997; Marshall 2004; Elder 2009), and use the same types of fallback resources (Palombit 1997; Marshall 2004; Lappan 2009a; Harrison and Marshall 2011). In fact, dietary overlap was found to be higher between species than between same-species groups at the study site (unpubl. data). There are clear dominance relationships between sympatric hylobatids. At Way Canguk (Chapter 3) the much heavier siamangs (adult female=10.7 kg) were found to win 98% of decided encounters with agile gibbons (adult female= 5.8 kg; Smith and Jungers 1997). Furthermore, the majority of these encounters were initiated by siamangs, encounters were frequently agonistic (including dangerous incidents of escalated aggression), and encounters were energetically costly for losing groups (Chapter 3). Long-term demographic data suggest that agile gibbons are at a disadvantage at Way Canguk. Compared with sympatric siamangs in this system, agile gibbons have lower population density, higher infant and juvenile mortality, longer interbirth intervals (IBIs), and lower birth rates (O'Brien et al. 2004; O'Brien and Kinnaird 2011). Furthermore, the reproductive performance of agile gibbons at Way Canguk (IBI= 3.8 years) is low compared to several other hylobatid populations (Table 4.1; reviewed in O'Brien and Kinnaird 2011), including congeneric species living allopatrically from siamangs in both similar (e.g., *H. albibarbis* in Kalimantan) and more seasonal, less productive forests (e.g., *H. lar* in Thailand). Average IBIs for agile gibbons at Way Canguk fall within the range of IBIs reported for *H. lar* living sympatrically with siamangs in northern Sumatra (Table 4.1). In contrast, with an IBI of 2.6 – 2.8 years (O'Brien et al. 2003; Lappan 2008), the rate of reproduction in the sympatric siamangs is among the fastest for hylobatids (Table 4.1). Thus, for agile gibbons at Way Canguk the costs of coexistence may be high relative to siamangs.

Despite the costs of interference competition imposed by siamangs, agile gibbons are hypothesized to persist in this system either by 1) acting as fugitive species or 2) using competition refuges. Due to their lower body mass, agile gibbons have lower travel costs and lower absolute energy requirements than siamangs (Fleagle 1976; 1980; Raemaekers 1984). Theoretically, therefore, agile gibbons should be better adapted for a fugitive species strategy. If agile gibbons are fugitives, then (compared with siamangs) they should have 1) equal size, but more productive feeding patches (i.e., use the same patches as siamangs, but when yields are higher), 2) earlier first feeding bouts, 3) higher food intake rates, 4) higher rates of feeding patch use (i.e., more patches per day), 5) longer feeding bouts, and 6) higher percentages of time spent traveling. Alternatively, agile gibbons may prioritize avoiding dangerous encounters with siamangs and, therefore, use feeding resources that are competition refuges. In that case, agile gibbons should have 1) lower quality feeding patches (i.e., different patches from siamangs, but of the same species and with either smaller size or lower productivity), 2) lower food intake rates, 3) lower rates of feeding patch use (i.e., fewer patches per day), 4) shorter feeding bouts, and 5) higher percentages of time spent resting.

MATERIALS AND METHODS

Study site

This study was conducted at Way Canguk Research Area (5° 39’ S, 104° 24’ E, 50 m a.s.l.), Bukit Barisan Selatan National Park, Sumatra, Indonesia. Way Canguk, which is managed by the Indonesian Ministry of Forestry and the Wildlife Conservation Society Indonesia Program (WCS-IP), includes 900 ha of primary lowland rain forest within a 3,568 km^2 protected area, and a grid of 105 km of trails at 200 m intervals (O'Brien et al. 2004). During the study the mean annual temperature was 28° C and annual rainfall ranged from 2,492 to 4,549 mm (mean=3,354 mm; WCS IP unpubl. data, 2007-2009).

Data collection

From September 2008 to October 2009, teams of two to three observers collected data on activity and feeding during all-day follows of four siamang (1,516 contact hours) and two agile gibbon (1,051 contact hours) groups. When additional assistants were available, either two focal groups or two focal individuals from the same group were followed simultaneously. A total of 269 all-day follows were completed, comprising 161 siamang days and 108 agile gibbon days. Each siamang group had two adult males, one adult female, and two to three immature individuals, while each agile gibbon group included one adult male, one adult female, and zero to one immature individual. In contrast with monogamous agile gibbon groups, siamang groups at Way Canguk are frequently polyandrous (Lappan 2005; Lappan 2009b). Thus, the compositions of the focal groups are typical for the study populations. Each focal group was observed for a minimum of three consecutive days per month. Focal individuals included all adult siamangs (8 males and 4 females) and agile gibbons (2 males and 2 females). After one hour, focal individuals were rotated to ensure that all individuals were sampled evenly across the active period.

Activity data. Instantaneous focal sampling was used for one-hour protocols with one-minute intervals (Martin and Bateson 1993) to record the individual's general activity state (i.e., traveling, resting, feeding, social, and singing defined below). Data were collected for a total of 2,486 focal hours, including 1,585 hours for siamangs and 901 hours for agile gibbons. Focal hours exceeded contact hours for siamangs due to occasional simultaneous follows of two individuals. Activity budgets were later assessed from these focal data. Five mutually exclusive activities were used: 1) *traveling* included directed movement (i.e., brachiating, climbing, bipedal walking and leaping), 2) *resting* was inactive and/or stationary behavior (excluding intra-group social interactions), 3) *feeding* was the preparation and/or intake of any food item (including figs, fruits, seeds, flowers, foliage, shoots, stems, petioles, and invertebrates), 4) *social* comprised intragroup interactions (i.e., grooming, agonistic, and sexual behaviors), and 5) *singing* was the production of calls. Because of the nature of the predictions, in the following, only traveling, resting and feeding activities were considered.

Feeding behavior. A feeding bout was defined operationally as the total number of minutes an individual fed continuously, including pauses in feeding of less than 10 minutes (2,817 bouts for siamangs and 1,161 bouts for agile gibbons). Feeding recorded during instantaneous focal samples was used to determine the times of arrival to and exit from feeding patches, as well as starts and stops in feeding for each individual. The beginning of the first feeding bout of a given day was recorded during all-day follows for each focal group.

Observers opportunistically assessed ingestion rates by counting the number of food items eaten by adult individuals per minute of feeding time for each food item. Ingestion rates were recorded when the focal individual was clearly visible, such that exact numbers of individual fruits, flowers, leaves, or shoots could be counted as they were picked and masticated. Only items fully masticated and swallowed were included in ingestion rates.

Feeding patch characteristics. A patch was defined following Chapman (1988) as an aggregation of food allowing for uninterrupted feeding activity by an individual. A patch was most often an individual tree, but could also be a patch of continuously-connected lianas of the same species and stage of food production. During each bout, patch height was recorded with a laser range finder and patch diameter was visually estimated to the nearest meter. The percentage of a patch covered by food items was visually estimated during each feeding bout as measure of patch productivity.

Food samples. At the end of each contact period (3-4 days per group each month), the observers returned to collect samples of all food items observed to be eaten by focal individuals. Each fresh sample was weighed prior to drying, reweighing, and packing it for nutritional analyses (detailed in Chapter 2). Fresh and dry weights for each food item (i.e., part of the same maturity per plant species) were repeated across individual samples (minimum sample sizes=20 different individuals/distinct food item) and a mean was calculated to represent masses per item. Samples were dried at low heat (40° C) in a gas-powered oven that I constructed in the field.

Data analyses

Feeding patch yield was defined as the percentage of the crown covered by food items (i.e., patch productivity) relative to estimated patch volume. Due to the unavailability of data on crown depth, patch volume was calculated from measurements of patch diameter and (instead of crown depth) total height. To minimize the potential overestimations of patch volume, a parabolic shape (which has a low shape multiplier) was assumed for all calculations; patch volume = patch diameter^2 x patch height x 0.3927 (Coder 2000).

To compare feeding rates between siamangs and agile gibbons, mean ingestion rates (i.e., N food items/min) were calculated for the same food items for each primate species. Mass data from nutritional samples were used to calculate the mass ingested (i.e., N grams dry mass/min). A Wilcoxon signed-ranks test (Siegel and Castellan 1988) was used to compare observed intake rates between siamangs and agile gibbons for matched pairs of food items consumed by both species.

Because food intake rates scale with body mass (BM; Shipley et al. 1994), larger-bodied species should ingest a higher mass per unit time than smaller-bodied species. Maximum intake rate (I=g dry matter/min) was found to scale as $BM^{0.71}$ across a diverse sample of mammalian herbivores, including two monkey species (Shipley et al. 1994) and as $BM^{0.9-1.0}$ in primates alone (Nakagawa 2008). Siamangs, therefore, should be able to masticate more food, faster than smaller-bodied gibbons. This was found to be the case for the intake rates of sympatric siamangs and lar gibbons (*Hylobates lar*) for one food item in Malaysia (Raemaekers 1979) and six food items in northern Sumatra (Grether et al. 1992; Nakagawa 2008). Thus, to control for the effect of body mass on food intake, Wilcoxon signed-ranks tests (Siegel and Castellan 1988) were also used to compare observed intake (i.e., mean intake per primate species per food item) with expected maximum intake (here: max rate=$BM^{0.90}$). Based on each hylobatid species' body mass (Smith and Jungers 1997), maximum expected rates are 8.44 g dry matter/min for siamangs and 4.87 g dry matter/min for agile gibbons.

For all remaining parameters, daily values were averaged over each month, and these mean values were used as the units of measurement for all subsequent analyses. Mixed model nested ANOVAs (Sokal and Rohlf 1995) were used to determine whether siamangs and agile gibbons significantly differed for each parameter. In these designs, species was a fixed factor and group was a random factor nested within species. In addition to testing for interspecific differences in these parameters, results for differences between conspecific groups are given for comparison. To meet the assumptions of normality, residuals were checked for skewness and kurtosis; data on feeding times, bout lengths, and patch yields were log transformed, while data on activity budgets and rates of feeding patch use were square-root transformed. Statistical tests were conducted using STATISTICA 7 and SPSS Statistics 17.0 at an alpha level of 0.05.

RESULTS

Feeding patch characteristics

Feeding patch yield. Siamangs and agile gibbons used feeding patches with similar yields (Fig. 4.1; Nested ANOVA: $F(1,68)=0.13$, $p>0.05$), containing on average 1,960 m^3 ($\sigma=2,298$ m^3) and 2,240 m^3 ($\sigma=2,759$ m^3) of food respectively. Furthermore, there were no differences in patch yields between conspecific groups (Nested ANOVA: $F(4,68)=1.39$, $p>0.05$).

Feeding patch dimensions. Hylobatid species diverged in the dimensions of their feeding patches. Compared with siamangs, agile gibbons used feeding patches that were taller ($\bar{x}=29$ m vs. $\bar{x}=33$ m; Fig. 4.2; Nested ANOVA: $F(1,74)=8.34$, $p<0.01$), as well as wider in diameter ($\bar{x}=14$ m vs. $\bar{x}=16$ m; Fig. 4.3; Nested ANOVA: $F(1,74)=7.17$, $p=0.06$).

Feeding patch productivity. Despite their larger size, feeding patches used by agile gibbons were less productive compared with siamangs' feeding patches; agile gibbon fed in patches with an average of 30% ($\sigma=14.21\%$) of the crown covered with food, while siamangs utilized patches with 36% ($\sigma=12.14\%$) mean productivity (Fig. 4.4; Nested ANOVA: $F(1,69)=4.52$, $p<0.05$).

Feeding patch use

First feeding bouts. Siamangs and agile gibbons did not differ in the timing of first feeding bouts (Fig. 4.5; Nested ANOVA: $F(1,61)=2.76$, $p=0.18$; siamangs: $\bar{x}=$6:40; $\sigma=25.04$ min, agile gibbons: $\bar{x}=$6:56; $\sigma=36.13$ min), while differences in first feeding times among conspecific groups reached a statistical trend (Fig. 4.5; Nested ANOVA: $F(4,61)=2.19$, $p=0.08$).

Feeding intake rates. Complete data necessary for calculating intake rates were available for 41 food items (Table 4.2) eaten by both siamangs and agile gibbons. Intake rates were numerically higher for siamangs ($\bar{x}$ =2.99; σ=2.48 g dry matter/min) than for agile gibbons ($\bar{x}$ =2.11; σ=3.59 g dry matter/min). Furthermore, hylobatid species significantly differed in food intake rates for matched pairs of the same food items (Fig. 4.6; Wilcoxon signed-ranks test: z=-3.83, p<0.001). For the majority of food items (32/41), agile gibbons fed at lower rates than siamangs (Table 4.2); on average, agile gibbon rates were 83% of siamang rates. Furthermore, siamangs fed at higher rates than agile gibbons across food types (Fig. 4.7), more rapidly consuming the majority of non-fig fruit (72%), fig (91%), flower (100%), and leaf, petiole, and shoot (75%) species used in matched comparisons.

Siamangs' intake rates (median=1.41 g dry matter/min) significantly differed from their expected maximum rate (Fig. 4.6; Wilcoxon signed-ranks test: z=-4.87, p<0.001). For 85% of items, siamangs fed at rates lower than predicted by body mass. Similarly, agile gibbons' observed (median=1.25 g dry matter/min) and expected maximum intake rates significantly differed (Fig. 4.6; Wilcoxon signed-ranks test: z=-4.74, p<0.001). Agile gibbons fed at significantly lower rates than their expected maximum for the majority of food items (90%).

Rate of feeding patch use. On average, siamangs used a higher number of feeding patches each day ($\bar{x}$ =13.03; σ=5.03 patches/day) than did agile gibbons ($\bar{x}$ =6.94; σ=2.99 patches/day; Fig. 4.8; Nested ANOVA: $F(1,77)$=18.72, p=0.02). Significant differences were also found in the rates of feeding patch use among groups of conspecifics (Nested ANOVA: $F(4,77)$=2.58, p=0.04).

Duration of feeding patch use. On average, each agile gibbon individual fed for 14 minutes per bout (σ= 5.01 min), while each siamang individual fed for 21 minutes (σ=7.16 min;

Fig. 4.9; Nested ANOVA: $F(1,75)=27.33$, $p=0.009$). Taking interspecific differences in group size into account (mean group sizes: siamangs=4.75; agile gibbons=2.00 individuals, excluding infants), the disparity between siamangs and agile gibbons in total feeding minutes available per patch is magnified. On average, feeding patches provided siamangs 21 minutes x 4.75 individuals=99.75 individual feeding minutes, while agile gibbons were provided only 14 minutes x 2 individuals= 28 individual feeding minutes.

Activity budgets

Significant differences were found in the activity budgets of hylobatid species (Fig. 4.10). While siamangs and agile gibbons spent about equal proportions of time traveling ($\bar{x}=15.12$ %; $\sigma= 3.71$% and $\bar{x}=14.36$ %; $\sigma= 4.82$% respectively; Nested ANOVA: $F(1,71)=0.21$, $p>0.05$), agile gibbons spent a lower proportion of time feeding than siamangs ($\bar{x}=16.44$ %; $\sigma=5.77$ % vs. $\bar{x}=34.50$ %; $\sigma=9.02$ %; Nested ANOVA: $F(1,71)=27.04$, $p=0.007$) and a higher proportion of time resting than siamangs ($\bar{x}=49.33$ %; $\sigma=4.82$ %; vs. $\bar{x}=36.67$ %; $\sigma=7.33$ %; Nested ANOVA: $F(1,71)=15.49$, $p=0.02$). Significant variation was also found among groups within a species in the percentages of time spent traveling (ANOVA: $F(4,71)=4.22$, $p=0.004$), feeding (ANOVA: $F(4,71)=4.80$, $p=0.002$), and resting (ANOVA: $F(4,71)=4.42$, $p=0.003$).

DISCUSSION

Are agile gibbons fugitives?

Results for feeding patch characteristics ran against expectations for fugitive species (Table 4.3). Feeding patches used by siamangs and agile gibbons were indistinguishable in yield, while patches used by agile gibbons were larger and less productive than siamangs' patches. Additionally, agile gibbons did not feed earlier than siamangs in the morning, and had lower food intake rates, lower rates of feeding patch use, and shorter feeding bouts. Also contrary to the predictions (Table 4.3), agile gibbons did not spend a higher percentage of time travelling than siamangs. Thus, agile gibbons did not meet any of the expectations for fugitive species examined.

The crux of the fugitive species hypothesis is that competitively inferior species should be better dispersers (reviewed in Roxburgh et al. 2004). In the case of mobile species, this would mean that individuals of subordinate species should reach and exploit renewed patches before dominant species. Agile gibbon feeding behavior and activity budgets suggest that they did not access recently-renewed patches prior to siamangs. Instead, differences between hylobatid species in the dimensions and productivity of their feeding patches are evidence that agile gibbons, in fact, fed in different, less productive resources from siamangs. Furthermore, the low food intake rates of agile gibbons relative to the dominant siamangs suggests that they could not compensate for their lower resource holding potential by consuming a large amount prior to being displaced. Thus, agile gibbons did not benefit from exploitation competition (scramble *sensu* van Schaik 1989) and, most likely, do not function as fugitives in the system at Way Canguk. Unlike typical fugitive species, agile gibbons spent more time resting each day than their dominant, siamang competitors. Instead of foraging as much as possible, agile gibbons may minimize energy expenditure; agile gibbons were found to frequently become inactive within dense vegetation when reacting to approaching siamang groups at Way Canguk (Chapter 3). These findings suggest that agile gibbon’s survival at Way Canguk may depend on being as quiet as possible for as long as possible to minimize detection by siamangs and at the same time to conserve energy. Additional analyses are needed to confirm that siamangs and agile gibbons are not using the same, exact feeding patches during a given recovery period (i.e., the same continuous period as a patch is depleted). For example, simultaneous follows of overlapping siamang and agile gibbon groups could be used to determine whether the majority of each species' feeding patches are used to the exclusion of the other.

Do agile gibbons use competition refuges?

In contrast with the results for fugitive species, my findings were consistent with agile gibbon's use of competition refuges. Agile gibbons differed from siamangs in directions predicted by this hypothesis for nearly all parameters assessed (5/6), including patch characteristics, patch use, and activity budgets (Table 4.3). As lower quality feeding patches, competition refuges may have lower yields and/or be more dispersed (Durant 1998). Compared with siamangs, agile gibbons used feeding patches that were larger, but lower in productivity and for fewer individual feeding minutes (i.e., individual feeding bouts were shorter and groups smaller for agile gibbons). Therefore, like subordinate species in other systems (Durant 1998; Abramsky et al. 2001; Horgan 2005), agile gibbons may use a set of lower-quality feeding patches as competition refuges. For larger-bodied siamangs living in larger groups, using these patches may not be profitable and, therefore, agile gibbons may avoid direct interactions during feeding bouts. In further support of the competition refuge hypothesis (Table 4.3), agile gibbons fed at lower intake rates, used fewer feeding patches each day, and spent more time resting. Agile gibbons also had shorter feeding bouts than siamangs, but fed in patches equal in yield with those used by siamangs. At the end of agile gibbons' feeding bouts, therefore, these patches should not have been depleted. Potentially, after meeting energy requirements, agile gibbons may stop foraging and avoid risky encounters with dominant siamang groups by leaving feeding patches prior to detection and remaining inactive. If agile gibbons can decrease their energy expenditure without decreasing net energy below a level sufficient for survival and reproduction, then their use of competition refuges could facilitate stable coexistence with siamangs. Alternatively, however, if competition refuges are either too small or too poor in quality, then the subordinate species could have a lower energy balance than the dominant species, and coexistence would be unstable. In the long-term, subsistence on competition refuges would then eventually lead to the local extinction of the subordinate species.

Additional mechanisms of coexistence

Although divergence between siamangs and agile gibbons in their responses to resource heterogeneity may help to promote their coexistence, additional mechanisms may contribute to this system's stability. Under one such mechanism, coexistence can be at pseudo-equilibrium. That is, during occasional events, the dominance hierarchy is reversed and individuals of the typically dominant species undergo greater decreases in fitness than individuals of the formerly-subordinate species (Nee and May 1992; Neuhauser 1998). For example, El Niño Southern Oscillation (ENSO) events result in periods of extreme drought in the tropics. The severe ENSO of 1997, coupled with human activities, produced forest fires throughout Southeast Asia (Cochrane 2003), including parts of Way Canguk. Census data from Way Canguk revealed that five siamang groups disappeared from the burnt area, while, at the same time, one agile gibbon group colonized intact forest adjacent to the burnt area (O'Brien et al. 1998). Due to their lower population densities and potentially superior ability to move into newly-available areas, agile gibbon populations may be less severely impacted by, or even gain from, periodic habitat destruction compared with the more numerous, typically-dominant siamangs.

While this may seem a possible mechanism of coexistence for hylobatids, following the ENSO of 1997, agile gibbons did not seem to gain any advantage over siamangs that increased their reproductive fitness. Hylobatids have very slow life histories, including a prolonged period of juvenility resulting in delayed maturation (Reichard et al. 2012). On average, lar gibbons (a species closely-related to agile gibbons) dispersed at 7-8 years of age (Brockelman et al. 1998) and were 10.5 years old at the time of first reproduction (Reichard et al. 2012). Therefore, in the 11 years between the ENSO and the current study at Way Canguk, each agile gibbon group could at most rear one individual to adulthood. Furthermore, by 2003 siamang groups had re-populated burnt areas (O'Brien et al. 2003), and were maintaining high population density in the study area (O'Brien and Kinnaird 2011). In contrast, agile gibbon populations declined from nine to five groups (22 to 14 individuals) and all new groups (*n*=2) found to colonize the study area disappeared between 1998 and 2009 (O'Brien and Kinnaird 2011).

Alternatively, competing species may maintain local sympatry (but not stable coexistence) if they differ in larger-scale habitat adaptations. Source-sink models posit that individuals of one species may immigrate from a favorable source population into a sink population, where they are at an adaptive disadvantage (e.g., Pulliam 1988; Amarasekare and Nisbet 2001). Interspecific differences have been proposed for siamangs and agile gibbons in the relationship between elevation and population density (discussed in Chapter 2; O'Brien et al. 2004). If agile gibbons at Way Canguk are, in fact, a sink population, then their persistence would only be possible through periodic repopulation from a nearby source. Potential source populations lie to the north of Way Canguk, where agile gibbons live at higher densities in contiguous hill and submontane forests (O'Brien et al. 2004). Results presented here suggest that the sympatric hylobatid community at Way Canguk may not be a stable one and that source/sink dynamics could offer a plausible explanation for their coexistence.

FUTURE PERSPECTIVES

Future work could focus on more directly assessing if agile gibbons avoid detection by siamangs during feeding bouts. Specifically, one could evaluate whether agile gibbons select lower-quality feeding patches or if they switch to these locations only following displacements from contested, higher-quality feeding patches. In systems where interspecific competition is intense and individuals of one species consistently win encounters, ecological game theory (Maynard Smith 1982) predicts that subordinate species should favor strategies that increase avoidance of the dominant species. Agile gibbon's overall behavior seems to fit this model. Although agile gibbons continue to survive alongside competitively-superior siamangs, their reliance on lower-quality feeding patches, potentially lower energy balances, and the energetic costs of lost interspecific encounters (Chapter 3), should result in long-term fitness consequences. Agile gibbon's low population density and high infant mortality at Way Canguk (O'Brien et al. 2004; O'Brien and Kinnaird 2011) seem to corroborate this conclusion..

