Research paper

Dominance Rank and Interference Competition in Foraging among Six Species of Birds in a Park in Kaohsiung City, Taiwan

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【Summary】

Through body size, social interaction, and foraging behavior, we investigated the dominance rank and interference competition among 6 bird species foraging at a park feeding site in Kaohsiung City, Taiwan. Social interactions and foraging behaviors of these birds were recorded in June to September 2009. David's scores were calculated from an interspecific interaction matrix, and the score roughly increased with the body size of birds, but some exceptions were noted. Concerning foraging behavior, feral pigeons (*Columba livia*) and Spotted-necked Doves (*Streptopelia chinensis*) took over the food area once they appeared even though Tree Sparrows (*Passer montanus*) usually arrived first. A linear regression model indicated that the number of Tree Sparrows outside the food area was positively correlated with the number of feral pigeons and Spotted-necked Doves inside the food area. Feral pigeons and Spotted-necked Doves moved away as the food was gradually consumed, and smaller species accordingly increased their foraging in the food area. Nevertheless, the Tree Sparrow was also suppressed by other medium-sized birds, like the White-vented Myna (*Acridotheres javanicus*) and Chinese Bulbul (*Pycnonotus sinensis*), and they eventually occupied the food area in large numbers at a later stage. This study revealed that body size did matter and the Tree Sparrow was clearly the least dominant species among the 6. However, a discrepancy between the dominance status and interference competition in foraging was apparent. In addition to David's score, we suggest incorporating body size, group size, and interference competition to reach a more-comprehensive dominance hierarchy in bird communities.

Key words: David's score, dominance hierarchy, dove, foraging behavior, Tree Sparrow.

Chen CC, Wu HY, Liu TT, Shieh BS. 2011. Dominance rank and interference competition in foraging among six species of birds in a park in Kaohsiung City, Taiwan. Taiwan J For Sci 26(3):255-66.

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Received March 2011, Accepted June 2011. 2011年3月送審 2011年6月通過。

研究報告

高雄市六種公園鳥類之優勢位階及覓食競爭行為

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摘 要

本研究從2009年6月到9月間在高雄市三民公園的一處餵食地點，藉由探討體型、種間的交互作用及覓食行為來研究高雄市六種常見公園鳥類的優勢位階及覓食競爭行為。利用種間交互作用勝負表計算出來的David值與體型呈現不顯著正相關。在覓食行為上，當家鴿(*Columba livia*)及珠頸斑鳩(*Streptopelia chinensis*)來到餵食區時，牠們常無視於早已在場的麻雀(*Passer montanus*)，會立即佔領整個餵食區。因此麻雀在餵食區外的數量與家鴿及珠頸斑鳩在餵食區內的數量呈現顯著正相關。而當食物量慢慢下降，家鴿及珠頸斑鳩漸漸離開時，其他較小型鳥類在餵食區內覓食的比例才隨之增加。不過麻雀還是會受到白尾八哥(*Acridotheres javanicus*)及白頭翁(*Pycnonotus sinensis*)的干擾，要等到這些中型鳥類也都離開之後，麻雀才會重新佔據整個餵食區。本研究顯示體型與覓食競爭有相當密切的關係，且最小的麻雀是所有六種鳥類中最弱勢的。我們建議除了David值之外，應納入體型、鳥群大小、干預競爭等因子，以獲致鳥種間更全面的優勢位階關係。

關鍵詞：David值、優勢位階、珠頸斑鳩、覓食行為、麻雀。

陳炤杰、吳蕙妤、劉姿岑、謝寶森。2011。高雄市六種公園鳥類之優勢位階及覓食競爭行為。台灣林業科學26(3):255-66。

INTRODUCTION

In addition to intraspecific competition, competition for resources among different animal species may also result in dominance hierarchies (Fisler 1977, Millikan et al. 1985, Wallace and Temple 1987). Larger species usually have a higher dominance rank and access resources earlier or take more food than smaller species (Hogstad 1989, Jablonski and Lee 1999, French and Smith 2005). Once dominant species appear, they often occupy a better position and make subordinate species shift to other foraging sites (Alatalo 1981, Alatalo and Moreno 1987, Jablonski and Lee 2002). Morse (1980, 1989) stated that an uneven partitioning of resources usually stems from different social dominance ranks among birds.