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Table 4.1 Interbirth intervals in hylobatids (IBIs shown in years after surviving offspring)

Species	Population	Mean IBI	*n*	Reference
H. lar	Khao Yai, Thailand	3.40	22	(Reichard et al. 2012)
H. lar	Ketambe, Sumatra, Indonesia	3-4*	3	(Palombit 1995)
H. lar	Kuala Lompat, Malaysia	10.00	1	(Chivers and Raemaekers 1980)
H. albibarbis	Kutai, Kalimantan, Indonesia	3.20	5	(Mitani 1990)
H. agilis	Way Canguk	3.83	4	(O'Brien and Kinnaird 2011)
S. syndactylus	Way Canguk	2.6**; 2.8^ 2.81	?† 5	(O'Brien et al. 2003) (Lappan 2008)
S. syndactylus	Ketambe, Sumatra, Indonesia	≥3.17	3	(Palombit 1995)
S. syndactylus	Kuala Lompat, Malaysia	4.38	2	(Chivers and Raemaekers 1980)

*Mean IBI=2.21 for one female (*n*=2 intervals) and minimum IBI=4-5 years for a second female (*n*=1 interval); **Groups occupied home ranges outside of 1997 El Niño burn areas; ^groups occupied home ranges in areas which were partially burned; †24-37 census groups/year over 4 years

Table 4.2 Food items used in interspecific comparisons of hylobatid intake rates; *S.s.*=siamangs; *H.a.*=agile gibbons

Food item no.	**Family**	**Genus**	**Species**	**Part**	**Maturity**	**Mean intake [g dry matter/min]**	
						S.s.	***H.a.***
1	*Annonaceae*	*Saccopetalum*	*horsfeldii*	Fruits	Ripe	9.64	8.05
2	*Moraceae*	*Antiaris*	*toxicaria*	Leaves	Young	0.40	0.38
3	*Moraceae*	*Antiaris*	*toxicaria*	Fruits	Ripe	3.17	1.27
4	*Fabaceae*	*Dialium*	*platysepalum*	Leaves	Young	1.56	0.63
5	*Clusiaceae*	*Garcinia*	*parvifolia*	Fruits	Ripe	4.48	2.74
6	*Moraceae*	*Ficus*	*altissima*	Figs	Ripe	9.50	2.03
7	*Moraceae*	*Ficus*	*caulocarpa*	Figs	Ripe	0.88	0.66
8	*Moraceae*	*Ficus*	*kerkhovenii*	Figs	Ripe	1.40	1.25
9	*Moraceae*	*Ficus*	*drupaceae*	Figs	Ripe	10.49	7.20
10	*Moraceae*	*Ficus*	*elastica*	Figs	Ripe	4.44	2.72
11	*Moraceae*	*Ficus*	*sp*	Figs	Ripe	1.25	1.10
12	*Moraceae*	*Ficus*	*sp*	Figs	Ripe	1.14	1.11
13	*Moraceae*	*Ficus*	*sp*	Figs	Ripe	1.76	2.13
14	*Moraceae*	*Ficus*	*sp*	Petioles	----	1.01	0.88
15	*Moraceae*	*Ficus*	*sp*	Figs	Ripe	16.68	12.86
16	*Moraceae*	*Ficus*	*stupenda*	Figs	Ripe	8.89	3.51
17	*Moraceae*	*Ficus*	*sp*	Leaves	Young	0.64	0.67
18	*Sapindaceae*	*Xerospermum*	*norohianum*	Fruits	Ripe	0.92	0.84

Food item no.	Family	Genus	Species	Part	Maturity	Mean intake [g dry matter/min]	
						S.s.	***H.a.***
19	*Moraceae*	*Ficus*	*albipila*	Figs	Ripe	3.83	2.85
20	*Annonaceae*	*Stelacocarpus*	*burahol*	Leaves	Young	1.87	1.87
21	*Annonaceae*	*?*	*?*	Fruits	Ripe	1.47	1.57
22	*Convolvulaceae*	*Merremia*	*peltata*	Shoots	Young	0.62	0.63
23	*Piperaceae*	*Piper*	*sp*	Fruits	Ripe	1.38	3.98
24	*Annonaceae*	*Mitrepora*	*polypirena*	Flowers	----	0.56	0.47
25	*Annonaceae*	*Mitrepora*	*polypirena*	Fruits	Ripe	0.75	1.12
26	*Annonaceae*	*Mitrepora*	*polypirena*	Leaves	Young	2.38	1.35
27	*Achariaceae*	*Hydnocarpus*	*gracilis*	Flowers	----	1.06	0.78
28	*Sapotaceae*	*Payena*	*acuminata*	Fruits	Ripe	9.70	6.47
29	*Anacardiaceae*	*Dracontomelon*	*dao*	Fruits	Ripe	1.41	0.91
30	*Cannabaceae*	*Celtis*	*nigrescens*	Flowers	----	0.09	0.05
31	*Cannabaceae*	*Celtis*	*nigrescens*	Fruits	Ripe	1.06	0.81
32	*Dilleniaceae*	*Dillenia*	*excelsa*	Flowers	----	2.17	1.40
32	*Theaceae*	*Adinandra*	*acuminatissima*	Fruits	Ripe	1.26	0.77
33	*Meliaceae*	*Aglaia*	*sp*	Fruits	Ripe	1.27	1.58
34	*Alangiaceae*	*Alangium*	*griffithii*	Fruits	Ripe	1.86	0.64
35	*Phyllanthaceae*	*Aporosa*	*arborea*	Fruits	Ripe	2.66	2.47
37	*Moraceae*	*Artocarpus*	*sp*	Fruits	Ripe	1.23	1.43

Food item no.	**Family**	**Genus**	**Species**	**Part**	**Maturity**	**Mean intake [g dry matter/min]**	
						S.s.	***H.a.***
38	*Ebenaceae*	*Diospyros*	*aurea*	Fruits	Ripe	1.27	1.09
39	*Annonaceae*	*Polyalthia*	*grandiflora*	Leaves	Young	3.10	1.05
40	*Annonaceae*	*Polyalthia*	*laterfolia*	Fruits	Unripe	0.23	0.16
41	*Myrtaceae*	*Eugenia*	*sp*	Fruits	Ripe	3.32	3.05

Table 4.3 Summary of predictions and results

Agile gibbons (vs. siamangs):	**H1. As fugitive species**		**H2. Use competition refuges**	
Parameter	**Prediction**	**Result**	**Prediction**	**Result**
Patch characteristics:				
Patch yield (m^3 with food)	Higher	No (equal)	Lower	No (equal)
Patch size (height & crown diameter)	Same	No (larger)	Smaller	No (larger) BUT
Patch productivity (% crown with food)	Higher	No (lower)	Lower	**Yes** (lower)*
Patch use:				
First feeding bout	Earlier	No (equal)	No prediction	----
Food intake rate (g dry matter/min)	Higher	No (lower)	Lower	**Yes** (lower)
n of feeding patches/day	Higher	No (lower)	Lower	**Yes** (lower)
Feeding bout duration	Longer	No (shorter)	Shorter	**Yes** (shorter)
Activity budgets:				
% time traveling	Higher	No (equal)	No prediction	----
% time resting	No prediction	----	Higher	**Yes** (higher)

*Patches used as competition refuges are predicted to be either smaller OR to have lower productivity.

Fig. 4.1 Log feeding patch yields by species; *line*=mean, *box*=±SE, *whiskers*=±SD; Mixed model nested ANOVA: groups nested within species; NS=*p*>0.05

Fig. 4.1

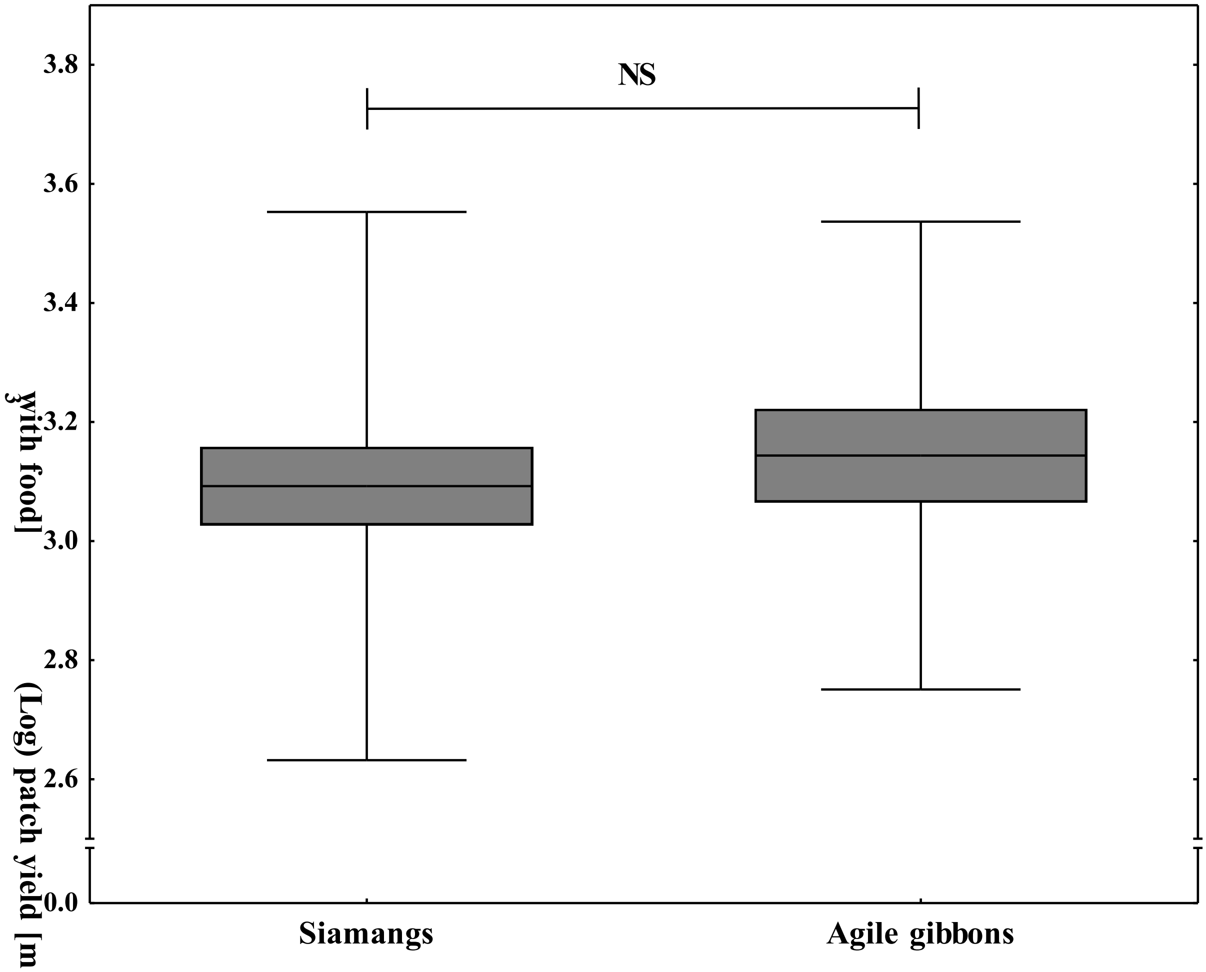

NS
3.8
3.6
3.4
3.2
3.0
2.8
2.6
0.0
(Log) patch yield [m3 with food]
Siamangs
Agile gibbons

Fig. 4.2 Feeding patch heights by siamang (*S.s.*) and agile gibbon (*H.a.*) groups; *line*=mean, *box*=±SE, *whiskers*=±SD; Mixed model nested ANOVA: groups nested within species; **=p<0.01, ***=p<0.001

Fig. 4.2

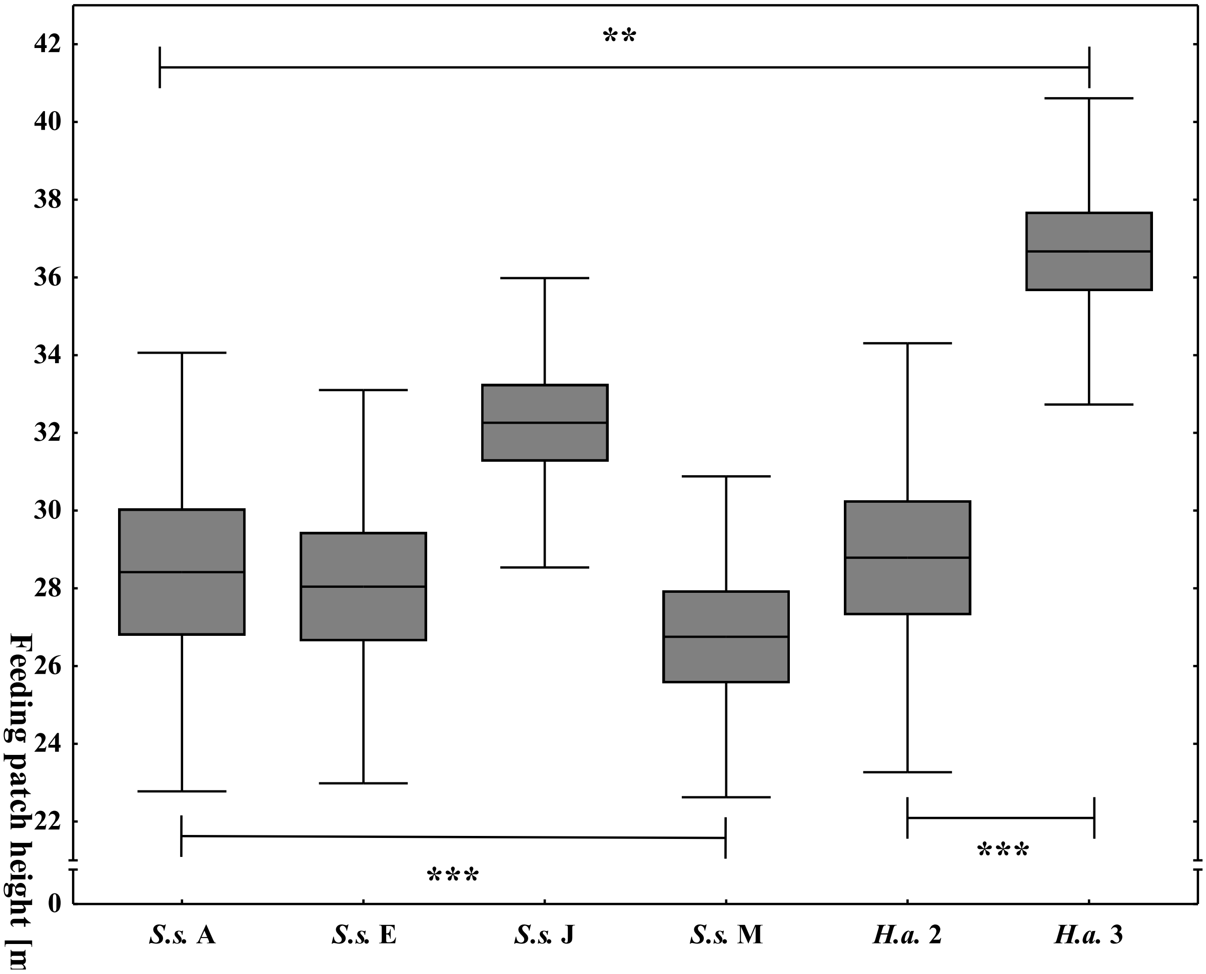
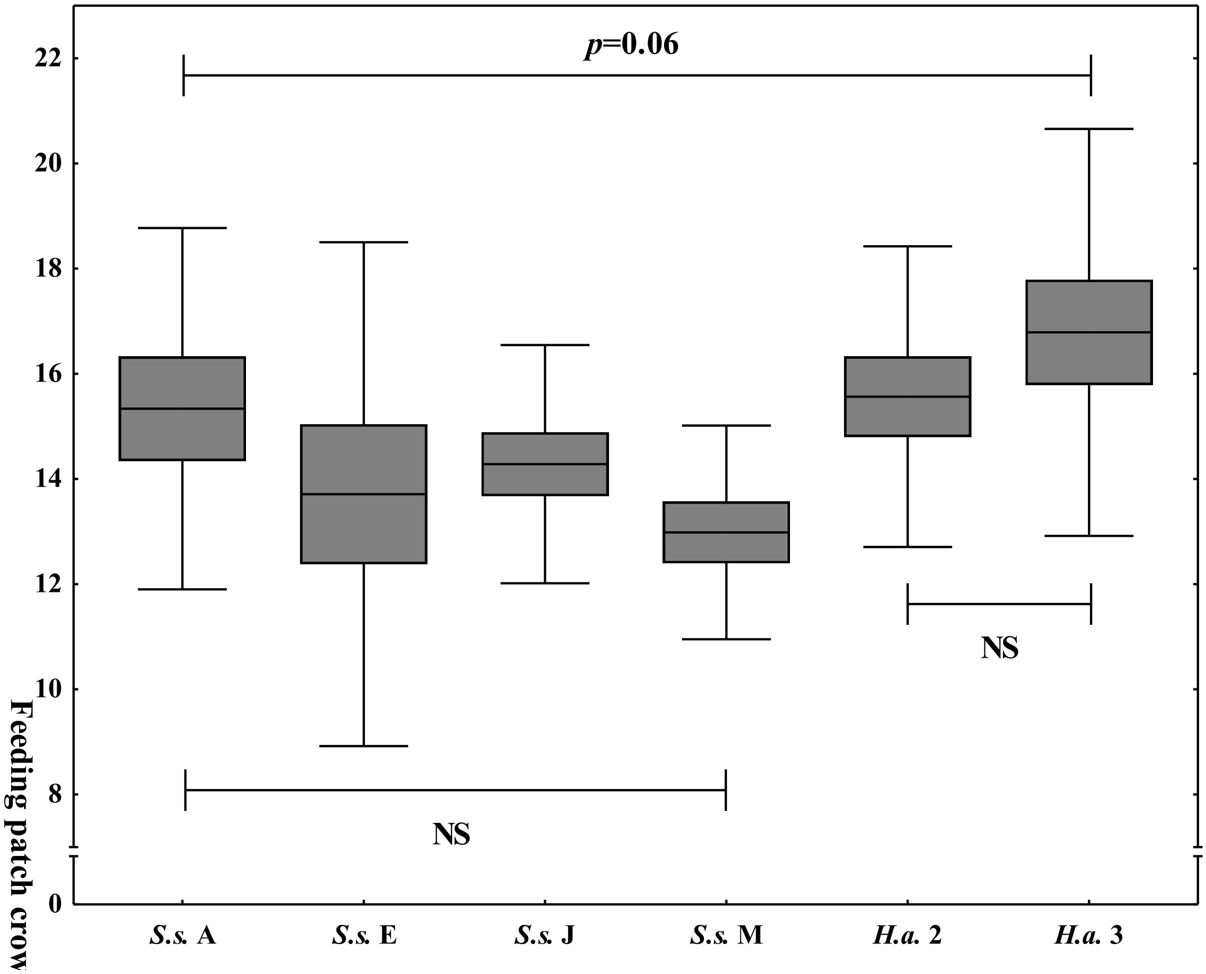

Feeding patch height [m
42
40
38
36
34
32
30
28
26
24
22
0
**
***
***
S.s. A
S.s. E
S.s. J
S.s. M
H.a. 2
H.a. 3

Fig. 4.3 Feeding patch crown diameters by siamang (*S.s.*) and agile gibbon (*H.a.*) groups; *line*=mean, *box*=±SE, *whiskers*=±SD; Mixed model nested ANOVA: groups within species; NS=p>0.05

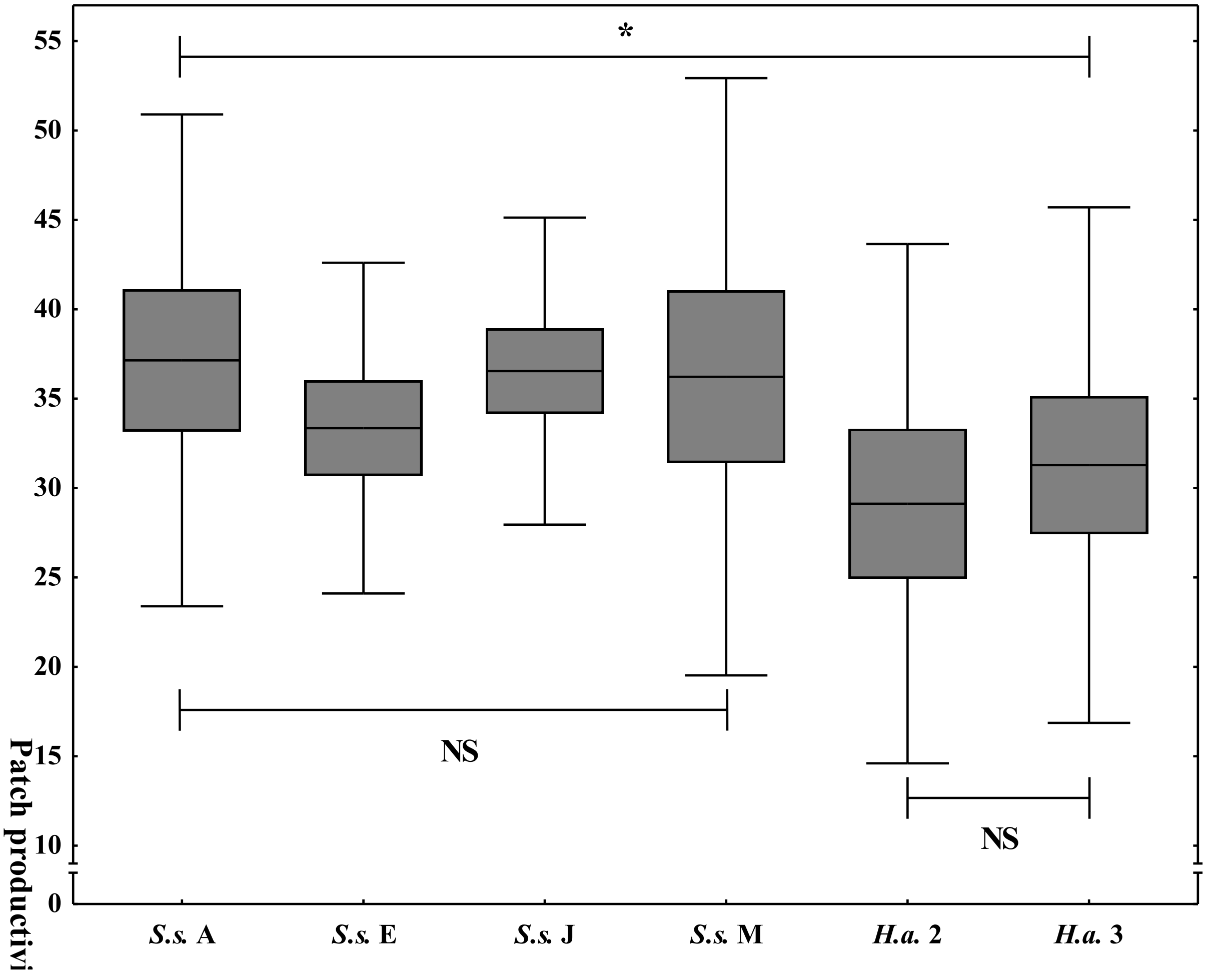
Fig. 4.3



p=0.06
NS
NS
22
20
18
16
14
12
10
8
0
Feeding patch crow
S.s. A
S.s. E
S.s. J
S.s. M
H.a. 2
H.a. 3

Fig. 4.4 Feeding patch productivity by siamang (*S.s.*) and agile gibbon (*H.a.*) groups; *line*=mean, *box*=±SE, *whiskers*=±SD; Mixed model nested ANOVA: groups within species; NS=$p>0.05$, *=$p<0.05$

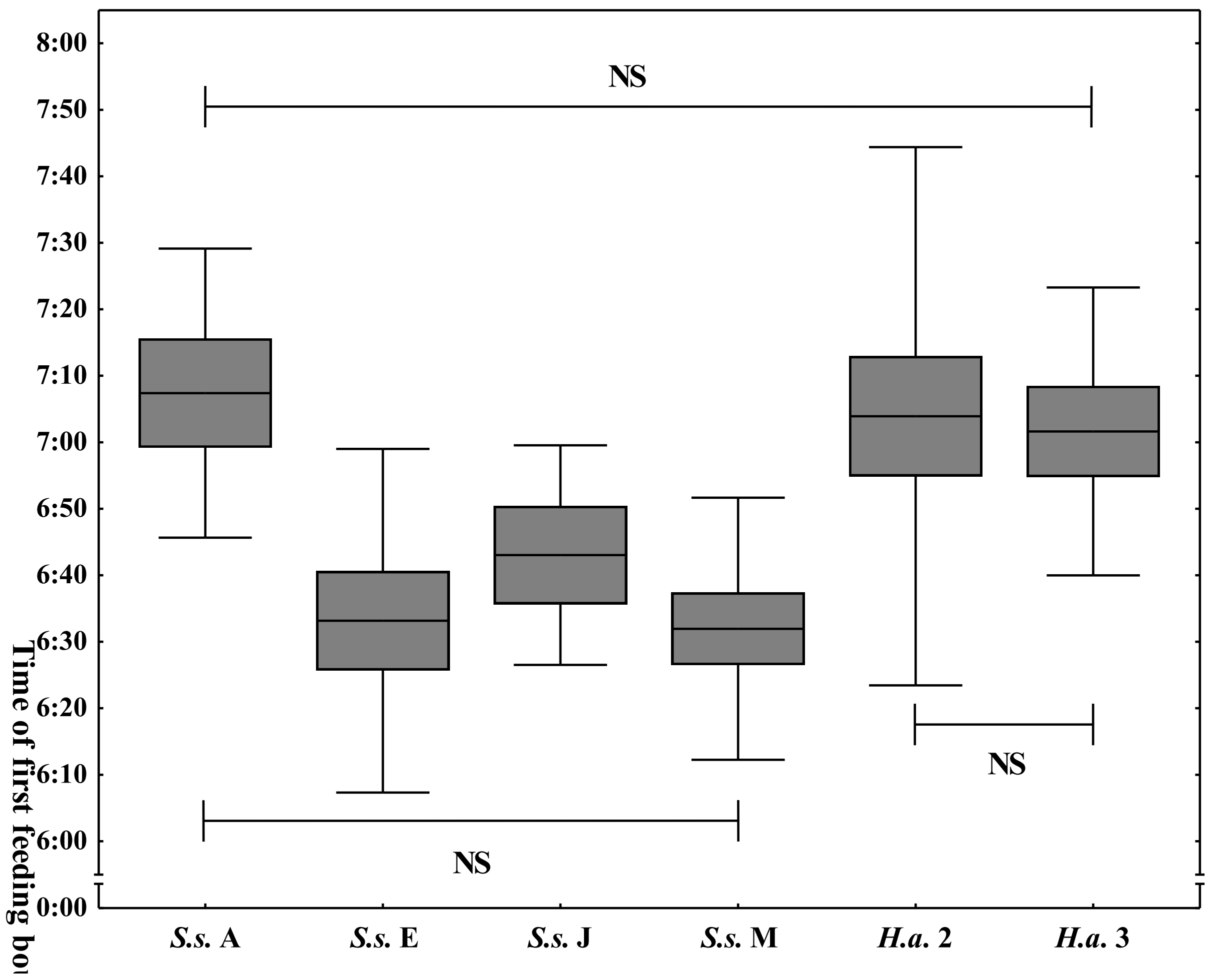
Fig. 4.4



*
55
50
45
40
35
30
25
20
15
10
0
Patch productivi
NS
NS
S.s. A
S.s. E
S.s. J
S.s. M
H.a. 2
H.a. 3

Fig. 4.5 Time of first feeding bouts by siamang (*S.s.*) and agile gibbon (*H.a.*) groups; *line*=mean, *box*=±SE, *whiskers*=±SD; Mixed model nested ANOVA: groups within species; NS=p>0.05

Fig. 4.5



8:00
7:50
7:40
7:30
7:20
7:10
7:00
6:50
6:40
6:30
6:20
6:10
6:00
0:00
Time of first feeding bo
NS
NS
NS
S.s. A
S.s. E
S.s. J
S.s. M
H.a. 2
H.a. 3

Fig. 4.6 Observed mean and expected maximum food intake rates for 41 items (detailed in Table 4.2) consumed by siamangs and agile gibbons; observed rates averaged across rates of adult individuals per primate species per food item; expected rates estimated as body mass$^{0.90}$, where siamang$_{max}$=8.44 g/min and agile gibbon$_{max}$=4.87 g/min; Wilcoxon signed-ranks tests; ***=p<0.001

Fig. 4.6

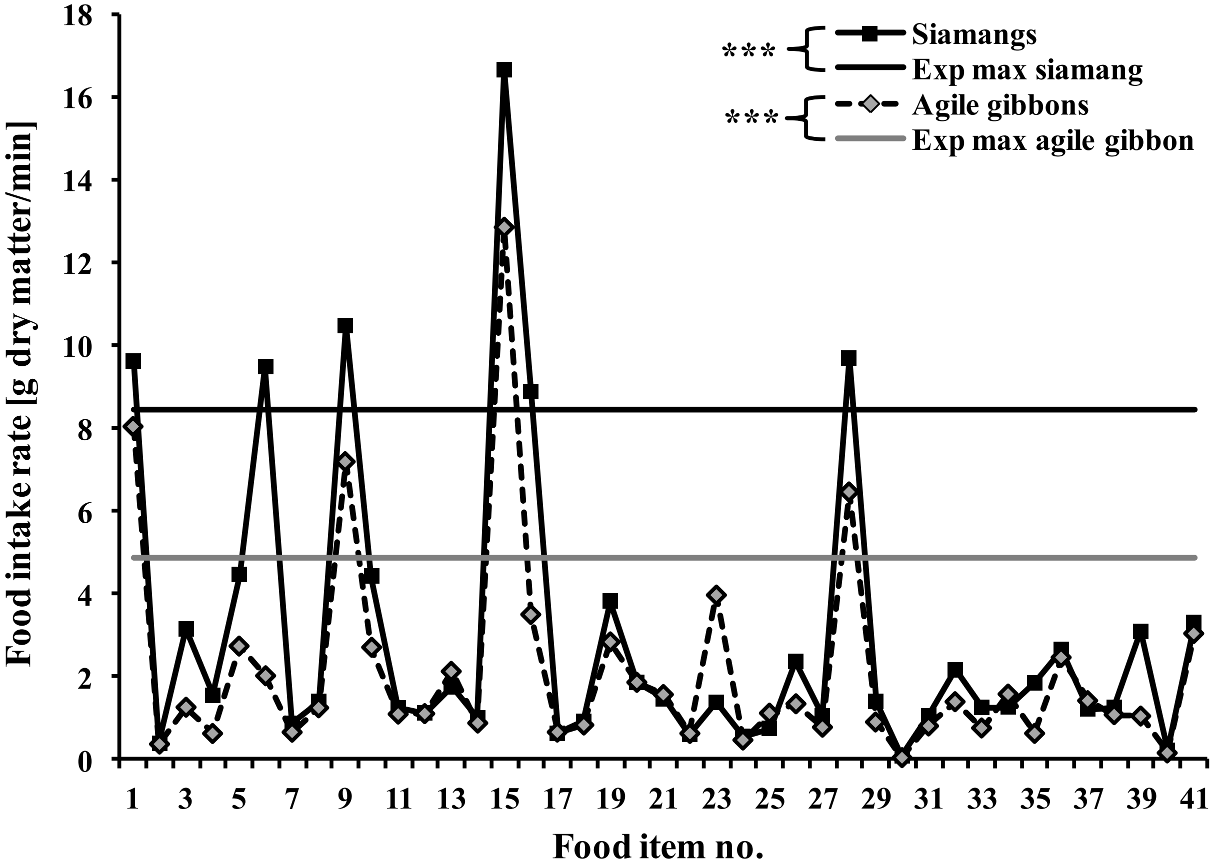
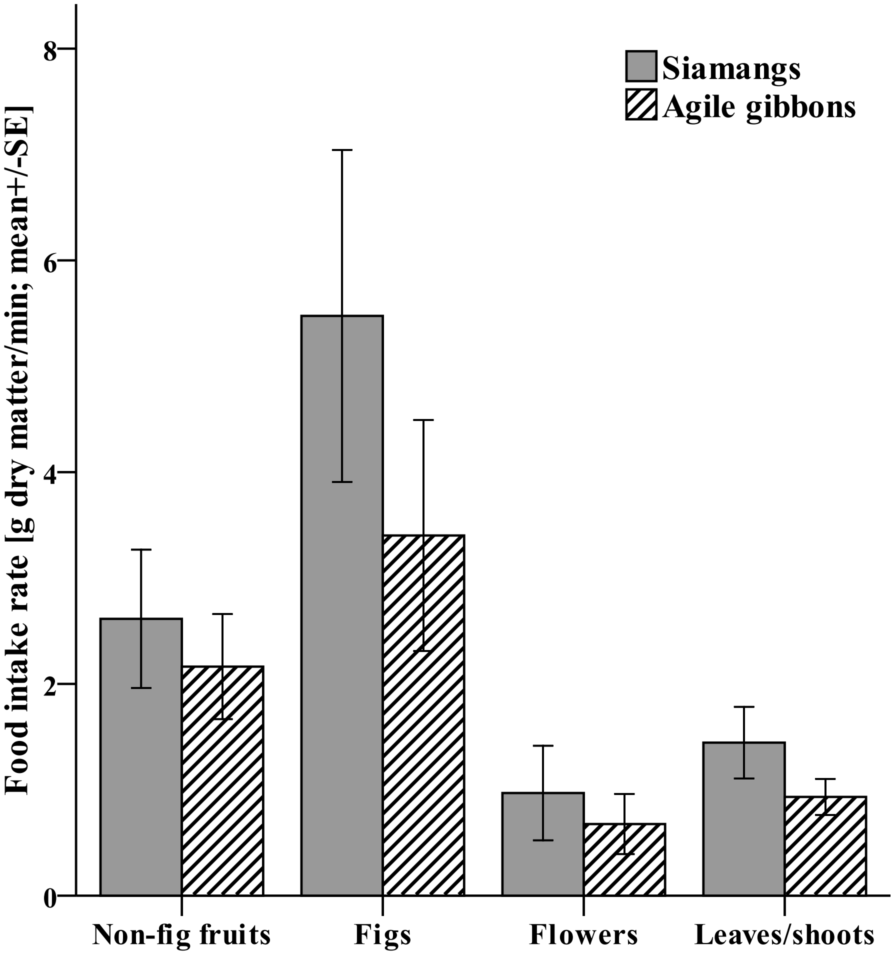

Food intake rate [g dry matter/min]
0
2
4
6
8
10
12
14
16
18
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
33
35
37
39
41
Food item no.
***
Siamangs
Exp max siamang
***
Agile gibbons
Exp max agile gibbon

Fig. 4.7 Food intake rates observed for siamangs and agile gibbons by food types

Fig. 4.7



Food intake rate [g dry matter/min; mean+/-SE]
0
2
4
6
8
Siamangs
Agile gibbons
Non-fig fruits
Figs
Flowers
Leaves/shoots

Fig. 4.8 Rate of feeding patch use by siamang (*S.s.*) and agile gibbon (*H.a.*) groups; *line*=mean, *box*=±SE, *whiskers*=±SD; Mixed model nested ANOVA: groups within species; NS=$p>0.05$, *=$p<0.05$

Fig. 4.8

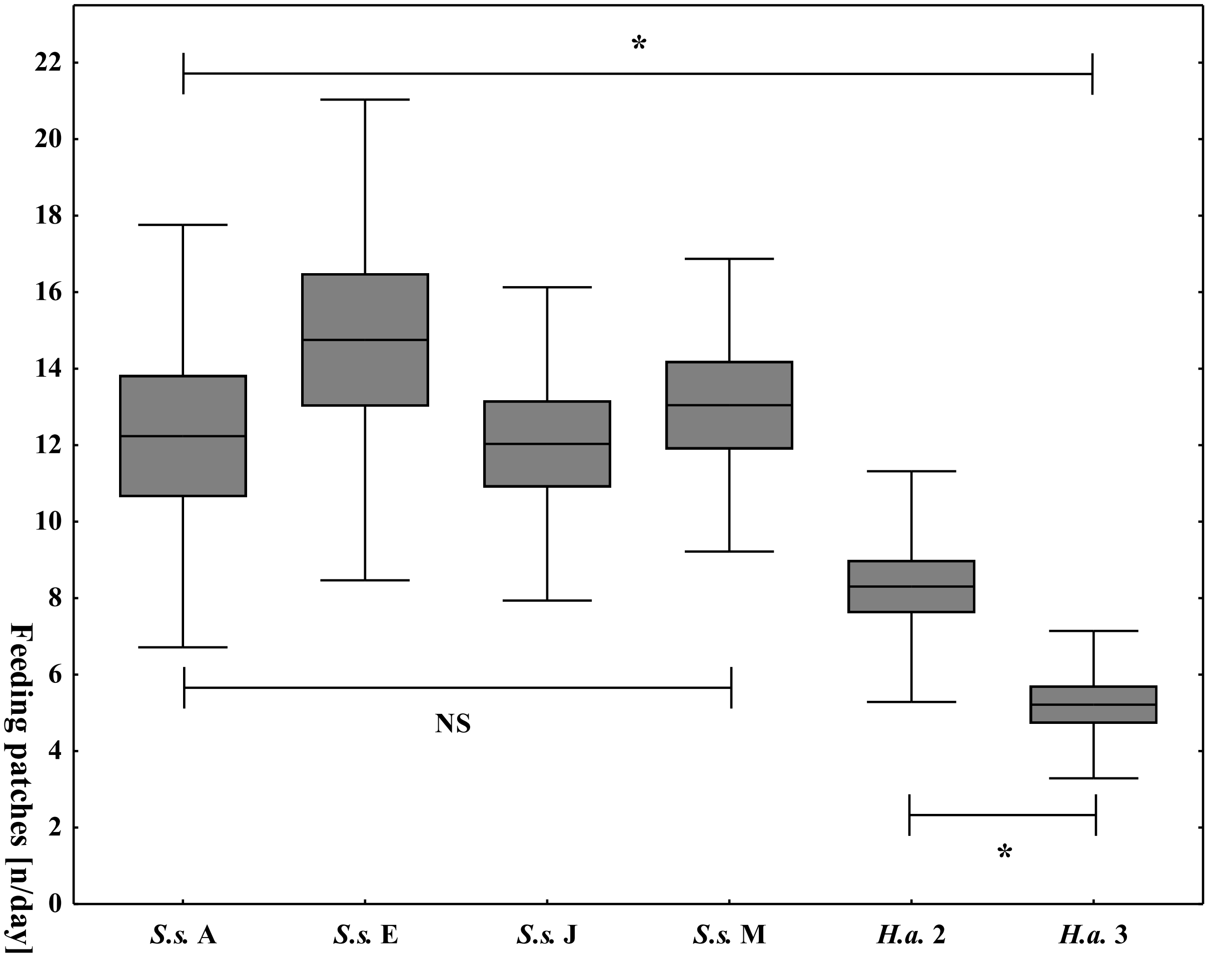
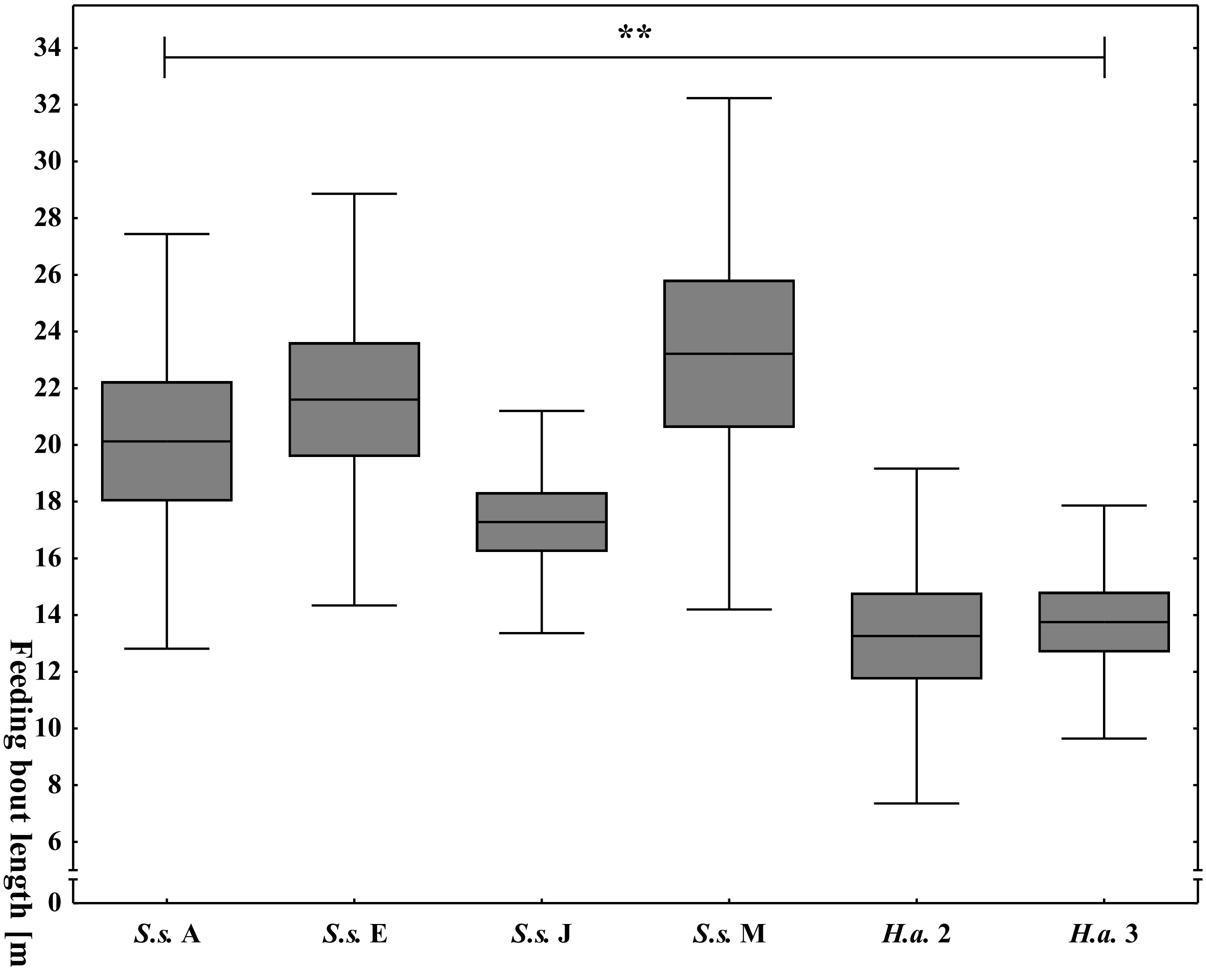

*
22
20
18
16
14
12
10
8
6
4
2
0
NS
*
Feeding patches [n/day]
S.s. A
S.s. E
S.s. J
S.s. M
H.a. 2
H.a. 3

Fig. 4.9 Feeding bout lengths by siamang (*S.s.*) and agile gibbon (*H.a.*) groups; *line*=mean, *box*=±SE, *whiskers*=±SD; Mixed model nested ANOVA: groups within species; between-species comparisons: **=*p*<0.01

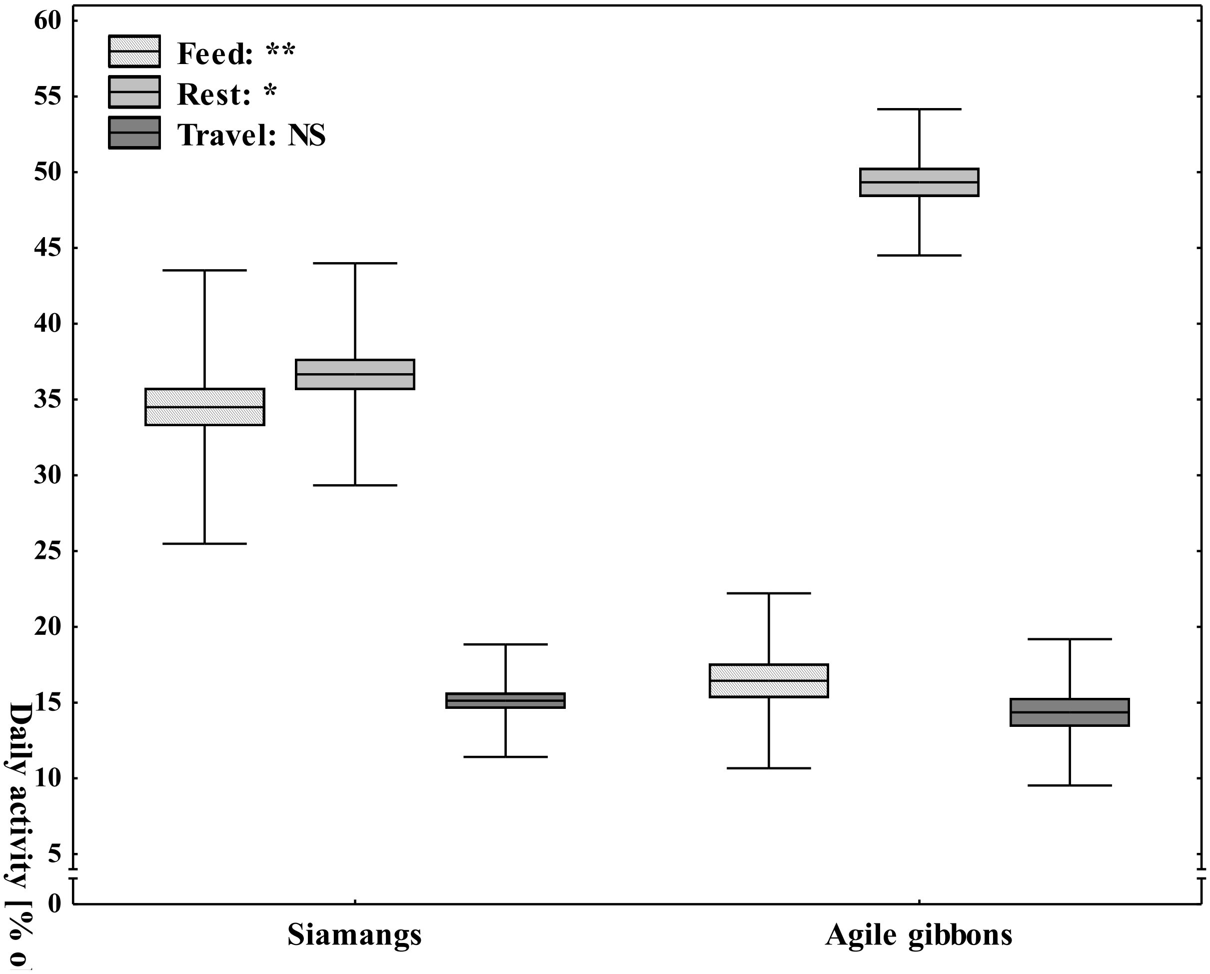
Fig. 4.9



**
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
0
Feeding bout length [m
S.s. A
S.s. E
S.s. J
S.s. M
H.a. 2
H.a. 3

Fig. 4.10 Activity budgets by species; *line*=mean, *box*=±SE, *whiskers*=±SD; Mixed model nested ANOVAs: groups within species; between-species comparisons: NS=$p>0.05$, *=$p<0.05$, **=$p<0.01$

Fig. 4.10


Feed: **
Rest: *
Travel: NS
Daily activity [% o
60
55
50
45
40
35
30
25
20
15
10
5
0
Siamangs
Agile gibbons

Chapter 5
The influences of predation avoidance and interspecific competition on sleeping strategies of three sympatric primate species

ABSTRACT

The selection of sleeping sites by diurnal animals seems to primarily reflect predation avoidance. Primates usually prefer emergent trees with large, open crowns and high locations near terminal branches, likely because they impede access for terrestrial predators and allow for their early detection. However, additional factors, such as interspecific competition may influence sleeping tree selection if subordinate species sleep closer to food, enter sleeping sites later, or exit earlier than dominant species to feed. Nevertheless, interspecific competition has rarely been considered in the selection of sleeping sites. Here I investigate how predation risk and interspecific competition may influence sleeping strategies in an Asian primate community. Data were collected from March 2008 through October 2009 on three agile gibbon groups (*Hylobates agilis*; 226 nights), four siamang groups (*Symphalangus syndactylus*; 223 nights), and one mitered langur group (*Presbytis melalophos*; 48 nights) living sympatrically at Way Canguk, Sumatra. In this system, siamangs dominate the ecologically-similar gibbons and dissimilar langurs. Consistent with predation avoidance, siamangs and langurs selected emergent trees with large, open crowns, which lacked lianas. Gibbons, on the other hand, selected significantly shorter, smaller-crowned trees and frequently slept hidden in dense foliage. Furthermore, gibbons did not sleep closer to feeding patches, enter sleeping sites later, or exit sites earlier than siamangs. To reduce the likelihood of encounters with siamangs, which were often intensely aggressive, gibbons instead may seek sleeping sites that facilitate avoidance. This study is one of

the first to suggest that interspecific dominance may exert at least as great an influence on sleeping strategies as predation avoidance.

INTRODUCTION

Sleeping sites are expected to fulfill a range of requirements, such as comfort, parasite and predator avoidance, thermoregulation, and foraging efficiency (reviewed in Anderson 1998). The majority of research into animal sleep has focused on the physiology and theoretical functions of inactivity (reviewed in Lima et al. 2005). The impact of ecological factors on sleeping strategies, however, has been largely limited to studies of primates (but see Winn and Bardach 1959; Christian et al. 1984; Clark and Gillingham 1990; Singhal et al. 2007). In diurnal primates in particular, the characteristics, location, and use of sleeping sites have been used to weigh the relative importance of factors influencing sleeping strategies.

During the night, diurnal animals contend with reduced visual acuity and are forced to spend long hours in inactivity. Thus, they are unable to detect and deter predators as efficiently as they can during the active period, and are particularly vulnerable (reviewed in Anderson 1984; 1998; 2000). It is expected, therefore, that diurnal animals should be selective when choosing their nightly sleeping sites, preferring locations that afford the best protection. Of all potential factors, predation avoidance likely exerts the greatest influence on the selection of sleeping sites because of its direct effect on survival. In fact for primates, sleeping site selection seems to be almost always consistent with predation avoidance (96% of 25 genera studied; Elder, unpublished review). Even if other factors, such as comfort, distance to feeding sites or home range defense, significantly contributed to sleeping site use, these were often in addition to predation avoidance (e.g., Phoonjampa et al. 2010) or in habitats where predation pressure had been recently reduced (Liu and Zhao 2004; Pontes and Soares 2005). Primates tend to select sites that distance them from potential predators, sleeping in large (e.g., Di Bitetti et al. 2000; Pozo 2005; Cui et al. 2006), emergent trees (review in Anderson 1998), on cliff faces (Hamilton 1982; Schreier and Swedell 2008; Zhou et al. 2009), and over water (Goodall 1962; Ramakrishnan and Coss 2001; Matsuda et al. 2010). Because they are difficult to climb, these high locations may limit access for terrestrial predators. Sleeping sites also tend to be relatively free of dense vegetation (Uhde and Sommer 2002; Rayadin and Saitoh 2009), allowing for a clear view of approaching predators and minimizing potential hiding places for ambush predators. Furthermore, individuals generally position themselves far away from the trunk (Bert et al. 1967; Gautier-Hion 1970; Hamilton 1982), which should increase the chances of early detection of approaching predators through branch vibrations.

Alternatively, smaller-bodied primate species (e.g., callitrichines) may use a cryptic strategy, choosing sleeping sites that provide the best concealment (Coimbra-Filho 1978; Zhang 1995; Day and Elwood 1999; Franklin et al. 2007). This is a strategy particularly useful against aerial predators, such as the large-bodied raptors and owls of South America and Madagascar (Hart 2007). However, the use of concealed sleeping locations (i.e., within tree holes) has not been reported for larger-bodied primates above 1.5 kg (review in Kappeler 1998).

Because many predators (e.g., pythons) also use chemical cues to detect potential prey (De Cock Buning 1983), it has been suggested that primates should minimize their olfactory presence (Hrdy 1977). In line with this argument, Reichard (1998) found that white-handed gibbons (*Hylobates lar*) used many different sleeping sites and rarely used the same sites on consecutive nights. Low consecutive use of sleeping trees has also been observed for snub-nosed monkeys (*Rhinopithecus bieti*) (Cui et al. 2006) and black-crested gibbons (*Nomascus concolor*) (Fan and Jiang 2008). The unpredictable use of sleeping trees, which should also minimize detection by predators, has been observed for the smaller, cryptic tamarin monkeys (*Saguinus sp*) (Caine 1987; Smith et al. 2007).

Besides predation avoidance, sleeping sites may fulfill additional requirements. For example, primates may select sleeping sites that offer the best physical comfort (Whitten 1982), and ultimately aid in parasite avoidance (Hausfater and Meade 1982; Largo et al. 2009) and thermoregulation (Barrett et al. 2004; Zhou et al. 2009; De Vere et al. 2010). In addition, the distance to feeding sites may influence sleeping site use (e.g., Goodall 1962; Chapman 1989; Pontes and Soares 2005). By selecting sleeping sites in close proximity to food patches, foraging efficiency is potentially maximized by reducing the costs of traveling between sleeping trees and food (di Bitetti et al. 2000). There has been speculation that between-group competition may additionally affect the selection of sleeping sites (discussed in Smith et al. 2007). However, while it has been suggested that a preference for sleeping sites located near the boundary of home ranges could assist in the early detection of incursions by neighboring groups (Day and Elwood 1999), little evidence has been found to support this hypothesis (but see Dawson 1979). In fact, by avoiding sites at the periphery of their home range, some primate species (e.g., gibbons - Reichard 1998; Phoonjampa et al. 2010) may reduce the chance of intergroup encounters.

In addition to resource defense against conspecifics, animals must also contend with between-species competition. The coexistence of ecologically-similar species in the absence of typical niche differentiation (*sensu* e.g., Brown and Wilson 1956; Schoener 1974) is likely a consequence of despotic coexistence (Morse 1971). In these systems, access to individual resources may be regulated by interspecific dominance relationships, where dominance is based on inequality in resource holding potential (RHP). Through interference competition, dominant species gain priority of access to resources over subordinate species (Morse 1971; 1974). It has been postulated, however, that it may be too energetically expensive for individuals of dominant species to exclude subordinate species from lower-quality resources (Morse 1974). This leaves room for subordinate species to subsist on these smaller, more dispersed, or less-protected resources (e.g., Navarrete and Castilla 1990; Horgan 2005). Moreover, if the location and outcome of encounters are uni-directional and predictable, then subordinate species should develop strategies to avoid dominant species (Maynard Smith 1982).