Although Basset (1995) considered body size to be the major factor determining dominance rank among birds, exceptions do occur. For example, the larger Black-backed Woodpeckers (*Picoides arcticus*) often stop foraging and move away when the smaller Hairy Woodpeckers (*P. villosus*) approach within 10 m (Villard and Beninger 1993). Apparently, other factors such as aggressiveness or group size may also affect the dominance rank (Burger and Gochfeld 1984, Chapman and Kramer 1996, Basset 1997, Sandlin 2000, Creel 2001). For example, the Grey-headed Junco (*Junco caniceps*) won social encounters at a higher rate in larger groups (Millikan et al. 1985). On the other hand, gender, age, experience, and residence time at feeding sites were proven to influence the dominance rank among conspecific individuals (Davies

1992, Stanback 1994, Emlem 1997, Martin et al. 1997, Pusey and Packer 1997).

The study of urban ecosystems has become quite popular in recent decades (Savard et al. 2000, Fontana et al. 2011). Although urban parks, especially forest parks, are considered habitat islands in an ocean of buildings, they are actually important habitats for bird communities living in big cities (Fernández-Juricic and Jokimäki 2001, Sandström et al. 2006). Furthermore, people may put out food at feeding areas of parks to provide birds with additional food (Orams 2002). According to the US Fish and Wildlife Service (1989), about 82 million Americans use many different ways to feed birds, and Cowie and Hinsley (1988) found that 75% of households put out food during winter in Cardiff, UK. In contrast, people in Taiwan seldom feed wild birds. A feeding site in a park in Kaohsiung City provided us the opportunity to study interspecific competition among some park bird species. Among them, the Tree Sparrow (*Passer montanus*), Chinese Bulbul (*Pycnonotus sinensis*), Spotted-necked Dove (*Streptopelia chinensis*), feral pigeon (*Columba livia*), Grey Treepie (*Dendrocitta formosae*), and White-vented Myna (*Acridotheres javanicus*) are common bird species in city parks of Kaohsiung (Chen et al. 2005) and frequently occur at the feeding site examined in this study. We investigated the dominance rank and interference competition in foraging among these 6 bird species.

MATERIALS AND METHODS

Study area

The study site is located within the San-Min Park (18.4 ha, 22º64′N, 120º31′E) in Kaohsiung City, southern Taiwan. It is a well-maintained park, full of trees and meadows. Owing to an enthusiastic resident who has been feeding birds in the park every day for a long period of time, hundreds of birds, including feral pigeons, Spotted-necked Doves, Tree Sparrows, etc, are attracted to the feeding site almost every day.

The food area was defined as the area of ground covered by food, and it was circular with a radius of about 1 m. Bread crumbs and bean sprouts were provided in the food area twice a day, once in the morning and once in the afternoon. The quantity of food was recorded whenever we began an observation. The quantity of food in the food area was divided into 3 levels: 1) abundant, when food had just been spread in the food area to about 75% of food remaining; 2) medium, the remaining food covering > 50% of the food area, and soil was clearly exposed in certain areas; 3) little, < 50% of the food area was covered by food, and dark brown soil was exposed in most parts of the circle.

Field methods

From 25 June to 30 September 2009, we recorded social interactions and foraging behaviors of these bird species at the feeding site. Concerning social interactions, we made note of the time, species involved, aggressive behavior, and outcome of the interaction. We scored a ‘win’ for birds that initiated aggressive behavior, and a ‘loss’ for the bird that displayed submissive behavior. Aggressive behavior included attacking others with the beak, chasing others, and threat displays with posture or sound. Birds which displayed submissive behavior usually retreated or yielded to the bird that initiated the aggressive behavior. For foraging behaviors, we recorded foraging techniques applied by each bird species at the feeding site. Foraging techniques included foraging within the food area, carrying food out of the food area, carrying food up to trees, or snatching food from other

individuals within the food area.

To estimate the abundance of each bird species at the feeding site, we used scan sampling at 10-min intervals (Martin and Bateson 1993) to count the number of each species in the feeding site. If birds had flown away because of a disturbance before the scanning time, we waited for another 10 min to repeat the scanning. In between the sampling points, we recorded social interactions among species and the foraging behaviors of each species.

We made additional observations to examine the distribution of Tree Sparrows inside and outside the food area and the abundances of large-sized bird species in the food area. We scanned the food area every 5 min to count the number of feral pigeons and Spotted-necked Doves inside the food area, and the number of Tree Sparrows staying inside and outside the food area.

Data analysis

We calculated David's score (DS = W + W_2 – L – L_2; David 1987) as a dominance index for each bird species based on an interspecific dominance matrix of the 6 bird species (Table 1). W and L represent the sum of species *i*'s wins and losses, and W_2 and L_2 represent the wins and losses of species defeated by species *i* (David 1987, de Vries 1998). Because our data had many interacting pairs with reversals, application of David's score was considered appropriate (Gammell et al. 2003, Bang et al. 2010). We then used the Spearman rank correlation coefficient to test if the dominance index was positively correlated with the body size of each bird species (SAS 1999). Body size indices were derived from PRIN1 through a principal component analysis (PCA), that integrated body length and weight of the 6 bird species (Table 2; SAS 1999), because body length and mass may both play a role in dominance displays (Robinson-Wolrath and Owens 2003). We used a Chi-squared test to examine whether different foraging techniques were applied homogeneously by the 6 bird species in the food area (SAS 1999). We performed a simple linear regression to examine if the number of Tree Sparrows staying outside the food area was related to the number of feral pigeons and Spotted-necked Doves foraging inside the food area. In addition, a Chi-squared test was also used to examine whether the distribution of Tree Sparrows and medium-sized birds (either Chinese Bulbul or White-vented Myna) were homogeneous across different food amount stages.

Table 1. Interspecific dominance matrix of 6 bird species foraging in the food area of a Kaohsiung City park. Species are arranged by body size. Winners are listed down the left column; losers are listed across the upper row

Winners	Losers						
	Feral pigeon	Grey Treepie	Spotted-necked Dove	White-vented Myna	Chinese Bulbul	Tree Sparrow	Total
Feral pigeon	-	1	33	2	2	48	86
Grey Treepie	1	-	10	0	7	19	37
Spotted-necked Dove	2	0	-	6	1	53	62
White-vented Myna	1	1	25	-	3	58	88
Chinese Bulbul	0	0	3	0	-	22	25
Tree Sparrow	12	2	24	3	10	-	51
Total	16	4	95	11	23	200	-

Table 2. Body weight, length, and derived body size index of the 6 bird species included in the study. Species are ranked by the body size index

Species	Body weight (g)[1)]	Body length (cm)	Body size index[2)]
Feral pigeon	267.5	32.5	1.81
Grey Treepie	105.0	38.0	0.95
Spotted-necked Dove	128.0	28.8	0.40
White-vented Myna	100.0	21.0	-0.44
Chinese Bulbul	29.9	19.0	-1.16
Tree Sparrow	23.5	14.5	-1.56

[1)] Body measurements were derived from *Handbooks of the Birds of the World* (del Hoyo et al. 1992-2010).

[2)] Body size index was the PRIN1 through the principal component analysis that integrated body length and weight of the 6 bird species.

RESULTS

Dominance rank

The Tree Sparrow was the smallest and least dominant species, and it was attacked or supplanted by other species up to 200 times (Table 1). The Spotted-necked Dove, although relatively large in size, usually yielded ground to other species and was ranked second as a loser. On the other hand, the White-vented Myna was the most aggressive species and chased other birds up to 88 times. The feral pigeon was also aggressive. When foraging in the food area, it moved boldly around and supplanted other nearby species. The feral pigeon ranked second as a winner. David's scores (dominance index) of the 6 species were as follows: White-vented Myna (9.54) > feral pigeon (8.46) > Grey Treepie (5.43) > Chinese Bulbul (-6.38) > Spotted-necked Dove (-7.87) > Tree Sparrow (-9.19) (Fig. 1). Obviously, the first 3 species were dominant over the latter 3 species in the food area.

We used a body size (or physique) index, extracted from PRIN 1 through the PCA that integrated body length and weight (Table 2). Although a positive correlation was found, the relationship between the dominance index and body size was not significant (r_s = 0.54, n = 6, p = 0.27, Fig. 1). David's score of the White-vented Myna was much higher than that predicted by body size, whereas the Spotted-necked Dove's score was far lower than expected.