Subordinate species may minimize home range overlap with their dominant, heterospecific competitors, as has been found in avian (e.g., Murray 1971), rodent (e.g., Heller 1971), and carnivore (e.g., Harrison et al. 1989) communities. In primates, however, such interspecific territoriality has very rarely been reported (but see Tilson and Tenaza 1982). If the likelihood of surviving the night is directly linked to gaining access to safe sleeping sites (e.g., Altmann 1974), then heterospecific groups occupying largely overlapping home ranges may contest over sleeping sites, where individuals of dominant species are predicted to displace subordinate species (e.g., Navarrete and Castilla 1990; Schwab 2000). Although tropical forests are rife with vegetation, very large, emergent trees are in limited supply and are preferentially selected as sleeping sites despite their rarity (Tenaza 1974; Phoonjampa et al. 2010). Interference competition over sleeping sites, however, remains little studied.

Due to ecological similarity, individuals from both dominant and subordinate species may benefit by selecting sleeping sites in close proximity to mutually-exploited feeding patches. Regardless of rank, whichever species first accesses and depletes preferred feeding resources in the morning will gain a foraging advantage. If feeding efficiency determines sleeping site selection, then, compared to dominant species, members of subordinate species are expected to:

(1) sleep in closer proximity (albeit in less-safe sleeping trees) to feeding patches, (2) enter sleeping sites later at night, and (3) exit sleeping sites earlier in the morning.

However, in cases where interspecific aggression is intense and/or the difference in RHP is large, individuals of subordinate species may be in danger of being attacked by individuals of dominant species, independent of the context of an encounter. For example, cheetahs (*Acinonyx jubatus*), which suffer direct predation by lions (*Panthera leo*) and hyenas (*Crcocuta sp*), have been reported to facultatively alter resource use to avoid these dominant competitors (Durant 1998). In primates, it was speculated, but not tested, that titi monkeys (*Callicebus coimbrai*) may select sleeping sites that promote avoidance of predatory capuchin monkeys (*Cebus apella*) (Souza-Alves et al. 2011).

Here I investigate the relative importance of predation risk and interspecific competition in determining sleeping strategies for an Asian primate community living at Way Canguk, Sumatra. By studying sympatric species, I control for both habitat type (i.e., resource availability and forest structure) and predation pressure, both of which may influence the selection of sleeping sites. Very few previous studies have analyzed sleeping strategies in a comparative framework (Tenaza 1974); thus more rigorous tests of predation avoidance in combination with interspecific competition are warranted. This study focused on the three most common primate species living at Way Canguk: the ecologically-similar siamang (*Symphalangus syndactylus*) and agile gibbon (*Hylobates agilis*), and the dissimilar mitered langur (*Presbytis melalophos*). Hylobatids (gibbons in the genera *Hylobates* and *Symphalangus*) coexist in spite of their very similar ecologies; thus, there is a high potential for interference competition between these taxa. Both siamangs and agile gibbons are ripe fruit specialists that use figs as fallback resources (Elder 2009). By contrast, mitered langurs, with their specialized digestive anatomy (Lambert

1998) can subsist on a diet that is more fibrous and consists of a lower proportion of fruits and figs (Davies et al. 1988). In this system, langurs provide a control to evaluate the influence of interspecific competition on sleeping strategies. Despite much larger mitered langur group sizes ($\bar{x}$ =15 individuals vs. siamang $\bar{x}$ =5.5; agile gibbon $\bar{x}$ =3.0), siamangs were found to be the dominant species at Way Canguk, winning 98% and 100% of agonistic encounters over agile gibbons and mitered langurs respectively (Chapter 3). Because siamangs (adult female $\bar{x}$ =10.7 kg) are nearly twice the body mass of agile gibbons and mitered langurs (adult female $\bar{x}$ =5.8 kg and 6.5 kg respectively; Smith and Jungers 1997), they were expected to dominate both species. The high RHP of siamangs may be further augmented by the presence of two adult males in about 25% of groups at Way Canguk (Lappan 2009; O'Brien et al., 2004).

Given that, for most primates, the selection of sleeping sites reflects the avoidance of terrestrial predators, all three primate species investigated were predicted to sleep in trees that were tall, large crowned, and open (i.e., free of dense vegetation and lianas). Individual sleeping locations within trees were predicted to be high, in close proximity to terminal branches, and in open areas of tree crowns. Consecutive use of sleeping sites should be low, resulting in a high number of different sleeping sites. Sleeping site selection should further be modified by interspecific competition. (1) Through interference competition the dominant species, the siamang, should have priority of access to the highest-quality (i.e., safest) sleeping sites, while other species may have to choose from less-protected sites (if sites of the safest class are in limited supply). (2) Assuming that subordinate species avoid encounters with dominant species, it was predicted that agile gibbons would (a) sleep in closer proximity to feeding patches, (b) enter sleeping trees later, and/or (c) exit sleeping trees earlier than siamangs to profit from critical times of reduced competition in the late evening or early morning. (3) If interspecific encounters are very risky, then subordinate species should select sleeping trees that facilitate the avoidance of these costly encounters.

METHODS

Study site

Data were collected at Way Canguk Research Area (5° 39’ S, 104° 24’ E, 50 m a.s.l.) in Bukit Barisan Selatan National Park, Lampung, Sumatra. Established in 1997, the site is co-run by the Indonesian Ministry of Forestry and the Wildlife Conservation Society Indonesia Program (WCS-IP). Way Canguk includes 900 ha of primary lowland rain forest within a 3,568 km^2 protected area (O'Brien et al. 2004). Annual rainfall ranges between 2,492 and 4,549 mm, with a very wet period (>200 mm/month) from September to April and a drier period (<100 mm/month) from May to August. The mean annual temperature was 28^{o} C (WCS-IP unpub. data, 2007-2009). The study area, bisected by the Canguk River, is divided into two sections crossed by 105 km of trails at 200 m intervals. In addition to siamangs, agile gibbons, and mitered langurs, the primate community includes slow lorises (*Nycticebus coucang*), Horsfield’s tarsiers (*Tarsius bancanus*), long-tailed (*Macaca fascicularis*) and pig-tailed macaques (*M. nemestrina*), and silvered langurs (*Trachypithecus cristatus*). However, lorises and tarsiers are nocturnal, and the latter three species occur at very low densities and/or predominantly range outside of the study area (WCS-IP unpub. data); thus, they were not included in this study.

The forest at Way Canguk supports an intact and diverse predator community, including species known to target primate prey. Furthermore, despite differences in body mass and group size among the primate species studied, all three are expected to avoid the same types of predators. From personal encounters and track and camera trap data, it is known that five species of felids live in the study area (Morino 2009; 2010; WCS-IP unpub. data). These include the marbled cat (*Pardofelis marmonata*), leopard cat (*Pronailurus bengalensis*), golden cat (*Catopuma temminckii*), Sunda clouded leopard (*Neofelis diardi*), and Sumatran tiger (*Panthera tigris sumatrae*). All of these felids may prey upon the local primates, and indeed clouded leopards have been observed to successfully prey on immature proboscis monkeys (Matsuda et al. 2008) and, at Way Canguk, a 3.7 kg juvenile siamang near its sleeping site (Morino 2010). In addition, reticulated pythons (*Python reticulatus*), which are adept climbers, have been observed to prey on cercopithecids (Shine et al. 1998; Palombit, pers comm) and hylobatids (Schneider 1906). However, unlike in Africa and South America, in Asia large-bodied aerial predators are rare, and likely pose a minimal threat to primates (Uhde and Sommer 2002; Hart 2007). The black eagle (*Ictinaetus malayensis*) and hawk eagles (*Spizaetus sp*), which likely occur at Way Canguk (MacKinnon and Phillipps 1993), have been observed to prey on immature monkeys at other sites (Rauf 1986; Fam and Nijman 2011). However, because these raptors are diurnal, hunting when primates are active, they should not affect the selection of nighttime sleeping sites.

Data collection

Data were collected from March 2008 through October 2009 on one group of mitered langurs (1 adult male, 5 adult females, and 11-15 immatures), four siamang groups (three groups with 2 adult males and 1 adult female; one group with 1 adult male and 1 adult female; plus 2-3 immatures per group), and three agile gibbon groups (all with 1 adult male and 1 adult female; plus 0-2 immatures per group). The groups were selected because they used the same habitat, resulting in extensive home range and resource-use overlap. While the home ranges of siamangs and agile gibbons had very little overlap with those of conspecific groups, the overlap was nearly complete with each other's home ranges, and the langur home range overlapped with two siamang and one agile gibbon group.

Sleeping tree characteristics. The height of each sleeping tree was measured with a laser range finder (Nikon Monarch; accuracy 0.5 m), and crown diameter was visually estimated to the nearest meter. The overall density of vegetation in each tree crown was ranked as "open" (coverage <25%), "moderate" (coverage 25-50%), or "closed" (coverage >50%), and the presence or absence of lianas was noted. All sleeping trees and all feeding patches were tagged for identification and their locations recorded. Location data were all recorded as xy coordinates following Way Canguk's trail grid (WCS IP). To assess the importance of proximity to feeding patches for sleeping site selection, Euclidean distances were calculated from the sleeping site to the first feeding patch of the following morning.

Patterns of sleeping site use. For each individual, the times of entry into and exit from sleeping trees were noted. In cases where more than one individual slept in the same location (e.g., adult female and immature offspring), the location was only included as a single sample point in analyses. The height of each individual sleeping location (within the chosen site) was measured with the laser range finder, and its proximity to terminal branches was classified as near trunk, mid-branch, or near terminal branch, where the crown was divided into equal thirds. We also noted whether individuals were visible or concealed from the ground. Because mitered langurs commonly entered sleeping trees at dusk, it was seldom possible to collect data on characteristics of sleeping locations. Thus, these data sets are restricted to siamangs and agile gibbons. Because only one langur group was studied, the sample sizes for langur sleeping sites are smaller than those for agile gibbons and siamangs. Furthermore, because one agile gibbon group was observed for many fewer days than the other two, it was excluded from calculations of group averages. Single-use sleeping trees were those used only once during this study. Consecutive use was defined as sleeping in the same site for consecutive nights by at least one group member (Phoonjampa et al. 2010).

Data analyses

Sleeping strategies of the three species were compared by analyzing characteristics of sleeping sites (i.e., tree height, crown diameter, density of vegetation, and liana presence/absence) and patterns of sleeping site use (consecutive and single use trees, number of trees used per group, time of entry and exit, and sleeping locations used within sites). One-way ANOVA's (Sokal and Rohlf 1994) were used to determine whether the heights and crown diameters of sleeping trees, and the heights of sleeping locations differed among those selected by mitered langurs, siamangs, and agile gibbons. To reduce skewness, crown diameters were log transformed. Tukey post-hoc tests or alternatively, if homogeneity of variances was violated, Games-Howell post-hoc tests were used. Chi-square tests of independence with Bonferroni correction (Siegel and Castellan 1988) were used pair-wise to determine whether the 1) density of vegetation and 2) presence of lianas in sleeping trees, 3) the proximity of sleeping locations to terminal branches and 4) the visibility of sleeping locations from the ground differed across species. A Kruskal-Wallis test (Siegel and Castellan 1988) was used to compare times of entry into sleeping sites across species. Post-hoc multiple comparisons (Siegel and Castellan 1988) for a significant Kuskal-Wallis value were calculated to examine differences between each species-pair. While exact times of entry could be determined because groups retired when visibility was good, it was often difficult to record precise times of exit from sleeping trees during the pre-dawn hours. Thus, to increase the sample size for times of exit, data were grouped in 30-minute time intervals (5:30-6:00, 6:01-6:30, 6:31-7:00, 7:01-7:30, or 7:31-8:00). Kolmogorov-Smirnov two-sample tests were used (two-tailed tests for large samples; Siegel and Castellan 1988) to determine whether the distributions of exit times from sleeping sites differed between each pair of species. A one-way ANOVA along with Tukey post-hoc tests (Sokal and Rohlf 1994) were used to determine whether the distance between sleeping sites and the first feeding patch of the following morning differed among species. Statistical tests were conducted using SPSS Statistics 17.0 at an alpha level of 0.05.

RESULTS

Sleeping tree characteristics

In the course of the study, mitered langurs used 41 individual trees over 48 nights, siamangs used 146 individual trees across 223 nights, and agile gibbons used 168 individual trees over 226 nights. The species significantly differed in the height of their sleeping trees (1-way ANOVA: $F(2,285)=71.02$, $p<0.001$; $\overline{x}=41.07$ m; $\sigma=8.63$ m; Fig. 5.1). Mitered langurs slept in the tallest trees, averaging 48 m ($n=30$), followed by siamangs which slept in trees averaging 45 m ($n=119$). Langurs selected trees that were significantly taller than those selected by siamangs (Games-Howell post-hoc test: $p=0.02$). Sleeping trees selected by agile gibbons were significantly shorter than those of both langurs and siamangs (Games-Howell post-hoc tests: *p's*<0.001), and averaged 36 m ($n=139$). At Way Canguk the maximum tree heights are about 55-60 m, while the forest canopy ranges from 20–30 m. Thus, langurs and siamangs often selected emergent trees as sleeping sites, in stark contrast to agile gibbons which used trees close to the canopy.

Sleeping trees also differed significantly in crown diameter (1-way ANOVA: $F(2,273)=14.04$, $p<0.001$; $\overline{x}=18.73$ m, $\sigma=7.85$ m; Fig. 5.2). Langurs ($\overline{x}=23$ m) and siamangs ($\overline{x}$

=20 m) slept in trees with similar crown diameters (Tukey post-hoc: p=0.29). In contrast, agile gibbons slept in trees with crowns that were significantly smaller ($\bar{x}$ =16 m) than both of the other two species (Tukey post-hoc tests: *p's*<0.001).

Pair-wise comparisons revealed that the density of vegetation in sleeping trees significantly differed between mitered langurs and siamangs (Chi-square test: χ^2=10.61, df=2, p=0.005). Both species mainly selected trees with open vegetation; 92% (n=37) of langur and 66% (n=123) of siamang sleeping trees had open crown structure, but more of siamangs' sleeping trees (26%) had moderate vegetation than did langurs' (3%). Sleeping trees used by agile gibbons significantly differed from those used by both siamangs (Chi-square test: χ^2=88.80, df=2, p<0.001) and mitered langurs (Chi-square test: χ^2=71.81, df=2, p<0.001). Agile gibbons were much more likely to sleep in trees with moderate to closed vegetation, and only rarely (17% of trees, n=125) in open trees (Fig. 5.3).

A similar result was found for the presence of lianas in sleeping sites. The trees chosen by langurs (n=37) and siamangs (n=123) rarely supported lianas (Chi-square test: χ^2=2.23, df=1, p=0.14), averaging 14% and 27% of the sleeping sites respectively. In contrast, sleeping trees used by agile gibbons (n=125) supported lianas (71%) significantly more often than siamangs (Chi-square test: χ^2=48.37, df=1, p<0.001) and mitered langurs (Chi-square test: χ^2=37.33, df=1, p<0.001; Fig. 5.4).

Sleeping location characteristics

There was significant variation in the height of individual sleeping locations between species (1-way ANOVA: $F(2,947)$=283.23, p<0.001; $\bar{x}$ = 37.88 m, σ=7.65 m; Fig. 5.5). Siamangs slept at the highest locations ($\bar{x}$ =41 m), langurs selected slightly lower locations ($\bar{x}$

=38 m), and agile gibbons slept at the lowest locations ($\bar{x}$ =30 m). Sleeping location height significantly differed between each pair of species (Games-Howell post-hoc tests; langurs vs. siamangs: p=0.003; siamangs vs. agile gibbons: p<0.001; agile gibbons vs. langurs: p<0.001).

Sleeping locations differed significantly in the proportion of near-trunk, mid-branch, and near-terminal branch locations (Chi-square test: χ^2=119.15, df=2, p<0.001). While the majority of siamangs' sleeping locations were near terminal branches (88% of nights), agile gibbons used these locations on only 51% of nights. Agile gibbons also much more frequently selected locations that were out-of-sight from the ground (26% of 309 versus 2% of 753 for siamangs' locations; Chi-square test: χ^2=166.89, df=1, p<0.001).

Patterns of sleeping site use

Throughout the study period, the cumulative number of sleeping trees per agile gibbon group (relative to the number of observation days) did not reach an asymptote (Appendix 3). For most siamang groups (Appendix 4) and the mitered langur group (Appendix 5) these relationships also failed to reach asymptotes, indicating that more trees would be added at a similar rate and that the total number of trees used is still unknown. For two siamang groups (A and J), however, the cumulative number of sleeping trees began to level off after about 40 observation nights (Appendix 4).

The species differed in the mean number of individual sleeping sites used per group. Due to differences among groups in the number of observation nights, comparisons were restricted to the first 37 nights per group. Siamangs ($\bar{x}$ =26.25 trees, n=4 groups, σ=3.78) used the fewest different sleeping trees, while mitered langurs (34 trees, n=1 group) and agile gibbons ($\bar{x}$ =35.5 trees, n=2 groups, σ=2.83) used about the same number of different trees. Due to langurs' comparatively large group size and late entry into sleeping trees, however, it is likely that some of their sleeping trees were overlooked. Thus, their number of individual sleeping trees was at least comparable to, but possibly higher than the mean number used by agile gibbon groups. To control for differences in group size, the mean number of sleeping trees per species (standardized to 37 observation nights) was divided by the mean number of trees used per night. The average agile gibbon group used the most sleeping trees (35.5 trees/1.71 trees per night=20.76), followed by siamangs (26.25 trees/1.65 trees per night=15.91), and finally mitered langurs (34 trees/2.83 trees per night=12.01). Furthermore, the mean number of individuals that shared each sleeping tree differed among species, such that sleeping groups were largest in langurs ($\bar{x}=7.42$ indiv. per tree), smaller in siamangs ($\bar{x}=3.11$ indiv. per tree), and smallest in agile gibbons ($\bar{x}=1.68$ indiv. per tree).

All three species rarely re-used sleeping trees on consecutive nights. Sleeping sites were used consecutively for 12% of 33 nights in mitered langurs, 10% of 368 nights in siamangs, and 11% of 181 nights in agile gibbons. On average, single-use sleeping trees accounted for 44% of langur, 45% of siamang, and 69% of agile gibbon sleeping sites.

There were significant differences among species in the times of entry into sleeping trees (Kruskal-Wallis test: $H=381.05$, $n=1200$, df=2, $p<0.001$; $\tilde{x}=16{:}03$, $\sigma=59.28$ min). Post-hoc comparisons revealed that agile gibbons ($\tilde{x}=15{:}35$, $\sigma=46.87$ min, $n=311$) entered almost half an hour, and thus significantly, earlier than siamangs (interspecific difference 179.30>critical difference 56.00), while siamangs ($\tilde{x}=16{:}03$, $\sigma=54.72$ min, $n=746$) entered significantly earlier than mitered langurs ($\tilde{x}=17{:}25$, $\sigma=19.97$ min, $n=143$; interspecific difference 501.57>critical difference 75.74). Agile gibbons also entered significantly earlier than mitered langurs (interspecific difference 680.87>critical difference 83.82). In contrast, for each pairwise comparison (siamangs vs. agile gibbons, siamangs vs. langurs; agile gibbons vs. langurs), species did not differ in their timing of exit from sleeping trees (Fig. 5.6; Kolmogorov-Smirnov two-sample tests: observed $D_{m,n}$ vs. critical $D_{m,n}=0.05<0.17$; $0.16<0.24$; $0.14<0.17$ respectively; $p>0.05$ each). Instead, exits from sleeping sites tended to occur around dawn across species (Fig. 5.6).

Proximity to feeding patches

A significant difference was found in the distance between sleeping trees and the first feeding patch of the next morning (1-way ANOVA: $F(2,309)=4.99$), $p=0.007$). Comparisons between each species-pair revealed that only sleeping trees selected by langurs and siamangs significantly differed in proximity to early morning feeding patches (Tukey post-hoc test: $p=0.009$), where siamangs slept further ($\overline{x}=130$ m, $n=142$, $\sigma=132$) than did langurs ($\overline{x}=51$ m, $n=34$, $\sigma=40$). With a mean of 97 m, agile gibbons slept at an intermediate distance from the first feeding patch of the day ($n=136$, $\sigma=161$); however, gibbons did not differ significantly from siamangs or langurs in this distance (Tukey post-hoc tests: $p=0.12$; $p=0.20$).

DISCUSSION

Predation avoidance

The sleeping strategies of mitered langurs and siamangs, like in the majority of diurnal primates (e.g., Bert et al. 1967; Gautier-Hion 1970; Anderson 1998; Uhde and Sommer 2002; Pozo 2005; Cui et al. 2006), are consistent with the predation avoidance hypothesis, because they chose tall, large trees without dense vegetation or lianas, and slept in open areas of the crown near terminal branches. Although langurs' sleeping trees were significantly higher than siamangs', it is unlikely that this 3 m difference is biologically-meaningful. Furthermore, langurs' significantly lower sleeping locations (versus siamangs') may result from their larger group size. If there are a limited number of sleeping locations per site, then some langur individuals are likely forced to sleep at lower heights. Agile gibbons, however, used significantly shorter, smaller sleeping trees with significantly more dense vegetation and that were significantly more likely to support lianas. The climbable lianas frequently found in these trees should provide easier access for terrestrial predators and hiding places for ambush predators, and therefore do not provide good protection from felids and snakes (Anderson 1984; Tenaza and Tilson 1985). By sleeping more frequently in close proximity to the tree trunk than the other two species, agile gibbons may, in addition, reduce the chance of detecting predators approaching from below. If agile gibbons were to select locations near terminal branches, like most primate species, then this would maximize the distance from approaching danger and could increase the efficiency of predator detection via branch vibrations (Anderson 1984). Interestingly, the results for agile gibbons also stand in contrast to previous studies for other gibbon species, which reported a preference for emergent trees with open vegetation (Table 5.1). Overall, there seems to be a large degree of variation in sleeping tree height and crown diameter across hylobatid populations (Table 5.1). This likely reflects differences in forest structure, and therefore sleeping tree availability, between localities. Such a relationship between sleeping site selection and habitat type, for instance, has been found for capuchin monkeys (Di Bitetti et al. 2000). While a similar analysis is beyond the scope of the present analysis, at Way Canguk agile gibbon's mean sleeping tree height of 36 m clearly falls within the canopy, while in montane China the 22-m tall sleeping trees of black-crested gibbons are emergent (Fan and Jiang 2008).

Sleeping sites were typically shared by multiple group members in siamangs and langurs, while in agile gibbon, individuals more commonly slept in separate sleeping trees. Similar to agile gibbons at Way Canguk, other populations of *Hylobates* gibbons have been found to frequently sleep solitarily (Srikosamatara 1984; Palombit 1996; Reichard 1998; Phoonjampa et al. 2010). Likewise, the communal use of sleeping sites by multiple group members observed for siamangs is consistent with observations for siamangs in northern Sumatra (Palombit 1996). The differences in sleeping group size between siamangs and langurs on one hand, and agile gibbons on the other, suggest divergence in their predation avoidance strategies. Siamangs and langurs may rely more on early detection of predators through larger sleeping groups within trees with clear views of the surrounding area (i.e., emergent trees with open vegetation), while agile gibbons may minimize their risk of detection by predators through solitary sleeping. The overall low number of sleeping trees recorded for the langur group may reflect their large sleeping groups. However, there is also a possible bias in this data set as a consequence of poor visibility at dusk when langurs typically enter sleeping sites.

The infrequent consecutive use of sleeping trees that was found for all three species is indicative of a similar predation threat and deterrence response across primate taxa, whereby the intensity of scent left in and under sleeping sites is minimized (Hrdy 1977). Because some predators hunt at least in-part by scent, potential primate prey may reduce the risk of their detection through infrequent use of sites on consecutive nights (discussed in Reichard 1998). Similar patterns of unpredictable sleeping site use have been reported for white-handed, black-crested, and pileated gibbons (Reichard 1998; Fan and Jiang 2008; Phoonjampa et al. 2010). However, agile gibbons at Way Canguk used more sleeping trees than sympatric siamangs and langurs, and had a higher percentage of single-use sleeping trees. Thus, agile gibbons may try to compensate for their use of densely-foliated and short trees by using a greater number of sleeping trees and more frequently varying their use, thereby reducing the olfactory traces left behind. Previous research on hylobatids has suggested that predation avoidance is the main factor governing their selection of sleeping sites (Tenaza and Tilson 1985; Reichard 1998; Cheyne 2010; Phoonjampa et al. 2010), while comfort (Whitten 1982) and proximity to food (Fan and Jiang 2008; Phoonjampa et al. 2010) may only play limited roles. The results of this study suggest that the sleeping strategy of agile gibbons at Way Canguk is impacted by one or more additional factors. I suggest that these factors may relate to interspecific competition (see below).

Due to their use of potentially-vulnerable sleeping sites, agile gibbons are expected to suffer higher losses to predation than other primates living at Way Canguk. In fact, O'Brien et al. (2004) found that agile gibbons at the study site live in smaller groups (2.6 individuals) and at a much lower density (0.67 groups/km^{-2}) than siamangs (mean 3.9 individuals/group; 2.23 groups/km^{-2}), but they did not speculate on a possible cause. Based on recent analyses, O'Brien and Kinnaird (2011) have suggested that agile gibbons suffer higher infant or juvenile mortality compared to other hylobatid populations. My present analysis suggests that higher predation rates on agile gibbons could be a consequence of their less-protected sleeping sites. But this leaves the question of why agile gibbons seem to use a sleeping strategy that puts them at such a risk? Potential explanations are: (1) feeding benefits that derive from gibbon's sleeping site selection may compensate for costs of increased vulnerability to predation or (2) the perceived danger of detection by and encounters with dominant species may be greater than encounters with predators.