Foraging behavior

Foraging techniques applied by the 6 bird species in the food area significantly differed (χ^2 = 69.81, df = 18, p < 0.001, Fig. 2). Feral pigeons and Spotted-necked Doves ate food completely in the food area. In contrast, the Grey Treepie carried food back to trees 93.1% of the time. The Chinese Bulbul mainly foraged in the food area, but carried a small portion of food to the trees. On the other hand, the White-vented Myna and Tree Sparrow fed mainly in the food area, with a few occasions of carrying food out of the food area.

The Tree Sparrow was usually the first species to appear after food was spread into the food area, and its number rapidly accumulated. Apparently, some of them had been waiting around prior to the feeding time. Once the feral pigeons and Spotted-necked Doves joined in, they immediately took over the food area. These larger species occupied the food area, causing Tree Sparrows to for-

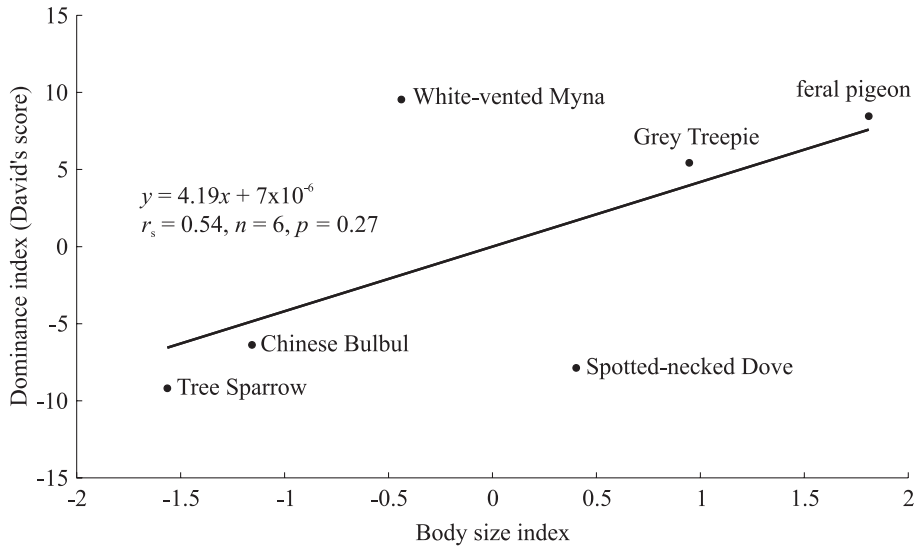

Fig. 1. Relationship between body size and the dominance index was not significant, showing that the dominance rank was not solely determined by body size. Note that the David's score for the White-vented Myna was larger than predicted by body size, whereas the Spotted-necked Dove had a much lower score than expected.