Proximity to feeding patches and feeding competition

There may be a tradeoff between feeding competition and predation pressure. That is, if agile gibbons were to choose sleeping sites that were in closer proximity to feeding patches, then they may gain an advantage in feeding competition with the dominant and ecologically-similar siamangs. The potential energetic gain and reduction in travel costs, however, would still be at the expense of increased predation risk if agile gibbons are forced to sleep in vulnerable sleeping sites. However, no support was found for this explanation; no significant difference was found between siamangs and agile gibbons in the distance between sleeping trees and the first feeding patches of the morning. Langurs were found to sleep significantly closer to the first feeding patch of the day, but likely this is not a consequence of direct competition with other taxa, as langurs overall seem to use more individual feeding sites that are more densely-distributed than either hylobatid. Despite their choice of sleeping sites equidistant from the first feeding patch as those of siamangs, if agile gibbons exited from sleeping trees earlier, then these individuals could still benefit from greater access to high quality, renewed feeding patches (e.g., figs) before their competitors (Schoener 1983). However, agile gibbons were found to exit sleeping trees no earlier than either siamangs or langurs. Instead, all three species began activities shortly before (5:30-6:00) or after (6:01-6:30) dawn, suggesting that they begin daily activities as soon as light conditions reach a minimal level for safe movement. Similar behavior was observed for other hylobatid species (e.g., Reichard 1998; Phoonjampa et al. 2010; Table 5.1). After not feeding for about 12.5 (langurs), 14 (siamangs), and 14.5 hours (agile gibbons) on average, hunger levels are expected to be at a maximum. In contrast, primate populations that live at higher latitudes (including gibbons) likely minimize energetic stress in these colder habitats by delaying the start of activity (Liu and Zhao 2004; Cui et al. 2006; Fan and Jiang 2008).

Interspecific dominance

Interspecific dominance, rather than predation avoidance and feeding competition, seems to better account for the unusual sleeping strategy of agile gibbons at Way Canguk. As predicted, siamangs were found to occupy and potentially monopolize safer sleeping sites. In three instances, when agile gibbons selected large, open sleeping trees they were chased out by siamangs the same evening. However, if agile gibbon's sleeping strategy was purely the result of interference competition with siamangs over the safest sleeping sites, then agile gibbons would be expected to use the next-best sites. That is, agile gibbons would still select relatively tall, large trees with open vegetation. Instead, agile gibbons had a fundamentally different sleeping strategy. Results here indicate that agile gibbons were significantly more likely than other primates at Way Canguk and other hylobatid populations (Table 5.1) to sleep in densely-foliated locations that rendered individuals virtually invisible. This assumes that poor visibility from the ground is equivalent to poor visibility from other levels of the forest. Nevertheless, this behavior is suggestive of a cryptic sleeping strategy, whereby those sites that provide maximum concealment are preferentially selected. I suggest that agile gibbons use these behaviors in an effort to hide from siamangs. As a subordinate species responding to the threat of interspecific aggression, agile gibbons seem to have prioritized strategies that may facilitate the avoidance of risky encounters with their dominant competitor. In extreme cases of interspecific aggression, such as in African (Durant 1998), European (Tannerfledt et al. 2002), and North American carnivore communities (Berger 2007), individuals of subordinate species are at risk of being killed by individuals of dominant species. Subordinate species have been reported to use local avoidance behaviors to prevent these fatal encounters (e.g., Durant 2000). Although siamangs have never been observed to kill agile gibbons, their interspecific encounters may be intensely aggressive, and often include long-distance chases, are energetically costly and have been observed to result in serious injuries (Chapter 3). Therefore, it seems that agile gibbons are juggling the risks of predation and interspecific competition, both of which may directly impact individual survival.

The cryptic sleeping strategy observed for agile gibbons may decrease the likelihood of detection by siamangs, but at the cost of increased predation risk due to the ease of access to agile gibbons' shorter, smaller, and liana-bearing sleeping trees. Similarly, subordinate crab species were found to suffer increased predation by using vulnerable resting sites as competition refuges (Navarrete and Castilla 1990). Within the primate order, Mentawai langurs (*Presbytis potenziani*) more frequently used shorter sleeping trees with heavier liana loads than did sympatric and dominant Kloss's gibbons (*Hylobates klossii*; Tenaza and Tilson 1985). Because local hunters access trees by climbing lianas, it was suggested that the higher mortality suffered by langurs to human predation was a consequence of their choice of sleeping sites.

Additionally, agile gibbon's selection of concealed sleeping sites may be influenced by differences between *Hylobates* gibbons and siamangs in the duration of daily activity. Agile gibbons were found to retire earlier in the evening than siamangs and langurs. These findings are comparable to those reported for other hylobatid populations (Table 5.1), where white-handed (*Hylobates* lar; Reichard 1998), white-bearded (*H. albibarbis*; Cheyne 2010), Mueller's (*H. muelleri*; Srikosamatara 1984), and pileated gibbons (*H. pileatus*; Phoonjampa et al. 2010) were found to retreat to sleeping trees well before dusk. Because many potential predators become active with the onset of darkness, it has been suggested that early retirement may also serve a predation avoidance function (Caine 1987). All hylobatids contend with the same types of predators; however, due to their larger body size, siamangs may be less sensitive to predation pressure than smaller-bodied *Hylobates* gibbons. Palombit (1992) reported greater variation in sleeping site entry times for siamangs than sympatric lar gibbons, where sometimes siamangs, but never lar gibbons, entered after 17:30. It is particularly interesting to point out that the entry times of Kloss's gibbons (Whitten 1980), which live on small islands without felid predators (Tenaza and Tilson 1985), were much later ($\bar{x}$ =16:40) than those of other *Hylobates* gibbons (Table 5.1). Furthermore, black-crested gibbons, which have body mass intermediate to other gibbons and siamangs (Smith and Jungers 1997) and live in a habitat where most predators have been extirpated (discussed in Sheeran 1993; Fan and Jiang 2008), had the latest reported entry times of any hylobatid (Table 5.1). Therefore, agile gibbons may be forced to follow the typical *Hylobates* gibbon pattern of retirement, but must also avoid encounters with still-active siamangs. At Way Canguk, in instances when siamangs travelled to areas nearby sleeping trees already occupied by agile gibbons, siamangs did not seem to detect the well-concealed, quiet gibbons. Co-sleeping was also never observed for agile gibbons and siamangs. Thus, agile gibbons may reduce the chance of aggressive interactions with siamangs by selecting sleeping trees with closed vegetation. If agile gibbons could enter sleeping sites later in the day, then the chance of being detected by siamangs would likely be much lower; agile gibbons could then select trees based on anti-predation characteristics. In sharp contrast, mitered langurs were occasionally observed to form loose polyspecific associations with siamangs, co-feeding in the same food patches and sleeping at the same sites. I suggest that the benefits gained (e.g., reduced predation pressure) from these associations outweigh the costs of feeding competition between the largely-frugivorous siamangs and the more folivorous langurs. Co-sleeping was never observed for agile gibbons and langurs, possibly because of the species' divergent sleeping strategies.

CONCLUSIONS

As hypothesized, the selection of primate sleeping sites at Way Canguk seems to largely reflect predation avoidance. However, the influence of interspecific competition may be equal to that of predation pressure in habitats where ecologically-similar species live in sympatry and in overlapping home ranges. Interspecific dominance may exert even greater selective pressure than predation if the perceived risk of between-species interactions outweighs that of potential predation events. Subordinate species (e.g., agile gibbons) may compete neither over the safest sleeping sites nor those sites in closest proximity to feeding resources, but instead put a priority on cryptic sleeping behavior as a tactic to seemingly avoid detection by and interaction with dominant species (e.g., siamangs).

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Table 5.1 Mean characteristics of hylobatid sleeping trees and sleeping site use across populations

Species	Height [m]	Crown diam. [m]	Location height [m]	Trees per group [*n*]	Trees w/ lianas [%]	Veg. type	Emer.	Entry time	Exit time	Cons. use [%]	References
H. agilis	-	-	-	30	-	-	Yes	15:59	6:41	-	5,9
H. agilis	36	16	30	71	71%	Cl	No	15:35	6:19	11	this study*
H. albibarbis	23	-	-	-	37%	-	Yes	-	-	-	15
H. klossii	45	22	-	-	0%	Op	Yes	-	-	-	3,12
H. klossii	-	-	-	26	-	Op	Yes	16:40	-	-	7,10
H. lar	-	-	>27	75	-	Op	Yes	15:45	6:00	-	2
H. lar	-	-	-	176	-	-	-	15:18	6:43	-	4,6*
H. lar	32	-	27	59	-	Op	Yes	15:02	6:14	4	13
H. moloch	-	-	-	19	-	-	Yes	-	-	-	8
H. muelleri	-	-	-	117	-	-	-	14:17	6:19	-	11
H. pileatus	39	-	-	71	55%	Op	Yes	15:12	6:11	9.5	16
H. pileatus	>25	-	-	-	-	-	Yes	14:27	6:00	-	11
N. concolor	22	8	17	65	36%	-	Yes	17:02	7:59	-	14
S. syndactylus	-	-	-	34	-	-	-	-	-	-	1*
S. syndactylus	-	-	-	70	-	-	-	16:32	6:42	-	4,6*
S. syndactylus	45	20	41	37	27%	Op	Yes	16:03	6:10	10	this study*

* Sympatric siamang/*Hylobates* gibbon populations; Crown diam. = crown diameter of sleeping tree; Veg .type = vegetation type in the majority of sleeping trees, where Cl = closed vegetation, Op = open vegetation; Emer. = sleeping trees emergent or non-emergent; Cons. use = % of nights that one or more individual used the same sleeping tree on consecutive nights; 1. Chivers 1974; 2. Ellefson 1974; 3. Tenaza 1974; 4. Raemaekers 1977; 5. Gittins 1979; 6. Gittins and Raemaekers 1980; 7. Whitten 1980; 8. Kappeler 1981; 9. Gittins 1982; 10. Whitten 1982; 11. Srikosamatara 1984; 12. Tenaza and Tilson 1985; 13. Reichard 1998; 14. Fan and Jiang 2008; 15. Cheyne 2010; 16. Phoonjampa et al. 2010

Fig. 5.1 Heights of sleeping trees selected by mitered langurs, siamangs, and agile gibbons (1-way ANOVA: $F(2,285)=71.02$, $p<0.001$); *line*=mean, *box*=±SE, *whiskers*=±SD, *asterisk*=significant pair-wise difference (Games-Howell post hoc tests: p's<0.05)

Fig. 5.1

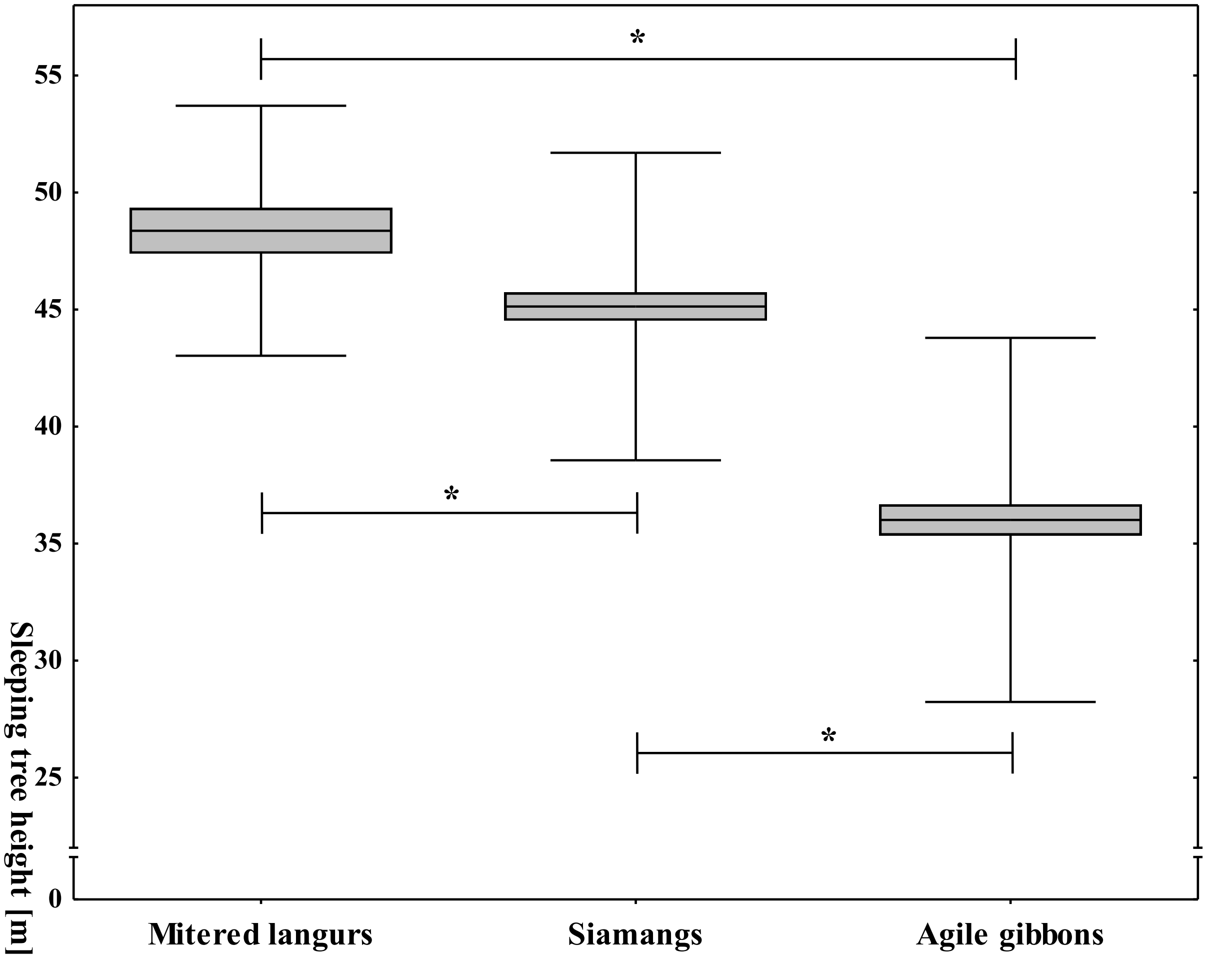

Sleeping tree height [m]
55
50
45
40
35
30
25
0
*
*
*
Mitered langurs
Siamangs
Agile gibbons

Fig. 5.2 Crown diameters of sleeping trees selected by mitered langurs, siamangs, and agile gibbons (1-way ANOVA: $F(2,273)=14.04$, $p<0.001$); *line*=mean, *box*=±SE, *whiskers*=±SD, *asterisk*=significant pair-wise difference (Tukey post-hoc tests: p's<0.001); NS=$p>0.05$

Fig. 5.2

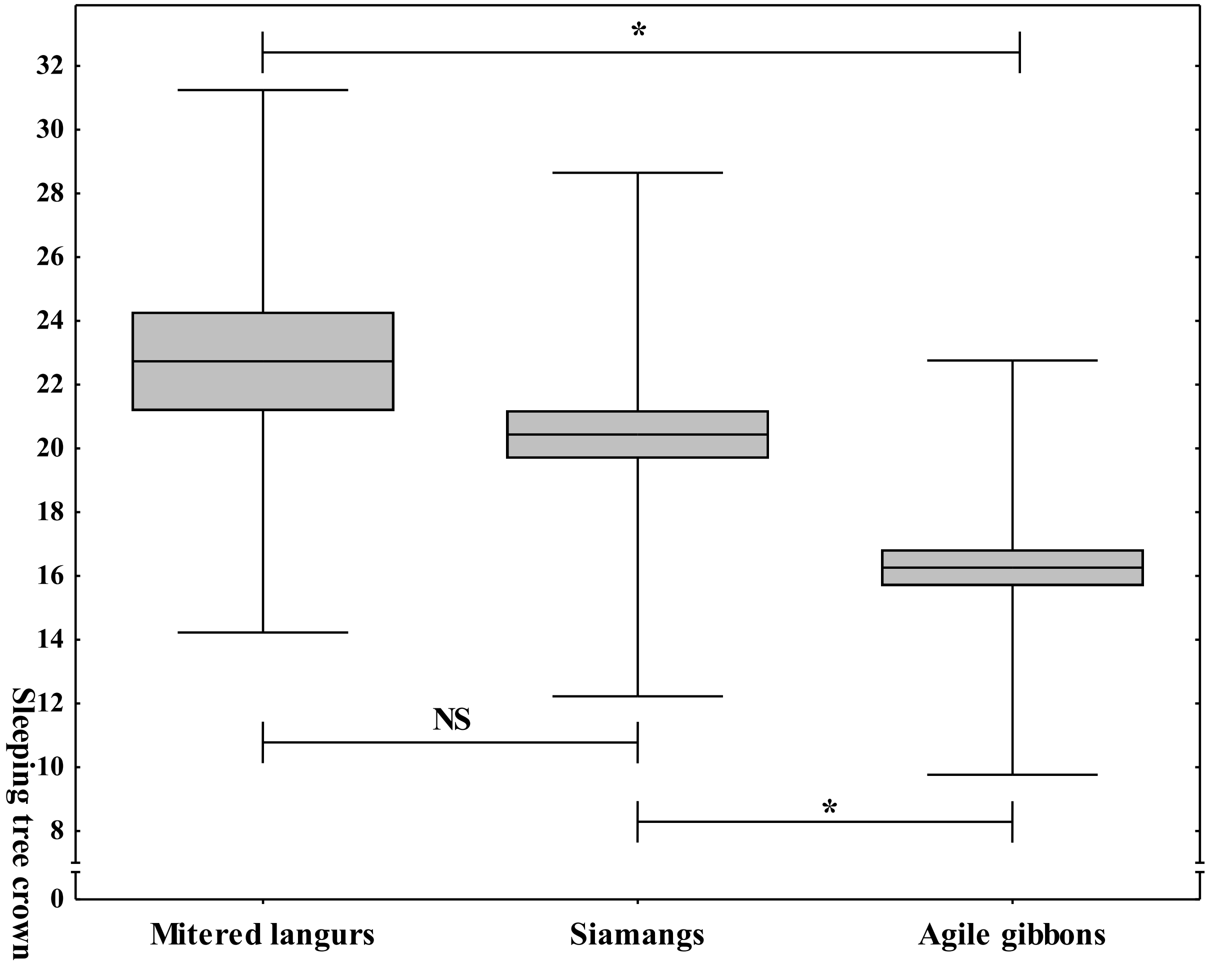
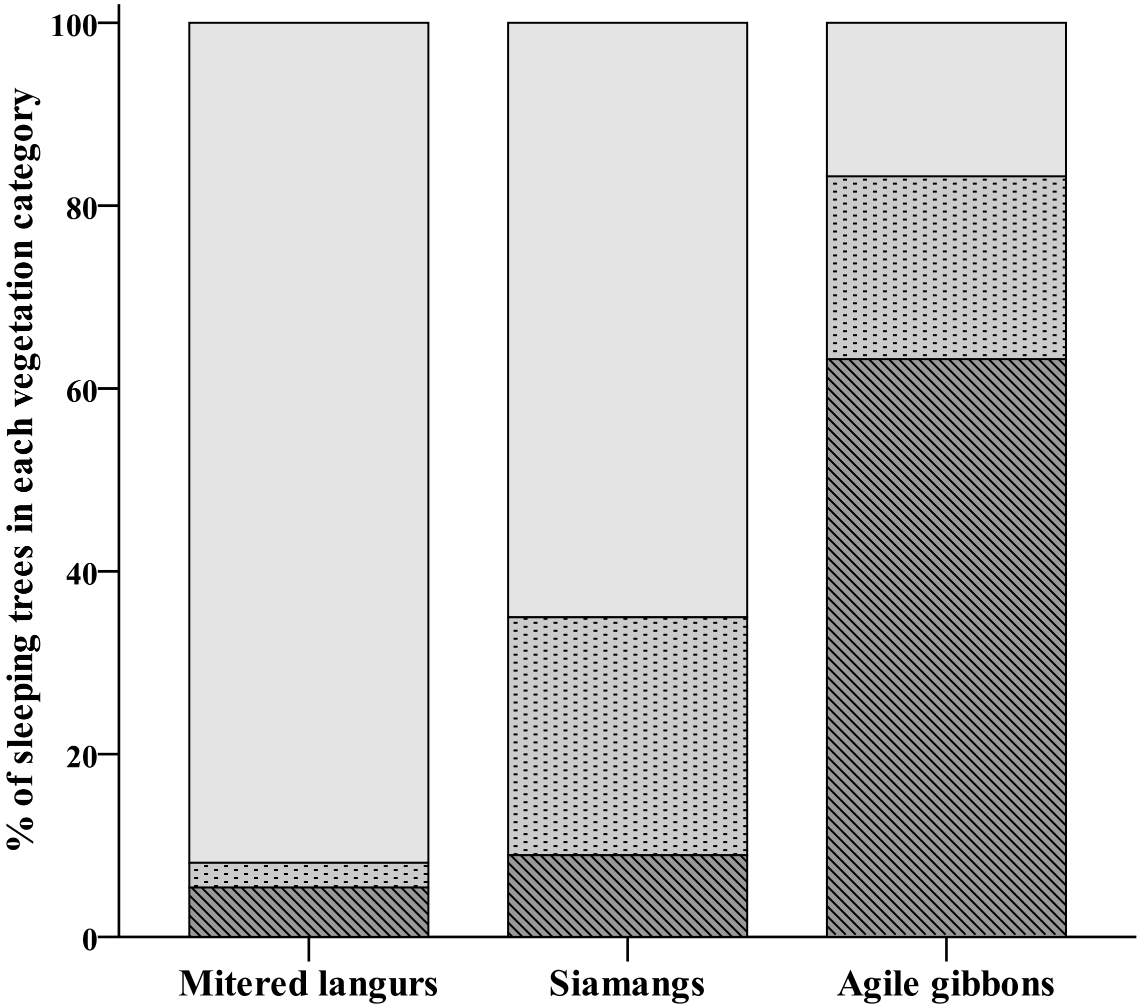

*
32
30
28
26
24
22
20
18
16
14
12
10
8
0
NS
*
Sleeping tree crown
Mitered langurs
Siamangs
Agile gibbons

Fig. 5.3 Density of vegetation in sleeping trees; *solid grey*=open vegetation, *dotted*=moderate vegetation, *slanted lines*=closed vegetation, *asterisk*=significant pair-wise difference (Chi-square tests of independence); mitered langurs versus siamangs (χ^2=10.61, df=2, p=0.005); agile gibbons versus mitered langurs (χ^2=71.81, df=2, p<0.001) and versus siamangs (χ^2=88.80, df=2, p<0.001)

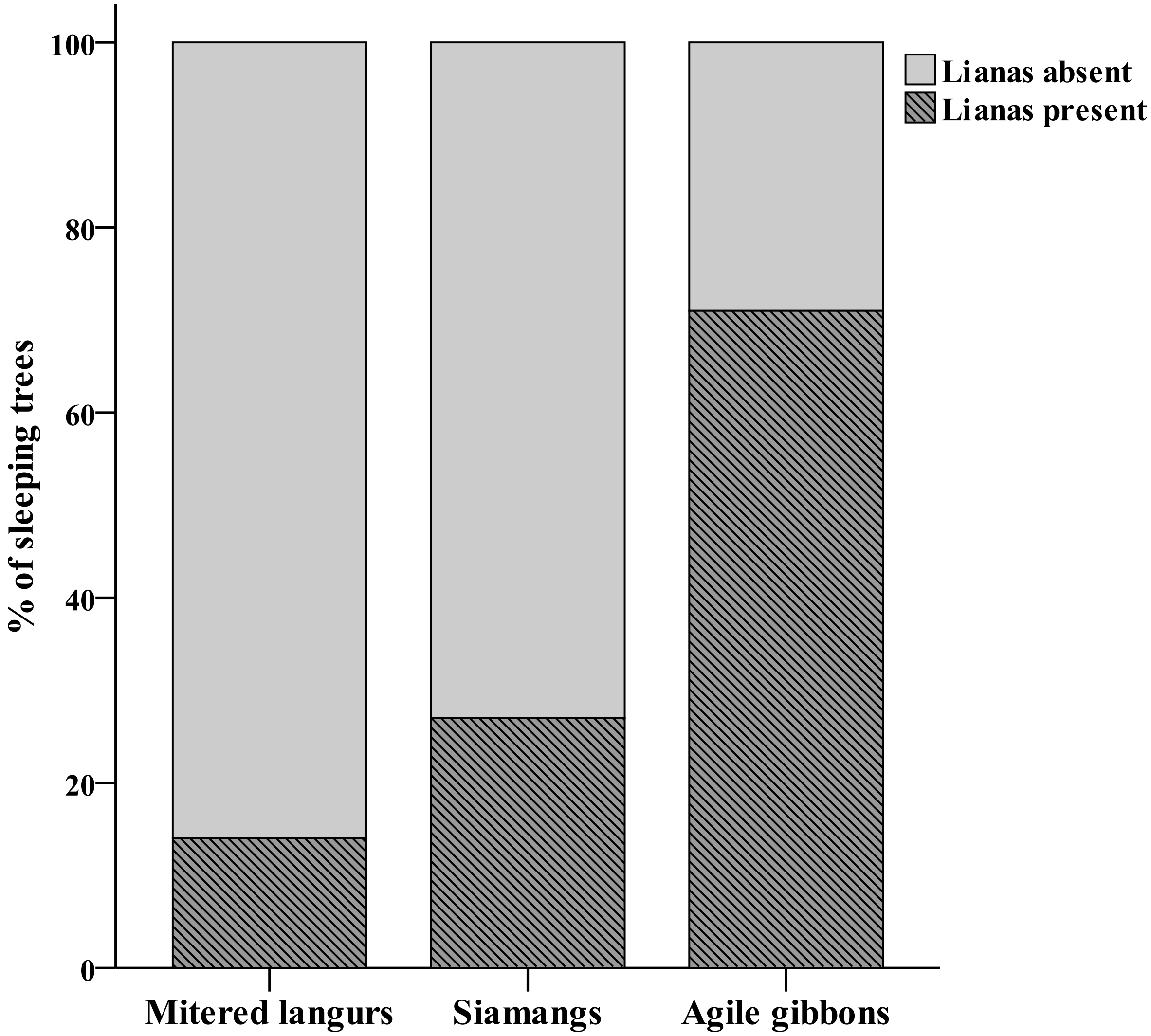
Fig. 5.3



% of sleeping trees in each vegetation category
0
20
40
60
80
100
Mitered langurs
Siamangs
Agile gibbons

Fig. 5.4 Presence of lianas in sleeping trees; *asterisk*=significant pair-wise difference (Chi-square tests of independence); mitered langurs versus siamangs (χ^2=2.23, df=1, p=0.14); agile gibbons versus mitered langurs (χ^2=37.33, df=1, p<0.001) and versus siamangs (χ^2=48.37, df=1, p<0.001)

Fig. 5.4



% of sleeping trees
100
80
60
40
20
0
Mitered langurs
Siamangs
Agile gibbons
Lianas absent
Lianas present

Fig. 5.5 Heights of sleeping locations selected by mitered langurs, siamangs, and agile gibbons (1-way ANOVA: $F(2,947)=283.23$, $p<0.001$); *line*=mean, *box*=±SE, *whiskers*=±SD, *asterisk*=significant pair-wise difference (Games-Howell post-hoc tests: p's<0.01)

Fig. 5.5

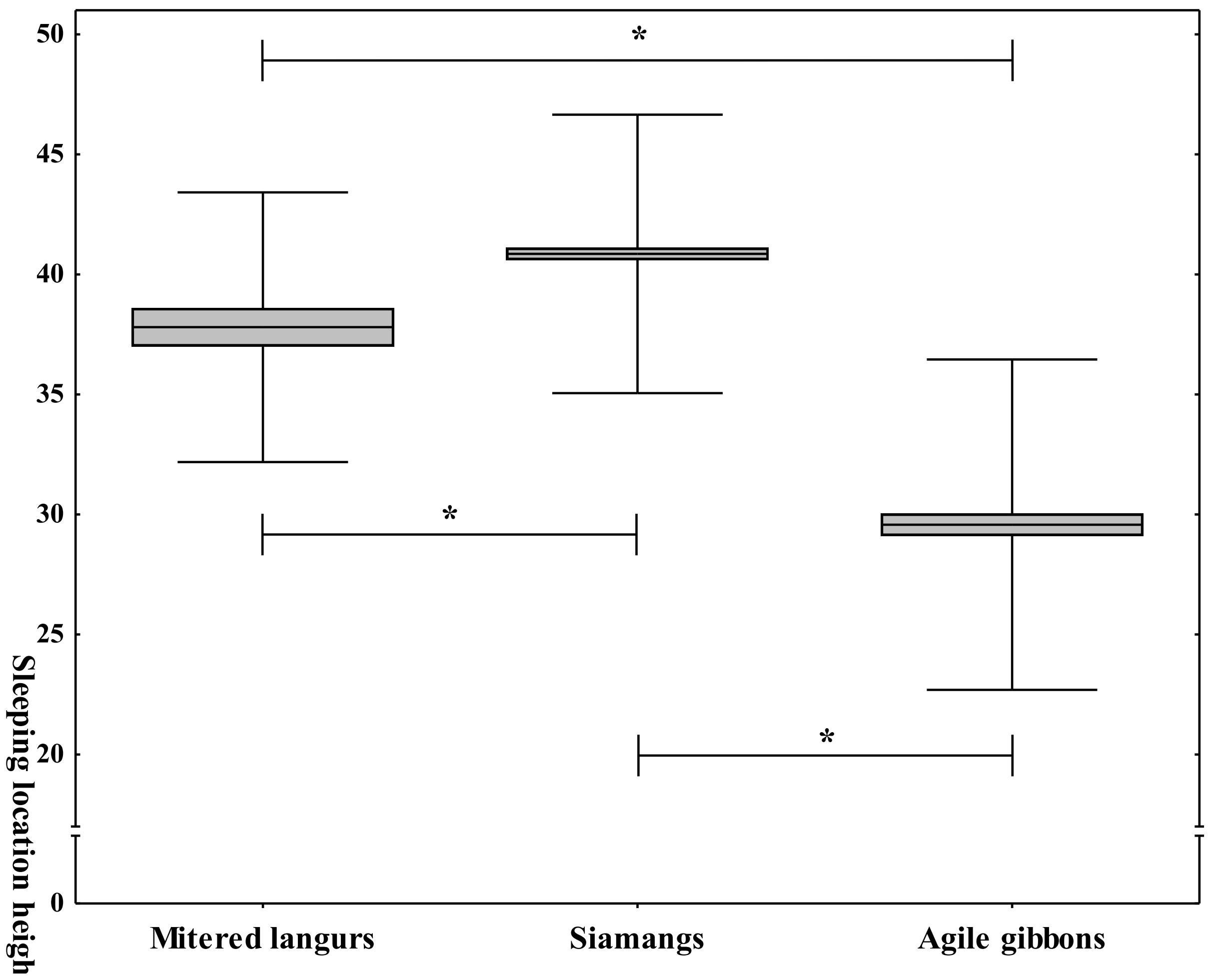
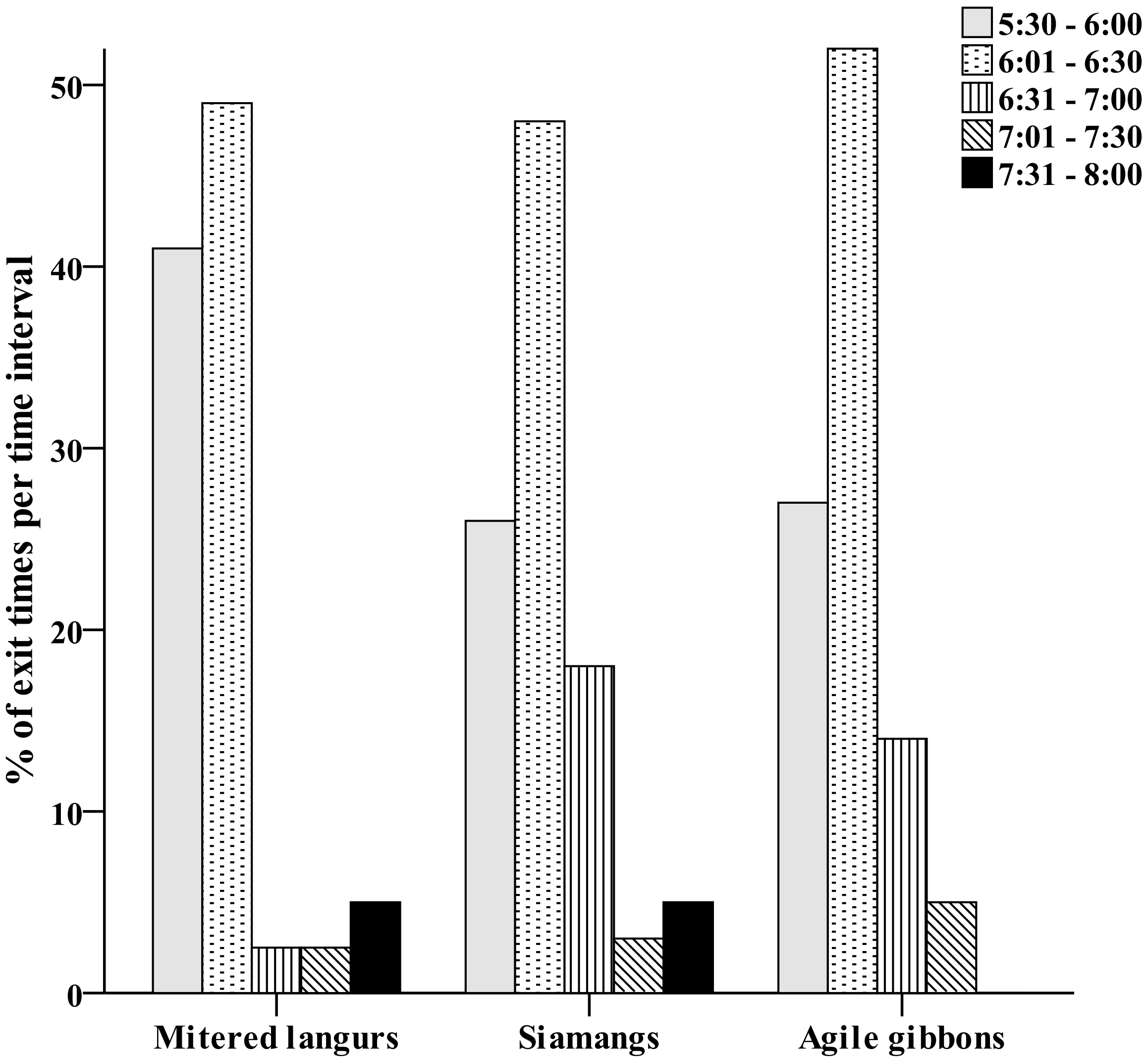

50
45
40
35
30
25
20
0
Sleeping location heigh
Mitered langurs
Siamangs
Agile gibbons
*
*
*

Fig. 5.6 Exit times from sleeping trees for mitered langurs, siamangs, and agile gibbons (Kolmogorov-Smirnov two-sample tests for each species-pair: observed $D_{m,n}$ < critical $D_{m,n}$; p's>0.05

Fig. 5.6


5:30 - 6:00
6:01 - 6:30
6:31 - 7:00
7:01 - 7:30
7:31 - 8:00
% of exit times per time interval
0
10
20
30
40
50
Mitered langurs
Siamangs
Agile gibbons

Chapter 6

Competition among sympatric primates: a synthesis of findings and future research

MODELS OF COMPETITION

Theories developed to understand the relationships between ecology and social interactions among conspecifics offer predictions for competition among heterospecifics. According to the socio-ecological model (van Schaik 1989; Sterck et al. 1997), competitive regimes may be distinguished by differential energy intake between individuals correlating with either rank or group size. Directed predictions have been made for competitive regimes depending on the spatiotemporal distribution of resources. When resources of low value occur in highly dispersed or very large patches, clear dominance relationships are not expected, as resources cannot be easily defended, but scramble competition (exploitation sensu Schoener 1983) may occur. On the other hand, contest competition (interference sensu Schoener 1983) is expected when resources of intermediate patch size are clumped in time or space. These resources are monopolizable and differential benefits should be gained by group rank. Although conceived for competition within species, the socio-ecological model should equally apply to forms of interspecific competition. Groups of dominant species should have the greatest advantage over subordinate species in habitats where preferred resources are clumped in distribution and, thereby, easily monopolized. If resources are more widely-distributed, then contest competition should decrease and scramble competition may increase. In such habitats, subordinate species may compensate for the energy costs of lost encounters with dominant species by more efficiently exploiting lower quality or more dispersed resources (Horn and

MacArthur 1972; Slatkin 1974; Roxburgh et al. 2004). Thus, a balance of contest and scramble competition could stabilize species coexistence.

RESEARCH GOALS

The main goals of this dissertation were to explore the competitive climate, as well as the mechanisms and consequences of coexistence among sympatric siamangs (*Symphalangus syndactylus*), agile gibbons (*Hylobates agilis*), and mitered langurs (*Presbytis melalophos*) living sympatrically at Way Canguk, Sumatra, Indonesia. In particular, I sought to explain the persistence of agile gibbons alongside siamangs, despite their high ecological overlap and the later species' likely superior resource holding potential. Mitered langurs (a colobine species), chiefly served as a control to distinguish interactions between the closely related and ecologically similar hylobatids (i.e., siamangs and agile gibbons) from those between distantly related species (i.e., siamang-mitered langur and agile gibbon-mitered langur interactions).

To address these goals, I investigated four main research topics: **(1) dietary niches**: what is the potential for interspecific feeding competition in the system - to what extent do the diets of each pair of primate species overlap and how do they differ, **(2) interspecific dominance**: a) what are the effects of ecological similarity, body mass, and group size on interspecific dominance relationships and heterospecific aggression and b) what are the energetic costs of being a subordinate species, **(3) divergent foraging strategies as mechanisms promoting coexistence for hylobatids**: are subordinates a) fugitive species or b) do they use competition refuges, and c) is this truly a stable system, and **(4) interspecific differences in sleeping strategies**: a) are differences in interspecific dominance reflected in each species' sleeping strategy, b) rather than reflecting predator avoidance, do subordinate species try to evade detection by and harassment from dominant species?

Results from this dissertation first suggested (Chapter 2) that there is a high potential for feeding competition between siamangs and agile gibbons, while competition between mitered langurs and either hylobatid is reduced through resource partitioning. Compared with the feeding ecology of mitered langurs, the diets of siamangs and agile gibbons were far more similar in overall composition and diversity. Furthermore, overlap in hylobatid diets was even more apparent in their use of the same top food items (i.e., those foods comprising the majority of feeding time). In light of the competitive climate established in Chapter 2, the results reported in Chapter 3 revealed that interspecific encounters were more frequent and more aggressive between ecologically similar species (i.e., siamangs and agile gibbons) than more divergent species (i.e., mitered langurs and each hylobatid species). Interspecific dominance rank was determined by body mass, but not group size; thus, siamangs dominated both agile gibbons and mitered langurs. However, being a subordinate agile gibbon in this system was much more costly than being either a siamang or a mitered langur. Lost encounters with siamangs resulted in both energetic costs and, occasionally, physical wounds for subordinate agile gibbons. Considering that displacements of agile gibbons resulted in increased access to higher-quality resources, siamangs likely benefited from the aggression they directed at agile gibbon. In contrast, agile gibbons were found to be at a clear disadvantage and to accrue energy costs directly from interactions with siamangs that might decrease their individual fitness. Agile gibbons emphasized avoidance behaviors, seemingly to reduce detection and harassment by siamangs. In Chapter 4, I sought to identify a mechanism of coexistence to explain the continued presence of agile gibbons in the study system. While agile gibbons met the expectations for a subordinate species using competition refuges (i.e., they used different, lower quality patches than siamangs), they could only achieve a neutral energy balance by minimizing energy expenditure. Taken together with daily energy intake that was consistently below that of siamangs, the results reported in Chapter 4 do not provide a clear route to stable hylobatid coexistence at Way Canguk. Interspecific competition at Way Canguk seemed to permeate all aspects of agile gibbon's behavioral ecology. Comparisons of sleeping strategies among siamangs, agile gibbons, and mitered langurs in Chapter 5 revealed that agile gibbons may select low quality (i.e., vulnerable to predation) sleeping sites just to reduce the risk of encounters with siamangs late in the day. Such a seemingly maladaptive sleeping strategy could further compromise the reproductive performance of agile gibbons in the study population due to increased predation pressure. Overall, my findings suggest that coexistence with siamangs is very costly for agile gibbons. In fact, without a comprehensible mechanism for the stable coexistence of hylobatids at Way Canguk, it may be concluded that their coexistence may not be stable. Instead, mechanisms that operate on periodic temporal scales (e.g., ENSO events) and/or larger spatial scales (e.g., source-sink dynamics) may contribute to agile gibbons' persistence in this system (Chapter 4). Increased perturbations of this forest (e.g., increased habitat loss due to human encroachment), therefore, may mean that the long-term prognosis for agile gibbons is local extinction.

Given what information this study has provided towards understanding species coexistence in hylobatids, I will now discuss my findings in light of those for other populations of sympatric hylobatids and attempt to describe larger-scale patterns that emerge across these populations. I will then offer suggestions for how to address remaining research questions that could be the focus of future studies on sympatric hylobatids.

SPECIES COEXISTENCE IN HYLOBATIDS

Results of this study imply that coexistence of competing hylobatid species at Way Canguk is not promoted by a tradeoff between competitive ability and efficiency in accessing feeding patches before. Agile gibbons are not fugitives and, instead, may minimize their energy expenditure, engage in prolonged inactivity, and emphasize the use of low-quality feeding patches as competition refuges. Furthermore, while the characteristics of sleeping trees reflected predation avoidance in siamangs and mitered langurs, agile gibbons were observed to use a sleeping strategy that could increase their risk of predation by felids or snakes. These findings, however, may not apply to all habitats where hylobatids occur in sympatry. Mechanisms of species coexistence should vary not only with the species' unique physiologies and morphologies, but also with local habitat characteristics. Most notably, between-site differences in the distribution, abundance, and quality of resources should shape the ecological role played by each species (e.g., Schoener 1983). Sympatric hylobatids, therefore, may use different foraging strategies depending on the availability (density and abundance) of preferred (figs and ripe fruits), as well as less-preferred food resources.

Sympatric siamangs and *Hylobates* gibbons

In addition to the population at Way Canguk, ecological comparisons have been made between sympatric siamangs and *Hylobates* gibbons living at Kuala Lompat, Malaysia (Raemaekers 1978a; 1978b; 1979; MacKinnon and MacKinnon 1980; Chivers 1984; Raemaekers 1984) and Ketambe, northern Sumatra (Palombit 1997). Each of these populations occupies a distinct habitat and is, thereby, subject to unique ecological conditions. Accordingly, differences in both ecological and behavioral interactions between hylobatid species are apparent among these sites.

Between-site variation. The three sites in question (Kuala Lompat, Ketambe, and Way Canguk) occur within the same West Malesian floral and faunal region (Whitten et al. 2000).

Subtle variation, however, in the abundance and distribution of resources, as well as population densities may contribute to differences in the strength of interspecific competition. In particular, between-site differences have previously been described in the availability of figs. Fig densities are highest at Ketambe (9.0 free-standing figs/ha; >27 strangler figs/ha; Palombit 1997), moderate at Kuala Lompat (7.7 free-standing figs/ha; Raemaekers et al. 1980), and lowest at Way Canguk (1.37 strangler figs/ha; Kinnaird and O'Brien 2005). Furthermore, figs at Way Canguk bear fruit at a density of one fig tree per 6 ha per month (Kinnaird and O'Brien 2005). Based on home range sizes reported in Chapter 3, each agile gibbon and each siamang group would have about four fruiting fig trees available each month. Fig production, however, is more constant at Way Canguk than at Ketambe (reviewed in Kinnaird and O'Brien 2005). The fig community at Way Canguk includes a mixture of coordinated, seasonal and asynchronous, aseasonal species; thus, at any given time figs are likely available in each home range. Based on the socio-ecological model (*sensu* van Schaik 1989), contest (interference) competition would be expected to be highest at Way Canguk (where preferred figs are most clumped and monopolizable), while scramble competition may be more important at Kuala Lompat and Ketambe (where individual fig patches are less defendable).

Hylobatid population densities also vary strongly among sites (Table 6.1). While densities at Kuala Lompat were more than twice as high for siamangs as for white-handed gibbons (Chivers 1974; Gittins and Raemaekers 1980), population densities were nearly equal for these same species at Ketambe (Palombit 1997). Conversely, at Way Canguk siamangs occur at far higher densities than sympatric agile gibbons (Table 6.1; O'Brien et al. 2004; O'Brien and Kinnaird 2011).

Coexistence in Malaysian hylobatids. Sympatric siamangs and white-handed gibbons were the subject of several studies at Kuala Lompat, Malaysia (Table 6.1). Similar to hylobatid populations at Way Canguk (Chapter 2), Malaysian siamangs and smaller, white-handed gibbons overlapped broadly in diet, particularly in their use of preferred fig patches (Raemaekers 1978; MacKinnon and MacKinnon 1980). Although siamangs dominated white-handed gibbons during encounters (Raemaekers 1978a), the nature of interspecific encounters differed between study sites. Contrasting with my findings (Chapter 4), siamang-lar gibbon encounters were infrequent and occurred disproportionately more often at fig patches, and siamangs at Kuala Lompat had lower success rates when attempting to displace white-handed gibbons from feeding patches (success rates: 35% vs. 98%; Raemaekers 1978a).

While acknowledging that feeding competition could theoretically occur between sympatric siamangs and *Hylobates* gibbons, Raemaekers (1978a; 1984) argued that interspecific differences in body mass (and thereby bioenergetics) result in adequate ecological separation for hylobatid coexistence. In particular, siamangs were cast as more folivorous and white-handed gibbons as more frugivorous (Raemaekers 1984). Due to their larger body mass and slower locomotion, siamangs should have higher travel cost (Raemaekers 1979; Fleagle 1976). Thus, the foraging decisions of siamangs were thought to be constrained by bioenergetics. Following this logic, siamangs would be forced to eat fruit predominantly from large, super-productive fig patches but rarely from small patches of higher-quality, sugary fruits and to consume more, lower quality leaves than smaller hylobatids (Raemaekers 1984). The lower travel costs of smaller, faster *Hylobates* gibbons, in contrast, would free them to exploit energy-rich fruit from widely-dispersed patches. Any displacements of white-handed gibbons by siamangs were discounted as non-significant because the smaller species could efficiently travel to an alternative food source (Raemaekers 1978a). Thus, interference competition did not seem to benefit siamangs, and *Hylobates* gibbons were portrayed, if anything, as somewhat ecologically superior to sympatric siamangs (e.g., Raemaekers 1984).

In light of the results of my research, I propose that *Hylobates* gibbons do, in fact, undergo costs as a result of competition with siamangs. Despite differences in the rate and outcome of their encounters with siamangs, both agile gibbons (Chapter 4) and white-handed gibbons had foraging strategies that could suggest the use of competition refuges. Compared with sympatric siamangs, white-handed gibbons fed in patches that were smaller, more dispersed, and provided fewer individual feeding minutes (Gittins and Raemaekers 1980; Raemaekers 1984). Although Raemaekers (1978a; 1984) made the assumption that fruits in these alternative patches were high in nutritional quality, I found this not to be true. When agile gibbons were supplanted from a fruit tree (both fig and non-fig) and travelled to a subsequent feeding patch, the fruit in that second patch contained less gross energy (Chapter 3). It cannot be determined whether white-handed gibbons experienced a similar caloric cost due to displacements by siamangs at Kuala Lompat, but results here suggest this as a possibility. Such low quality patches would fit expectations for competition refuges (Durant 1998; Abramsky et al. 2001; Horgan 2005). However, unlike results for agile gibbons (Chapter 4), white-handed gibbons did not minimize their energy expenditure. In fact, they likely had higher energy expenditure than Malaysian siamangs, Sumatran siamangs, and agile gibbons (Table 6.1); each day they spent far more time travelling, travelled much farther (twice the daily path lengths of sympatric siamangs), fed in many more patches (twice the number used by siamangs; MacKinnon and MacKinnon 1980), and covered a larger percentage of their home range (Raemaekers 1979; MacKinnon and MacKinnon 1980). Siamangs at Kuala Lompat, in turn, concentrated on the largest, most-productive feeding patches (e.g., figs), which left white-handed gibbons to use the lower quality patches. Under such a system, the chance of risky interspecific encounters should be reduced; indeed, this assertion gains support from the low frequency of interspecific encounters at Kuala Lompat compared with Way Canguk (see above). However, avoidance of the dominant species would not be enough to ensure species coexistence. Due to the seemingly high travel costs associated with accessing low-quality patches, it may be challenging for white-handed gibbons to achieve a neutral energy balance. Although the sample size is quite limited, interbirth intervals were reported to be very long (10 years) for white-handed gibbons in Malaysia (Chivers and Raemaekers 1980). Additionally, siamangs had higher population densities than white-handed gibbons (Table 6.1). Together, this might suggest that the smaller *Hylobates* gibbons in the system may have been energetically-compromised to the extent that the rate of reproduction was negatively affected. Similar reductions in energy intake have been linked to delayed infant growth (Roberts et al. 1985) and lower birth rates (Watts and Holekamp 2009).

Alternatively, if siamangs and white-handed gibbons diverge in diet, then feeding competition may be low enough at Kuala Lompat to compensate for energy losses. Hylobatids, in general, preferentially select figs, and the proportion of their feeding time spent on figs is best determined by the local availability of these foods (reviewed in Elder 2009). Figs are particularly critical to the success of hylobatid populations; in fact, hylobatid densities (across sites and species) are limited by the availability of figs (Mather 1992; Marshall 2004; Marshall and Leighton 2006). Furthermore, figs have been shown to be preferred over other fruits for several hylobatid species (Gittins and Raemaekers 1980; Palombit 1997; Marshall 2004) perhaps because figs occur in large, productive patches, require minimal handling time, provide easily-digested carbohydrates and protein at levels sufficient for survival, and may contain high levels of calcium (Conklin and Wrangham 1994; O'Brien et al. 1998). Due to body mass differences, siamangs and *Hylobates* gibbons are expected to differ in how they supplement their fig-dominated diets (Raemaekers 1984). Travel costs are higher in siamangs as a result of their heavier mass, shorter strides (Raemaekers 1979), and slower mode of locomotion (Fleagle 1976). Thus, it was hypothesized and observed in Kuala Lompat that siamangs supplement more with easy-to-find leaves, while smaller-bodied, white-handed gibbons target more dispersed ripe fruits (Raemaekers 1979; 1984).

Coexistence in northern Sumatran hylobatids. In the fig-rich forest at Ketambe, feeding competition seems to be even lower between sympatric siamangs and white-handed gibbons. Fig consumption was particularly high in this system (Table 6.2). Furthermore, siamangs and white-handed gibbons differed neither in the percentage of feeding time spent on figs (Table 6.2) nor their activity budgets (Table 6.1). Thus, both species likely had access to multiple patches of their preferred foods (i.e., fig resources were too many to be monopolized). Feeding competition between species was likely further diminished because siamangs and white-handed gibbons diverged in how they supplemented their fig-heavy diets. Similar to patterns observed at Kuala Lompat, at Ketambe siamangs supplemented with more young leaves and white-handed gibbons ate more ripe fruits (Table 6.2). Both hylobatid species spent comparatively high percentages of feeding time on insects (Table 6.2), which could potentially further increase their daily energy intake and provide key sources of protein.

COEXISTENCE AT WAY CANGUK REVISITED

About 35 years ago, Raemaekers (1977; 1978a; 1978b; 1979; 1980; 1984) provided a body of work on the ecology of sympatric siamangs and white-handed gibbons that lay the foundation for my study of interactions between siamangs and agile gibbons at Way Canguk. Although Raemaekers suggested that resource competition could occur between hylobatid species, he stated that: “There is as yet no sound evidence that interspecific competition between large and small species affects either species’ dietary niche or population density in sympatry, even though there is a large dietary overlap” (Raemaekers 1984: 218). I submit that my dissertation now provides some of the first evidence that interspecific competition is indeed actively occurring between siamangs and a *Hylobates* gibbon species.