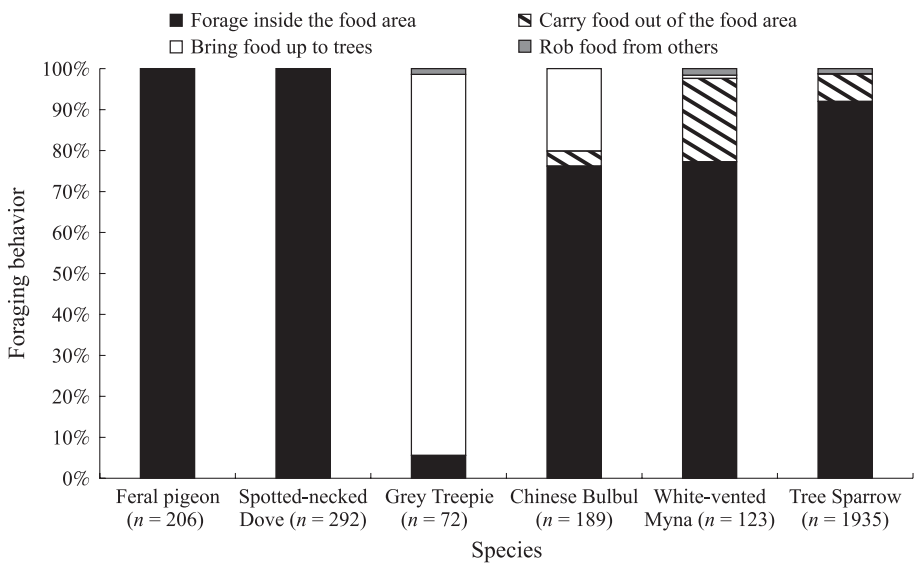

Fig. 2. Foraging techniques in the food area significantly differed among the 6 bird species ($\chi^2 = 69.81$, df = 18, $p < 0.001$). Five species foraged mainly in the food area, but the Grey Treepie carried food back to trees most of the time.

age peripherally or stay outside the food area. Consequently, the number of Tree Sparrows outside the food area increased as the number of feral pigeons and Spotted-necked Doves in the food area increased ($R^2 = 0.3228$, df = 195, $p < 0.0001$, Fig. 3).

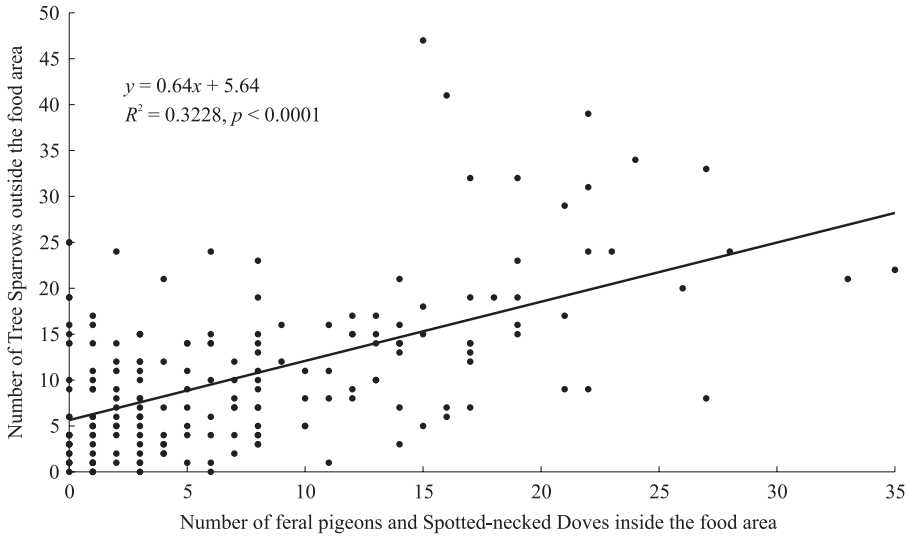

Fig. 3. Number of Tree Sparrows outside the food area was positively correlated with the total number of feral pigeons and Spotted-necked Doves inside the food area.

As food was consumed and the amount declined, numbers of feral pigeons and Spotted-necked Doves decreased as well (Fig. 4). In contrast, proportions of Chinese Bulbul (Fig. 4a), White-vented Myna (Fig. 4b), and Tree Sparrows (Fig. 4c) that foraged inside the food area accordingly increased. Although total numbers of Chinese Bulbul (Fig. 4a) and White-vented Myna (Fig. 4b) also decreased as food was gradually consumed, the number of Tree Sparrows inversely increased (Fig. 4c). Numbers of individuals appearing in the feeding site were not homogeneous at different stages of food amount between the Tree Sparrow and medium-sized birds (for Chinese Bulbul, $\chi^2 = 112.34$, df = 2, $p < 0.001$, Fig. 5a; for White-vented Myna, $\chi^2 = 50.74$, df = 2, $p < 0.001$, Fig. 5b). Eventually, the number of Tree Sparrows greatly increased in the final stage when little food was left.