Compared with sympatric hylobatid populations at Kuala Lompat and Ketambe, the system at Way Canguk may exemplify extreme conditions for species coexistence. Despite their larger body mass, siamangs can overcome the constraints of high travel costs because preferred figs occur at low densities, yet are consistently available and highly productive (Kinnaird and O'Brien 2005). That is, siamangs will nearly always have a patch to monopolize, as well as maximally exploit to the exclusion of agile gibbons. Accordingly, siamangs spent a higher percentage of feeding time on figs than agile gibbons (Chapter 2; Table 6.2). Furthermore, because siamangs occur at high densities and have fairly small home ranges (Table 6.1), they can likely afford to cover more of their home range each day than siamangs at Kuala Lompat. This reduction in travel costs could lead to more frequent encounters with and, therefore, displacements of *Hylobates* gibbons. Similar to white-handed gibbons at Kuala Lompat (Raemaekers 1984) and Ketambe (Palombit 1997), agile gibbons spent more time eating non-fig fruits than sympatric siamangs (Chapter 2; Table 6.2). However, insectivory was much lower for both species at Way Canguk than at Ketambe (Palombit 1997), suggesting that there is variation between northern and southern Sumatra in the availability of insects. Additionally, hylobatid species at Way Canguk did not greatly differ in their consumption of leaves. At Way Canguk, an unusually high percentage of feeding time was spent on flowers, which may serve as an alternative to insects as good sources of protein (Chapter 2; Table 2.1). However, because flowers made up an equal proportion of each hylobatid species' diet, agile gibbons likely did not disproportionately benefit from these resources relative to siamangs. Subordinate agile gibbons are left with literally nowhere to run and little to eat, and must either subsist on competition refuges or hide and perish.

FUTURE RESEARCH

The next step to understanding the persistence of agile gibbons at Way Canguk would be to evaluate whether hylobatid coexistence is compatible with a source-sink dynamic (Pulliam 1988; Amarasekare and Nisbet 2001). Namely, is the agile gibbon population at Way Canguk (the "sink") periodically re-populated from a nearby population (the "source")? Because Way Canguk (which lies within Bukit Barisan Selatan National Park) is contiguous with higher elevation forests to the North, those are the most likely source populations. To address this research question, one would need to conduct a population-wide study of genetic relatedness among agile gibbon individuals. If individuals are indeed colonizing Way Canguk from the northern sections of the forest, then the average relatedness between individuals within Way Canguk would be no different than relatedness between any two individuals chosen at random from the larger population (e.g., the wider gene pool available within Bukit Barisan Selatan National Park). That is, reproductive rates do not match mortality rates within Way Canguk, so the local population is maintained by immigration of random, distantly-related individuals from sources nearby.

Hylobatid coexistence at Way Canguk may be at the edge of natural systems. Siamangs are dominant, seem to benefit from the aggression they direct at agile gibbons, and live at very high population densities. Although this may be one of the few systems described where coexistence is long-term, but possibly not stable, such areas should theoretically exist for most populations (Pulliam 1988). It is, therefore, theoretically important and informative to study these systems. Furthermore, understanding how habitat characteristics (e.g., fig density) impact species coexistence should have implications for the conservation of these communities.

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Table 6.1 Activity budgets, daily path lengths (DPLs), home range sizes (HR), and densities of sympatric siamangs (*S. s.*) and *Hylobates* gibbons (*H. lar* and *H. agilis*)

Species	**Population**	**% Feed**	**% Rest**	**% Travel**	**DPL [m]**	**HR [ha]**	**Density [indiv/km^2]**	***n* groups**	**References**
S. s.	Kuala Lompat, Malaysia	55	29*	16	870	34	5.0	1	Chivers 1974; Chivers 1984
		50	28	22	740	47		1	Raemaekers 1979
		----	----	----	640	28		1	MacKinnon and MacKinnon 1980
		50	25	22	738	----		1	Gittins and Raemaekers 1980
	Population mean	**52**	**27**	**20**	**747**	**36**			
	Ketambe, Sumatra	40	44	12	----	----	4.0	2	Palombit 1997
	Way Canguk, Sumatra	36	35	17	1148	20	10.3	5	O'Brien et al. 2004; Lappan 2005
		35	37	15	1228	23		4	THIS STUDY
	Population mean	**36**	**36**	**16**	**1188**	**22**			
H. lar	Kuala Lompat, Malaysia	42	26*	32	1670	55		1	Chivers 1984
		42	25	33	1500	57		1	Raemaekers 1979
		42	20	32	1217	54	2.0	1(2)	Gittins and Raemaekers 1980
		---	---	---	1850	53		1	MacKinnon and MacKinnon 1980
	Population mean	**42**	**24**	**32**	**1559**	**55**			
	Ketambe, Sumatra	34	45	16	----	----	4.7	2	Palombit 1997
H. agilis	Way Canguk, Sumatra	16	49	14	1010	24	1.4	2	THIS STUDY; O'Brien et al. 2004

* % time spent resting estimated as 100% - (% feed + % travel); *n* groups given in parentheses were not focal groups, but were used in calculation of mean home range size

Table 6.2 Diets of sympatric siamangs (*S. s.*) and *Hylobates* gibbons (*H. lar* and *H. agilis*)

Population	Species	% Fruits	% Figs	% Leaves	% Flowers	% Insects	References
Kuala Lompat, Malaysia 3° N, 102° E	*S. s.*	14	22	43	6	15	Raemaekers 1977
	S. s.	41*	----	48	5	6	Chivers 1974
	S. s.	44*	----	44	4	8	MacKinnon and MacKinnon 1980
	H. lar	28	22	29	7	13	Raemaekers 1977
	H. lar	36	27	31	1	5	MacKinnon and MacKinnon 1980
Ketambe, Sumatra 3° N, 97° E	*S. s.*	18	43	17	1	21	Palombit 1997
	H. lar	26	45	4	1	24	Palombit 1997
Way Canguk, Sumatra 5° S, 104° E	*S. s.*	34	22	32	12	0	Lappan 2005
	S. s.	40	27	24	9	<1	THIS STUDY^
	H. agilis	51	18	20	10	1	THIS STUDY^

Diets characterized as percentages of feeding time spent eating (non-fig) fruits, figs, leaves (young and mature combined), flowers, and insects (including all animal matter); *In cases when only the percentage of fruit is listed, the relative contributions of time eating figs vs. nonfig fruits was unknown; ^species means across 12 months

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Appendices

Appendix 1 Observed total diets of siamangs (*S.s.*), agile gibbons (*H.a.*), and mitered langurs (*P.m.*) at Way Canguk; *presence or absence of each food item in primate diets during the study period

				Food details			**Eaten by***		
Local/common name	**Family**	**Genus**	**Species**	**Type**	**Mature**	**Part**	***Ss***	***Ha***	***Pm***
Paitan	*Achariaceae*	*Hydnocarpus*	*gracilis*	Flowers		Whole	1	1	
	Alangiaceae	*Alangium*	*griffithii*	Flowers		Whole			1
	Alangiaceae	*Alangium*	*griffithii*	Fruit	Ripe	Pulp	1	1	1
	Alangiaceae	*Alangium*	*javanicum*	Fruit	Ripe	Pulp	1	1	
	Alangiaceae	*Alangium*	*javanicum*	Fruit	Semiripe	Pulp			1
Rao	*Anacardiaceae*	*Dracontomelon*	*dao*	Flowers		Whole			1
Rao	*Anacardiaceae*	*Dracontomelon*	*dao*	Fruit	Ripe	Pulp	1	1	
Rao	*Anacardiaceae*	*Dracontomelon*	*dao*	Fruit	Unripe	Pulp	1	1	
Mangga hutan	*Anacardiaceae*	*Mangifera*	*sp* (*griffithii*?)	Fruit	Ripe	Pulp	1	1	
Mangga hutan	*Anacardiaceae*	*Mangifera*	*sp* (*griffithii*?)	Leaves	Mature	Stems			1
Mangga hutan	*Anacardiaceae*	*Mangifera*	*sp* (*griffithii*?)	Leaves	Young	Whole	1		1
Liana "Panut"	*Annonaceae*	*Uvaria*	*sp*(*littoralis*?)	Fruit	Ripe	Pulp	1	1	
Kembang	*Annonaceae*	*Cananga*	*odorata*	Leaves	Mature	Stems			1
Kembang	*Annonaceae*	*Cananga*	*odorata*	Leaves	Young	Whole			1
	Annonaceae	*Cyathocalyx*	*sumatranus*	Fruit	Ripe	Pulp	1		
Sawoh sawohan	*Annonaceae*	*Latrimitra* ?	*siamensis*	Fruit	Ripe	Pulp	1	1	
Sawoh sawohan	*Annonaceae*	*Latrimitra* ?	*siamensis*	Leaves	Young	Whole			1
	Annonaceae	*Meiogyne*	*sp*	Leaves	Young	Whole	1		1
	Annonaceae	*Meiogyne*	*virgata*	Fruit	Ripe	Pulp & seeds	1		
	Annonaceae	*Meiogyne*	*virgata*	Leaves	Young	Whole	1		
Pohon dekat camp	*Annonaceae*	*Mitrepora*	*polypirena*	Flowers		Petals	1	1	1
Pohon dekat camp	*Annonaceae*	*Mitrepora*	*polypirena*	Fruit	Ripe	Pulp & seeds	1	1	
Pohon dekat camp	*Annonaceae*	*Mitrepora*	*polypirena*	Leaves	Mature	Whole	1		
Pohon dekat camp	*Annonaceae*	*Mitrepora*	*polypirena*	Leaves	Young	Whole	1	1	1
	Annonaceae	*Polyalthia*	*becaari*	Fruit	Unripe	Whole			1
	Annonaceae	*Polyalthia*	*becaari*	Leaves	Young	Whole	1		

				Food details			Eaten by*		
Local/common name	**Family**	**Genus**	**Species**	**Type**	**Mature**	**Part**	***Ss***	***Ha***	***Pm***
	Annonaceae	*Polyalthia*	*grandiflora*	Leaves	Young	Whole	1	1	1
	Annonaceae	*Polyalthia*	*laterfolia*	Flowers		Whole	1		1
	Annonaceae	*Polyalthia*	*laterfolia*	Fruit	Ripe	Skin & pulp	1	1	
	Annonaceae	*Polyalthia*	*laterfolia*	Fruit	Unripe	Seeds	1	1	1
	Annonaceae	*Polyalthia*	*laterfolia*	Leaves	Young	Whole	1		
	Annonaceae	*Polyalthia*	*rumpii*	Fruit	Ripe	Skin & pulp	1	1	
	Annonaceae	*Polyalthia*	*sp*	Flowers		Petals	1		1
	Annonaceae	*Polyalthia*	*sp*	Flowers		Whole	1	1	
	Annonaceae	*Polyalthia*	*sp*	Flowers		Whole	1		
	Annonaceae	*Polyalthia*	*sp*	Fruit	Ripe	Skin & pulp	1	1	
	Annonaceae	*Polyalthia*	*sp*	Fruit	Ripe	Skin & pulp	1		
	Annonaceae	*Polyalthia*	*sp*	Fruit	Ripe	Skin & pulp	1	1	
	Annonaceae	*Pseuduvaria*	*reticulata*	Flowers		Whole	1		1
Anopucuk	*Annonaceae*	*Saccopetallum*	*horsfeldii*	Flowers		Whole			1
Anopucuk	*Annonaceae*	*Saccopetallum*	*horsfeldii*	Fruit	Ripe	Pulp	1	1	
Anopucuk	*Annonaceae*	*Saccopetallum*	*horsfeldii*	Fruit	Unripe	Seeds			1
Anopucuk	*Annonaceae*	*Saccopetallum*	*horsfeldii*	Leaves	Young	Whole			1
Kepel	*Annonaceae*	*Stelacocarpus*	*burahol*	Flowers		Whole	1	1	
Kepel	*Annonaceae*	*Stelacocarpus*	*burahol*	Fruit	Ripe	Whole	1		
Kepel	*Annonaceae*	*Stelacocarpus*	*burahol*	Leaves	Young	Whole	1	1	1
Liana "Ungu"	*Annonaceae*			Flowers		Petals	1	1	
	Annonaceae			Flowers		Petals	1		
Liana "Merah di dalam"	*Annonaceae*			Fruit	Ripe	Pulp	1	1	
Liana "Panjang"/“Pisang”	*Annonaceae*			Fruit	Ripe	Pulp	1	1	
Liana "Ungu"	*Annonaceae*			Fruit	Ripe	Pulp	1	1	
Liana "Mana lagi"	*Annonaceae*			Fruit	Ripe	Pulp & seeds	1	1	
Liana "Tarmin"	*Annonaceae*			Fruit	Ripe	Skin & pulp			1
Liana "Ungu"	*Annonaceae*			Leaves	Young	Whole	1		

				Food details			Eaten by*		
Local/common name	**Family**	**Genus**	**Species**	**Type**	**Mature**	**Part**	***Ss***	***Ha***	***Pm***
	Annonaceae			Leaves	Young	Whole			1
Pule	*Apocynaceae*	*Alstonia*	*sp*	Flowers		Whole		1	
Liana "Geta putih"	*Apocynaceae*			Fruit	Ripe	Pulp	1	1	1
Cembirit	*Apocynaceae*			Leaves	Mature	Whole			1
Liana "Geta putih"	*Apocynaceae*			Leaves	Young	Whole			1
Rattan	*Arecaceae*	*Daemonorops*	*sp*	Fruit	Ripe	Pulp	1	1	
Rattan "Suti"	*Arecaceae*	*Daemonorops*	*sp*	Fruit	Ripe	Pulp	1		
Rattan "Lelok"	*Arecaceae*	*Daemonorops*	*sp*	Fruit	Ripe	Pulp	1		
Liana "Rayutan"	*Asteraceae*	*Mikania*	*cordata*	Leaves	Mature	Whole			1
Liana "Rayutan"	*Asteraceae*	*Mikania*	*cordata*	Leaves	Young	Whole			1
Randu alas	*Bombacaceae*	*Bombax*	*valentonii*	Leaves	Young	Whole		1	
Kenari	*Burseraceae*	*Canarium*	*sp*	Leaves	Young	Whole	1		
Seltis	*Cannabaceae*	*Celtis*	*nigrescens*	Flowers		Whole	1	1	1
Seltis	*Cannabaceae*	*Celtis*	*nigrescens*	Fruit	Ripe	Skin & pulp	1	1	
Pacal kidang	*Cannabaceae*	*Gironniera*	*subaequalis*	Fruit	Ripe	Whole	1		
Pacal kidang	*Cannabaceae*	*Gironniera*	*subaequalis*	Leaves	Young	Whole	1		1
	Celastraceae	*Bhesa*	*paniculata*	Fruit	Ripe	Pulp & seeds	1	1	1
Kindo	*Celastraceae*	*Siphonodon*	*celastrineus*	Fruit	Ripe	Skin & pulp	1	1	
	Chrysobalanaceae	*Atuna*	*racemosa*	Leaves	Young	Whole	1		
Assam kandis	*Clusiaceae*	*Garcinia*	*parvifolia*	Fruit	Ripe	Pulp & seeds	1	1	
Assam kandis	*Clusiaceae*	*Garcinia*	*parvifolia*	Leaves	Mature	Whole	1		
Assam kandis	*Clusiaceae*	*Garcinia*	*parvifolia*	Leaves	Young	Whole	1		
Assam ?	*Clusiaceae*	*Garcinia*	*sp*	Fruit	Ripe	Pulp	1	1	
Red garcinia	*Clusiaceae*	*Garcinia*	*sp*	Fruit	Ripe	Pulp	1		
Assam ?	*Clusiaceae*	*Garcinia*	*sp*	Leaves	Young	Whole	1		
Ketapang	*Combretaceae*	*Terminalia*	*catapa*	Fruit	Ripe	Skin	1		1
Liana "Mantangan"	*Convolvulaceae*	*Merremia*	*peltata*	Flowers		Whole	1	1	
Liana "Mantangan"	*Convolvulaceae*	*Merremia*	*peltata*	Pith	Mature	Woody li			1

				Food details			**Eaten by***		
Local/common name	**Family**	**Genus**	**Species**	**Type**	**Mature**	**Part**	***Ss***	***Ha***	***Pm***
Liana “Mantangan”	*Convolvulaceae*	*Merremia*	*peltata*	Shoots	Young	Whole	1	1	1
Simpur	*Dilleniaceae*	*Dillenia*	*excelsa*	Flowers		Petals	1	1	1
Meluang	*Dipterocarpaceae*	*Dipterocarpus*	*retusus*	Fruit	Ripe	Seeds			1
	Dipterocarpaceae	*Shorea*	*chloriflora*	Flowers		Whole			1
Damar	*Dypterocarpiceae*	*Shorea*	*javanicum*	Leaves	Mature	Lamina	1		
Damar	*Dypterocarpiceae*	*Shorea*	*javanicum*	Leaves	Young	Whole	1		
Koyo	*Dypterocarpiceae*	*Shorea*	*ovalis*	Flowers		Petals		1	
Samang	*Ebenaceae*	*Diopsyros*	*aurea*	Fruit	Ripe	Pulp	1	1	
Samang	*Ebenaceae*	*Diopsyros*	*aurea*	Leaves	Mature	Whole	1		
Samang	*Ebenaceae*	*Diopsyros*	*aurea*	Leaves	Young	Whole	1		
	Ebenaceae	*Diopsyros*	*korthalsiana*	Fruit	Ripe	Pulp & seeds	1	1	
Rayoh	*Ebenaceae*	*Diopsyros*	*macrophylla*	Fruit	Ripe	Pulp	1	1	
	Ebenaceae	*Diopsyros*	*pendula*	Leaves	Young	Whole	1		
	Ebenaceae	*Diopsyros*	*sp*	Fruit	Ripe	Pulp	1	1	
	Ebenaceae	*Diopsyros*	*sp*	Leaves	Mature	Lamina	1		
	Ebenaceae	*Diopsyros*	*sp*	Leaves	Young	Whole	1		1
	Ebenaceae	*Diospyros*	*sp*	Fruit	Unripe	Pulp & seeds			1
	Ebenaceae	*Diospyros*	*sp*	Leaves	Young	Whole			1
Tupa	*Euphorbiaceae*	*Blumeodendron*	*tokbrai*	Leaves	Young	Whole			1
	Euphorbiaceae	*Neoscortechinia*	*nicobarica*	Leaves	Young	Whole		1	1
	Euphorbiaceae			Leaves	Young	Whole			1
Jering	*Fabaceae*	*Archidendron*	*bubalinum*	Fruit	Ripe	Pulp & seeds			1
Jering	*Fabaceae*	*Archidendron*	*bubalinum*	Leaves	Young	Whole	1		1
Meribung	*Fabaceae*	*Dialium*	*patens*	Leaves	Young	Whole	1		
Arap meribung	*Fabaceae*	*Dialium*	*platysepalum*	Leaves	Young	Whole	1	1	
Kupang	*Fabaceae*	*Ormosia*	*sumatrana*	Leaves	Young	Whole			1
Liana “Kupu kupu’	*Fabaceae*	*Phanera*	*sp*	Leaves	Young	Whole	1	1	1
Liana “Kupu kupu”	*Fabaceae*	*Phanera*	*sp*	Leaves	Young	Whole	1		

				Food details			Eaten by*		
Local/common name	**Family**	**Genus**	**Species**	**Type**	**Mature**	**Part**	***Ss***	***Ha***	***Pm***
Liana “Kupu kupu”	*Fabaceae*	*Phanera*	*sp (glauca?)*	Flowers		Whole	1		
Liana “Kupu kupu”	*Fabaceae*	*Phanera*	*sp (glauca?)*	Leaves	Young	Whole	1	1	1
	Fagaceae	*Lithocarpus*	*sp*	Fruit	Ripe	Seeds			1
Semut/Ants	*Formicidae*			Insects		Whole	1	1	
Sembayung	*Lageraceae*			Leaves	Mature	Whole	1		
Sembayung	*Lageraceae*			Leaves	Young	Whole	1		
Laban	*Lamiaceae*	*Vitex*	*pinnata*	Flowers		Whole	1		
Laban	*Lamiaceae*	*Vitex*	*pinnata*	Fruit	Ripe	Skin & pulp	1	1	
Laban	*Lamiaceae*	*Vitex*	*pinnata*	Leaves	Mature	Whole	1		1
Laban	*Lamiaceae*	*Vitex*	*pinnata*	Leaves	Young	whole	1		1
Medang	*Lauraceae*	*Actinodaphne*	*bornensis*	Fruit	Ripe	Skin & pulp	1		1
Medang	*Lauraceae*	*Alseodaphne*	*falcata*	Fruit	Ripe	Skin & pulp	1	1	
Medang	*Lauraceae*	*Alseodaphne*	*falcata*	Fruit	Unripe	Seeds			1
	Lauraceae	*Beilschmiedia*	*sp*	Fruit	Ripe	Pulp		1	
Medang	*Lauraceae*	*Cryptocarya*	*ferea*	Fruit	Ripe	Whole	1		1
Medang	*Lauraceae*	*Cryptocarya*	*ferea*	Leaves	Young	Whole			1
	Lauraceae	*Dehaasia*	*microsepala*	Fruit	Ripe	Skin & pulp	1	1	
	Lauraceae	*Dehaasia*	*sp*	Fruit	Unripe	Pulp & Seeds			1
	Lauraceae	*Dehaasia*	*sp*	Fruit	Unripe	Seeds			1
Medang	*Lauraceae*	*Litsea*	*resinosa*	Fruit	Ripe	Skin & pulp	1	1	
Medang	*Lauraceae*	*Litsea*	*resinosa*	Fruit	Unripe	Seeds			1
Medang	*Lauraceae*	*Litsea*	*sp*	Flowers		Buds			1
	Leeaceae	*Leea*	*indica*	Fruit	Ripe	Whole	1		
Cempaka	*Magnoliaceae*	*Michelia*	*champaka*	Flowers		Whole	1		
Cempaka	*Magnoliaceae*	*Michelia*	*champaka*	Leaves	Mature	Lamina	1		
Duren/Durian	*Malvaceae*	*Durio*	*zibethinus*	Flowers		Buds			1
Duren	*Malvaceae*	*Durio*	*zybethinus*	Leaves	Young	Whole	1	1	1
	Meliaceae	*Aglaia*	*argenta?*	Fruit	Ripe	Pulp	1	1	

Local/common name	Family	Genus	Species	Food details Type	 Mature	 Part	Eaten by* *Ss*	 *Ha*	 *Pm*
	Meliaceae	*Aglaia*	*rubiginosa*	Fruit	Ripe	Pulp	1		
	Meliaceae	*Aglaia*	*sp*	Flowers		Whole	1		
	Meliaceae	*Aglaia*	*sp*	Fruit	Ripe	Pulp	1	1	
	Meliaceae	*Aglaia*	*sp*	Fruit	Ripe	Pulp	1	1	
	Meliaceae	*Aglaia*	*sp*	Fruit	Ripe	Pulp	1	1	
	Meliaceae	*Aglaia*	*sp*	Fruit	Ripe	Pulp	1		
	Meliaceae	*Aglaia*	*sp*	Fruit	Ripe	Pulp	1	1	
	Meliaceae	*Aglaia*	*sp*	Fruit	Ripe	Whole	1	1	
	Meliaceae	*Aglaia*	*sp*	Fruit	Unripe	Seeds			1
	Meliaceae	*Aglaia*	*sp*	Fruit	Unripe	Seeds			1
	Meliaceae	*Aglaia*	*sp*	Leaves	Young	Whole	1		
	Meliaceae	*Aglaia*	*sp*	Leaves	Young	Whole			1
Kulut	*Meliaceae*	*Dysoxylum*	*renniformes*	Fruit	Ripe	Skin & pulp		1	
Kulut (red)	*Meliaceae*	*Dysoxylum*	*sp*	Fruit	Unripe	Pulp & seeds			1
Kulut	*Meliaceae*	*Dysoxylum*	*sp*	Fruit	Unripe	Seeds			1
Suren	*Meliaceae*	*Toona*	*sureni*	Fruit	Ripe	Whole		1	
	Menispermaceae	*Anamirta*	*cocculus*	Flowers		Whole	1	1	
	Menispermaceae	*Anamirta*	*cocculus*	Shoots/Leaves	Young	Whole	1		
	Moraceae	*Antiaris*	*toxicaria*	Flowers		Whole	1		
	Moraceae	*Antiaris*	*toxicaria*	Fruit	Ripe	Skin & pulp	1	1	
Nangkan	*Moraceae*	*Antiaris*	*toxicaria*	Leaves	Young	Whole	1		
	Moraceae	*Arctocarpus*	*dada*	Fruit	Ripe	Skin & pulp	1		
Jackfruit	*Moraceae*	*Arctocarpus*	*heterophyllus?*	Fruit	Ripe	Pulp	1	1	
	Moraceae	*Arctocarpus*	*rigidus*	Fruit	Ripe	Pulp & seeds	1		
Bendo lagan	*Moraceae*	*Arctocarpus*	*sp*	Fruit	Ripe	Pulp	1		
	Moraceae	*Arctocarpus*	*sp*	Fruit	Ripe	Whole	1	1	1
	Moraceae	*Arctocarpus*	*sp*	Fruit	Ripe	Whole	1	1	
Bendo lagan	*Moraceae*	*Arctocarpus*	*sp*	Leaves	Young	Whole	1		

				Food details			**Eaten by***		
Local/common name	**Family**	**Genus**	**Species**	**Type**	**Mature**	**Part**	***Ss***	***Ha***	***Pm***
	Moraceae	*Arctocarpus*	*sp*	Leaves	Young	Whole	1		
	Moraceae	*Artocarpus*	*sp*	Leaves	Young	Whole			1
Fig	*Moraceae*	*Ficus*	*albipila*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*albipila*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*altissima*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*altissima*	Leaves	Young	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*altissima*	Shoots	Young	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*benyamina*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*caulocarpa*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*caulocarpa*	Leaves	Mature	Whole	1		
Fig	*Moraceae*	*Ficus*	*caulocarpa*	Leaves	Young	Whole	1	1	1
Fig	*Moraceae*	*Ficus*	*caulocarpa*	Leaves	Young	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*clasiramea*	Fig fruit	Ripe	Whole	1	1	1
Fig	*Moraceae*	*Ficus*	*depresa*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*drupaceae*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*drupaceae*	Fig fruit	Unripe	Whole			1
Fig	*Moraceae*	*Ficus*	*drupaceae*	Leaves	Young	Whole	1		1
Fig	*Moraceae*	*Ficus*	*elastica*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*globosa*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*globosa*	Fig fruit	Ripe	Whole	1	1	1
Fig – Free-standing	*Moraceae*	*Ficus*	*globosa* like	Fig fruit	Ripe	Whole	1		
Fig – Free-standing	*Moraceae*	*Ficus*	*hispida*	Fig fruit	Unripe	Whole			1
Fig	*Moraceae*	*Ficus*	*kerkhovenii*	Fig fruit	Ripe	Whole	1	1	1
Fig	*Moraceae*	*Ficus*	*kerkhovenii*	Leaves	Young	Whole	1		
Fig – Free-standing	*Moraceae*	*Ficus*	*pale*	Fig fruit	Ripe	Whole	1		1
Fig – Free-standing	*Moraceae*	*Ficus*	*pale*	Fig fruit	Unripe	Skin			1
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	