DISCUSSION

Although the Spearman rank correlation coefficient ($r_s = 0.54$, $p = 0.27$) indicated a poor fit between body size and dominance index, the feral pigeon, Grey Treepie, Chinese Bulbul, and Tree Sparrow were located very close to the regression line. This indicates that body size may be important for some species in determining the dominance rank, but definitely not for every species. It implies that the dominance rank of birds is also influenced by other factors besides body size. The dominance index of the White-vented Myna was much higher than predicted by body size. The White-vented Myna is the most abundant introduced starling in Taiwan (Lin 2001). It has white spots, is aggressive toward other native species, and often scared away other species by jumping and running around in the food area while foraging. In contrast, the Spotted-necked Dove was timid and easily intimidated by other bird species in the food area; it ranked second in the frequency of submissive behavior, and thus its dominance index was much lower than expected from its body size. On the other hand, when food was abundant, all species fed intensively and tolerated one another to some extent, and thus very few

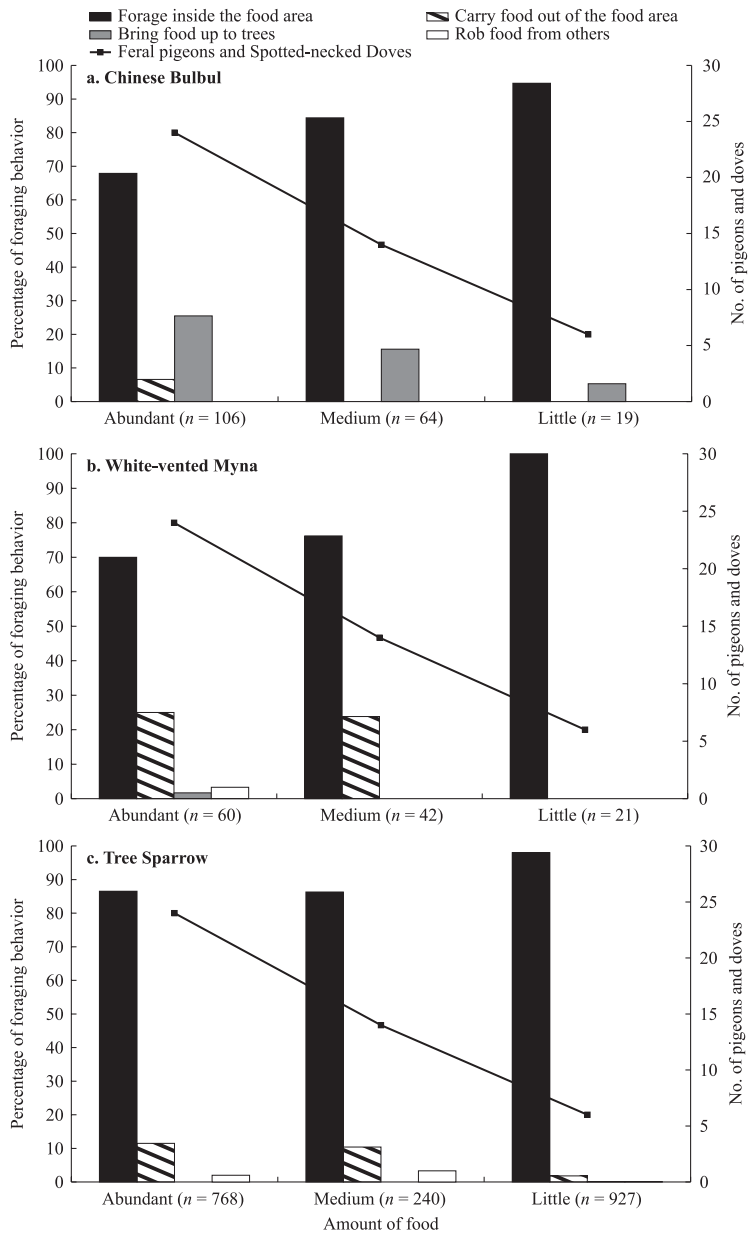

Fig. 4. Proportions of individuals foraging inside the food area increased for Chinese Bulbul (a), White-vented Myna (b), and Tree Sparrow (c) when the number of feral pigeons and Spotted-necked Doves decreased in accordance with the amount of food left.

clashes were observed. It is obvious that an abundant food supply lessened the intensity of conflict and consequently the frequency of social interactions (Suhonen et al. 1992). Therefore, the dominance rank was not completely determined by body size; other factors such as aggressiveness, submissiveness, food amount, group size, and foraging behavior may all influence the dominance ranking.