				Food details			**Eaten by***		
Local/common name	**Family**	**Genus**	**Species**	**Type**	**Mature**	**Part**	***Ss***	***Ha***	***Pm***
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	1
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	1
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	whole	1	1	1
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	

				Food details			Eaten by*		
Local/common name	Family	Genus	Species	Type	Mature	Part	***Ss***	***Ha***	***Pm***
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Ripe	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Fig fruit	Unripe	Skin			1
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Mature	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Mature	Whole	1		1
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		1
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole			1
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole			1
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1	1	
Fig – Free-standing	*Moraceae*	*Ficus*	*sp*	Leaves	Young	Whole	1		
Fig	*Moraceae*	*Ficus*	*sp*	Petioles		Whole		1	
Fig	*Moraceae*	*Ficus*	*stupenda*	Fig fruit	Ripe	Whole	1	1	1
Fig	*Moraceae*	*Ficus*	*stupenda*	Leaves	Young	Whole	1	1	
Fig	*Moraceae*	*Ficus*	*variegata*	Fig fruit	Ripe	Whole	1		1
Fig	*Moraceae*	*Ficus*	*virens*	Fig fruit	Ripe	Whole	1	1	1
	Myristicaceae	*Horsfieldia*	*sp*	Fruit	Ripe	Pulp	1	1	
	Myristicaceae	*Horsfieldia*	*sp*	Fruit	Ripe	Pulp	1	1	

				Food details			**Eaten by***		
Local/common name	**Family**	**Genus**	**Species**	**Type**	**Mature**	**Part**	***Ss***	***Ha***	***Pm***
	Myristicaceae	*Horsfieldia*	*sp*	Fruit	Ripe	Pulp	1	1	
	Myristicaceae	*Horsfieldia*	*sp*	Fruit	Unripe	Whole	1	1	
	Myristicaceae	*Horsfieldia*	*sp*	Leaves	Young	Whole			1
Nutmeg	*Myristicaceae*	*Myristica*	*sp*	Fruit	Ripe	Arillus		1	
Nutmeg	*Myristicaceae*	*Myristica*	*sp*	Fruit	Unripe	Seed			1
	Myristicaceae	*Sterculia*	*sp*	Leaves	Young	Whole	1		
	Myristicaceae			Leaves	Young	Whole	1		
Gelam ungu	*Myrtaceae*	*Eugenia*	*acutissima*	Fruit	Ripe	Skin & pulp	1	1	
Gelam	*Myrtaceae*	*Eugenia*	*javanica?*	Fruit	Ripe	Skin & pulp	1	1	
Gelam	*Myrtaceae*	*Eugenia*	*sp*	Fruit	Ripe	Skin		1	
Gelam	*Myrtaceae*	*Eugenia*	*sp*	Fruit	Ripe	Skin & pulp	1	1	
Gelam	*Myrtaceae*	*Eugenia*	*sp*	Fruit	Ripe	Skin & pulp	1	1	
Gelam merah	*Myrtaceae*	*Eugenia*	*sp*	Fruit	Ripe	Skin & pulp	1	1	
Terongan	*Olacaceae*	*Strombosia*	*javanicum*	Fruit	Ripe	Skin	1		
Terongan	*Olacaceae*	*Strombosia*	*javanicum*	Fruit	Unripe	Seeds			1
Terongan	*Olacaceae*	*Strombosia*	*javanicum*	Leaves	Young	Whole			1
Terongan	*Olacaceae*	*Strombosia*	*zelica*	Fruit	Unripe	Seeds			1
	Phyllanthaceae	*Aporosa*	*arborea*	Fruit	Ripe	Pulp & seeds	1	1	
	Phyllanthaceae	*Aporosa*	*sp*	Leaves	Young	Whole			1
Assam lampung	*Phyllanthaceae*	*Baccaurea*	*lancelata*	Fruit	Ripe	Pulp & seeds	1		
	Phyllanthaceae	*Baccaurea*	*sp*	Fruit	Ripe	Pulp & seeds	1	1	
Kalandri	*Phyllanthaceae*	*Cleistanthus*	*monoicus*	Fruit	Ripe	Whole	1	1	
Serih	*Piperaceae*	*Piper*	*betle*	Leaves	Mature	Whole	1	1	1
Serih	*Piperaceae*	*Piper*	*betle*	Leaves	Young	Whole	1	1	1
	Piperaceae	*Piper*	*sp*	Fruit	Ripe	Whole	1	1	1
	Polygalaceae	*Xanthophyllum*	*sp*	Fruit	Unripe	Whole			1
	Polygalaceae	*Xanthophyllum*	*sp*	Leaves	Young	Whole	1		
	Polygalaceae	*Xanthophyllum*	*sp*	Leaves	Young	Whole	1		

Local/common name	Family	Genus	Species	Food details Type	Mature	Part	Eaten by* *Ss*	*Ha*	*Pm*
	Polygalaceae	*Xanthophyllum*	*sp*	Leaves	Young	Whole	1		1
	Polygalaceae	*Xanthophyllum*	*sp*	Leaves	Young	Whole			1
	Polygalaceae	*Xanthophyllum*	*sp*	Leaves	Young	Whole			1
	Putranjivaceae	*Drypetes*	*sp*	Leaves	Young	Whole			1
	Putranjivaceae	*Drypetes*	*sp*	Leaves	Young	Whole			1
Pohon "Wiono"	*Putranjivaceae*			Leaves	Young	Whole		1	1
Nangi	*Rubiaceae*	*Adina*	*polycephala*	Leaves	Young	Whole			1
Kelampean	*Rubiaceae*	*Anthocephalus*	*chinensis*	Flowers		Petals			1
Kelampean	*Rubiaceae*	*Anthocephalus*	*chinensis*	Fruit	Ripe	Skin & pulp	1	1	
Kopi hutan	*Rubiaceae*	*Coffea*	*sp*	Fruit	Unripe	Seeds			1
	Rubiaceae	*Nauclea*	*officinalis*	Fruit	Ripe	Whole	1		1
	Salicaceae	*Flacourtia*	*rukam*	Fruit	Ripe	Whole	1		
	Salicaceae	*Homalium*	*grandiflorum*	Leaves	Mature	Stems			1
	Sapindaceae	*Lepisanthes*	*sp*	Shoots/leaves	Young	Whole	1		
Rambutan	*Sapindaceae*	*Nephilium*	*sp*	Fruit	Ripe	Pulp	1	1	1
Rambutan merah	*Sapindaceae*	*Nephilium*	*sp*	Fruit	Ripe	Pulp		1	
Rambutan keras	*Sapindaceae*	*Nephilium*	*sp*	Fruit	Unripe	Seeds			1
Rambutan	*Sapindaceae*	*Nephilium*	*sp*	Leaves	Young	Whole			1
Geruntang	*Sapindaceae*	*Xerospermum*	*noronhianum*	Fruit	Ripe	Pulp	1	1	
Geruntang	*Sapindaceae*	*Xerospermum*	*noronhianum*	Fruit	Semiripe	Pulp & seeds			1
Geruntang	*Sapindaceae*	*Xerospermum*	*noronhianum*	Leaves	Young	Whole	1		1
	Sapindaceae			Fruit	Ripe	Skin & pulp	1		
	Sapindaceae			Leaves	Young	Whole	1		1
Red "Geruntang"	*Sapindaceae?*			Fruit	Ripe	Seeds			1
Dadap serep	*Sapotaceae*	*Erythrina*	*lethosperma*	Leaves	Mature	Whole			1
Dadap serep	*Sapotaceae*	*Erythrina*	*lethosperma*	Leaves	Young	Whole			1
	Sapotaceae	*Madhuca*	*pallida*	Flowers		Whole	1	1	1
	Sapotaceae	*Madhuca*	*pallida*	Leaves	Young	Whole	1	1	

				Food details			**Eaten by***		
Local/common name	**Family**	**Genus**	**Species**	**Type**	**Mature**	**Part**	***Ss***	***Ha***	***Pm***
	Sapotaceae	*Madhuca*	*sp*	Leaves	Young	Whole	1		
	Sapotaceae	*Palaquium*	*ferox*	Fruit	Ripe	Skin & pulp	1	1	
	Sapotaceae	*Palaquium*	*sp*	Fruit	Ripe	Pulp	1	1	
	Sapotaceae	*Palaquium*	*sp*	Fruit	Ripe	Pulp & seeds	1	1	1
	Sapotaceae	*Palaquium*	*sp*	Fruit	Ripe	Skin & pulp	1		
	Sapotaceae	*Palaquium*	*sp*	Fruit	Ripe	Whole	1	1	
Payena	*Sapotaceae*	*Payena*	*sp*	Fruit	Ripe	Pulp	1	1	1
Payena	*Sapotaceae*	*Payena*	*sp*	Fruit	Ripe	Seed			1
	Simaroubaceae	*Ailanthus*	*malabarica*	Fruit	Unripe	Skin & pulp			1
Liana	*Simaroubaceae*	*Ailanthus*	*mulocanus*	Fruit	Unripe	Seeds			1
Bayur	*Sterculiaceae*	*Pterospermum*	*javanicum*	Flowers		Petals	1		1
Bayur	*Sterculiaceae*	*Pterospermum*	*javanicum*	Fruit	Ripe	Whole	1		1
Bayur	*Sterculiaceae*	*Pterospermum*	*javanicum*	Leaves	Young	Whole	1		1
Termites	*Termitoidae*			Insects		Larvae	1	1	1
Sepatau	*Theaceae*	*Adinandra*	*acuminatissima*	Fruit	Ripe	Whole	1	1	
Sepatau	*Theaceae*	*Adinandra*	*sp*	Fruit	Unripe	Whole	1	1	
Sudu	*Tiliaceae*	*Microcos*	*florida*	Fruit	Ripe	Whole	1		
Sudu	*Tiliaceae*	*Microcos*	*florida*	Leaves	Young	Whole			1
Pucung	UNRESOLVED	*Pangium*	*edule*	Leaves	Mature	Whole			1
	UNRESOLVED	*Selvitia*	*sp*	Fruit	Ripe	Whole		1	
Liana	*Verbiaceae*			Leaves	Young	Whole	1		1
	Violaceae	*Rinorea*	*sp*	Fruit	Ripe	Whole			1
Liana “Anggur”	*Vitaceae*	*Cissus*	*adnata*	Fruit	Ripe	Whole	1	1	
Liana				Flowers		Buds	1		
Liana “Petai” (purple)				Flowers		Buds	1	1	
Assam misos				Flowers		Whole			1
Liana				Flowers		Whole		1	
Liana "Lily pad"				Flowers		Whole	1		

Local/common name	Family	Genus	Species	Food details Type	 Mature	 Part	Eaten by* *Ss*	 *Ha*	 *Pm*
Liana "Pohon tidur amang"				Flowers		Whole	1		1
				Flowers		Whole	1	1	1
Liana				Fruit	Ripe	Pulp	1	1	
Liana "Kuning"				Fruit	Ripe	Pulp	1	1	
Liana "Merah"				Fruit	Ripe	Pulp	1	1	1
				Fruit	Ripe	Pulp	1	1	
				Fruit	Ripe	Pulp	1		1
Liana				Fruit	Ripe	Pulp & seeds		1	
Liana				Fruit	Ripe	Pulp & seeds		1	
Tembang bayur				Fruit	Ripe	Pulp & seeds			1
Ewil ewil				Fruit	Ripe	Seeds			1
Liana				Fruit	Ripe	Seeds			1
Benalu				Fruit	Ripe	Whole		1	
Klepu katak				Fruit	Ripe	Whole		1	
Liana bait asem				Fruit	Ripe	Whole	1		1
Liana krepok				Fruit	Ripe	Whole	1		1
				Fruit	Ripe	Whole	1	1	1
				Fruit	Ripe	Whole	1		
				Fruit	Ripe	Whole		1	
Ulat/caterpillars				Insects		Whole	1	1	
Ulat/caterpillars				Insects		Whole		1	
Eggs				Insects		Whole	1	1	
				Insects		Whole-large		1	
				Insects		Whole-large		1	
Liana "Lily pad"				Leaves	Mature	Lamina	1		
Liana				Leaves	Mature	Whole	1		
Liana				Leaves	Mature	Whole	1		
Liana				Leaves	Mature	Whole	1		

				Food details			**Eaten by***		
Local/common name	**Family**	**Genus**	**Species**	**Type**	**Mature**	**Part**	***Ss***	***Ha***	***Pm***
Liana – Fern				Leaves	Mature	Whole	1		
Assam misos				Leaves	Young	Whole			1
Epiphyte – Fern				Leaves	Young	Whole			1
Liana				Leaves	Young	Whole	1		
Liana				Leaves	Young	Whole	1		
Liana				Leaves	Young	Whole	1		
Liana				Leaves	Young	Whole	1		
Liana				Leaves	Young	Whole			1
Liana – Fern				Leaves	Young	Whole	1		
Liana "Abrasive"				Leaves	Young	Whole	1		1
Liana "Bait asem"				Leaves	Young	Whole			1
Liana "Lily pad"				Leaves	Young	Whole	1		
Liana "Pohon tidur amang"				Leaves	Young	Whole	1	1	1
Liana “Petai” (type 1)				Leaves	Young	Whole	1		
Liana “Petai” (type 2)				Leaves	Young	Whole	1		
Pakis "Cakar ayam"				Leaves	Young	Whole			1
				Leaves	Young	Whole	1		
				Leaves	Young	Whole	1	1	
				Leaves	Young	Whole	1		1
				Leaves	Young	Whole			1
				Leaves	Young	Whole			1
				Leaves	Young	Whole			1
Epiphyte (large lvs)				Leaves		Whole	1		
Epiphyte (medium lvs)				Leaves		Whole	1	1	

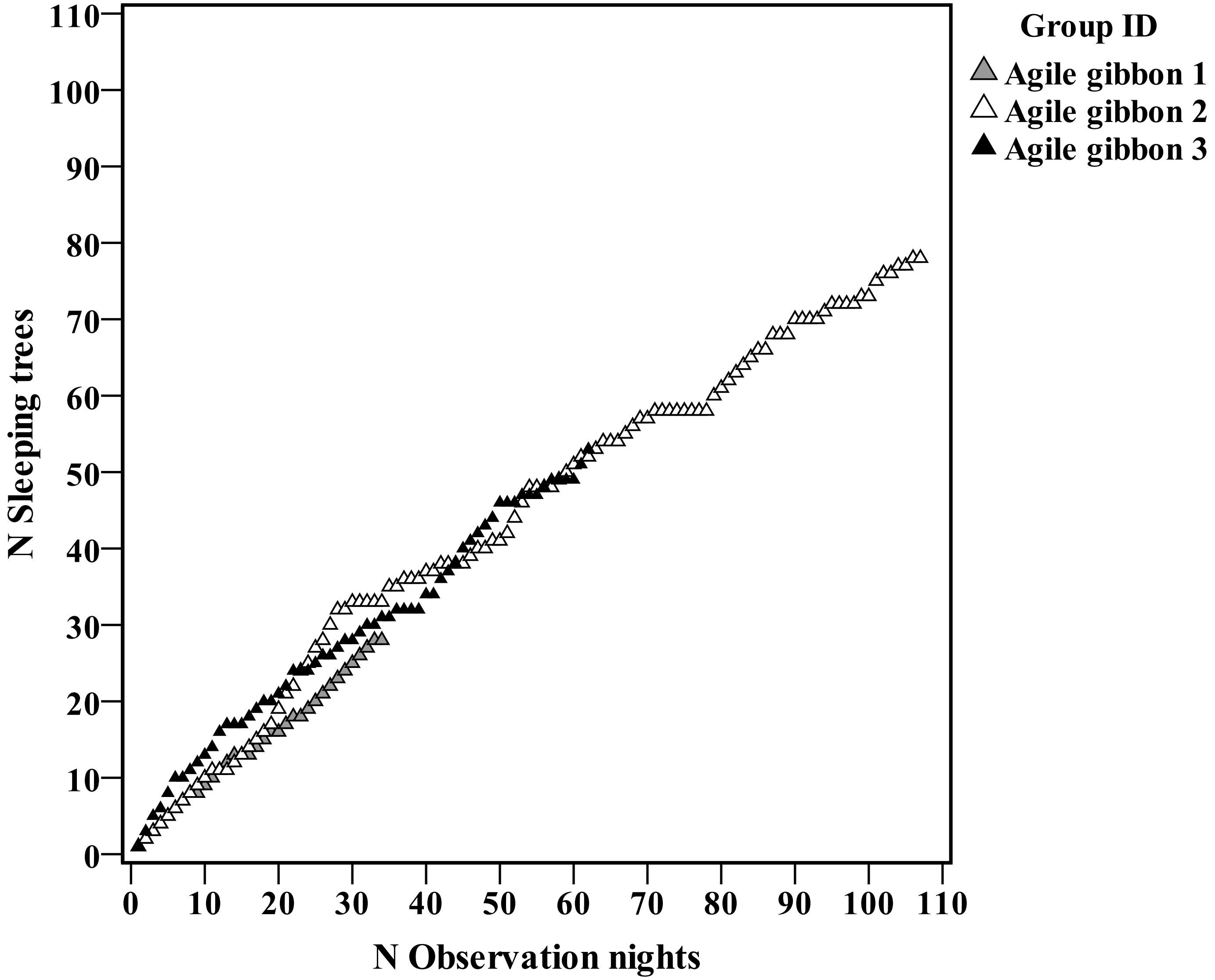
Appendix 2 Top 10 food items contributing to top 75% of daily feeding time for siamangs, agile gibbons, and mitered langurs

Primate species	Rank*	Name	Family	Genus	Species	Part
Siamangs	1	Fig	Moraceae	*Ficus*	*spp*	Fig fruit: Whole - Ripe
	2	Rao	Anacardiaceae	*Dracontomelon*	*dao*	Fruit: Pulp - Ripe
	3	Fig	Moraceae	*Ficus*	*spp*	Leaves - Young
	4	Medang	Lauraceae	*Cryptocarya*	*ferea*	Fruit: Skin/Pulp - Ripe
	6	Arek Meribung	Fabaceae	*Dialium*	*platysepalum*	Leaves - Young
	6	Liana anggur	Vitaceae	*Cissus*	*adnata*	Fruit: Skin/Pulp - Ripe
	7	Geruntang	Sapindaceae	*Xerospermum*	*noronhianum*	Fruit: Pulp - Ripe
	8	Laban	Lamiaceae	*Vitex*	*pinnata*	Fruit: Pulp - Ripe
	10	Kindo	Celastraceae	*Siphonodon*	*celastrineus*	Fruit: Skin/Pulp - Ripe
	10	Paitan	Achariaceae	*Hydnocarpus*	*gracilis*	Flowers: Whole
Agile gibbons	1	Rao	Anacardiaceae	*Dracontomelon*	*dao*	Fruits: Pulp - Ripe
	2	Fig	Moraceae	*Ficus*	*spp*	Fig fruits: Whole - Ripe
	5	Fig	Moraceae	*Ficus*	*spp*	Leaves - Young
	5	Liana mantangan	Convolvulaceae	*Merremia*	*peltata*	Shoots - Young
	5	Pohon dekat camp	Annonaceae	*Mitrepora*	*polypirena*	Fruit: Pulp - Ripe
	6	Pohon dekat camp	Annonaceae	*Mitrepora*	*polypirena*	Flowers: Whole
	7	Kindo	Celastraceae	*Siphonodon*	*celastrineus*	Fruit: Skin/Pulp - Ripe
	8	Paitan	Achariaceae	*Hydnocarpus*	*gracilis*	Flowers: Whole
	9	Assam kandis	Clusiaceae	*Garcinia*	*parvifolia*	Fruit: Pulp - Ripe

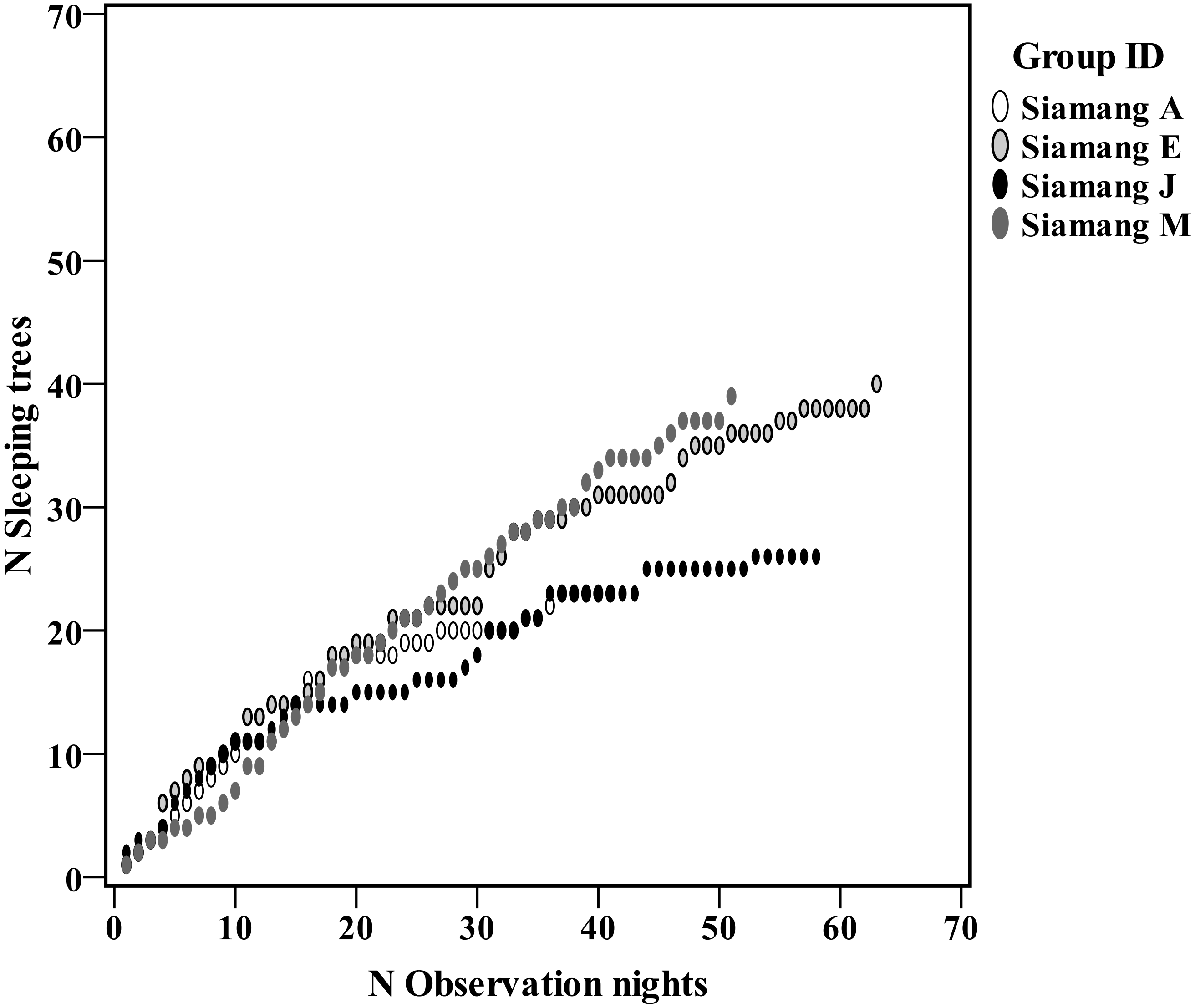
Primate species	Rank*	Name	Family	Genus	Species	Part
	10	Geruntang	Sapindaceae	*Xerospermum*	*noronhianum*	Fruit: Pulp - Ripe
Mitered langurs	1	Geruntang	Sapindaceae	*Xerospermum*	*noronhianum*	Fruit: Pulp - Ripe
	2	Terongan	Olacaceae	*Strombosia*	*javanicum*	Fruit: Seeds - Unripe
	5	Fig	Moraceae	*Ficus*	*spp*	Fig fruits: Unripe
	5	Kulut	Meliaceae	*Dysoxylum*	*sp*	Fruits: Seeds - Ripe
	5	Fig	Moraceae	*Ficus*	*spp*	Fig fruits: Ripe
	8	Seltis	Cannabaceae	*Celtis*	*nigrescens*	Flowers - Whole
	8	Antiaris	Moraceae	*Antiaris*	*toxicaria*	Fruit: Unripe
	8	Gelam	Myrtaceae	*Eugenia*	*sp*	Fruit: Whole - Unripe
	10	Medang	Lauraceae	*Alseodaphne*	*falcata*	Fruit: Pulp/Seed - Unripe
	10	Liana mantangan	Convolvulaceae	*Merremia*	*peltata*	Shoots - Young
	10	Liana bait asem	?	?	?	Fruit: Whole - Ripe
	10	Duren	Malvaceae	*Durio*	*zibethinus*	Leaves - Young
	10	Anopucuk	Annonaceae	*Saccopetallum*	*horsfeldii*	Leaves - Young

*Items ranked by frequency each occurred as daily top items across the study period; ties indicated by modified competition ranks

Appendix 3 Cumulative number of sleeping trees used by agile gibbon groups



Appendix 4 Cumulative number of sleeping trees used by siamang groups



Appendix 5 Cumulative number of sleeping trees used by mitered langurs