In terms of foraging behavior, larger spe-

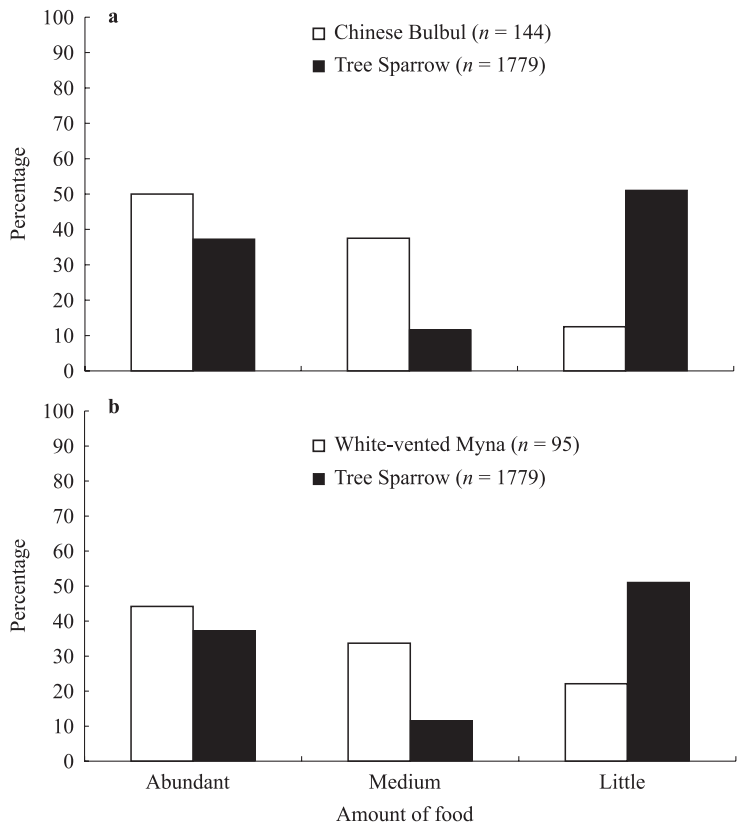

Fig. 5. Number of Tree Sparrows present at the feeding site was not homogeneous with that of Chinese Bulbul (a) or White-vented Myna (b) at different stages of food amount.

cies exhibit obvious advantages over smaller ones, and the presence of larger species does mean a considerable threat to smaller ones. In general, dominant birds often occupy a better position and have priority to use resources (Vehrencamp 1983, Hogstad 1989). Once the dominant species appear, subordinate species will yield and change their foraging sites (Alatalo 1981, Alatalo and Moreno 1987). In this study, a large number of Tree Sparrows often appeared in the food area soon after the food was spread. However, once feral pigeons and Spotted-necked Doves appeared, Tree Sparrows yielded the ground to these larger species and foraged peripherally or carried food out of the food area. Interference competition (Vahl et al. 2005, 2007) occurred in this case because feral pigeons and Spotted-necked Doves usurped the space previously occupied by Tree Sparrows. On the other hand, Tree Sparrows might increase their use of poorer sites to minimize interference (Johnson et al. 2006). As a result, the number of Tree Sparrows outside the food area was positively correlated with the total number of feral pigeons and Spotted-necked Doves inside the food area. Occupation of the food area by feral pigeons and Spotted-necked Doves also created some obstacles for medium-sized species entering, even though the myna had a higher dominance rank over the feral pigeon and Spotted-necked Dove. The proposition is supported by evidence that White-vented Mynas and Chinese Bulbuls

could only freely move into the food area after feral pigeons and Spotted-necked Doves had gradually left. At an even later stage, Tree Sparrows would occupy the food area again after all other species had mostly gone. It is evident that body size does matter when birds forage together at the same place, and that the Tree Sparrow was the least dominant species among the 6.

This study indicated that the dominance status determined by one-on-one social interactions is not consistent with those observed through foraging competition. The Spotted-necked Dove ranked fifth in one-on-one encounters; however, they co-occupied the food area with the feral pigeons, the most dominant species. Such observations imply that subordinate large species may eventually enhance their competition when their group size becomes large. Nevertheless, this rule might not be true for small species since the Tree Sparrow ranked the last in dominance regardless of its high numbers. As a result, we consider that David's score might not fully represent the dominance status of birds in a community. Since the scores are solely based on one-on-one interactions, they do not take into account the group size of competitive species. As the "square law" in Lanchester's "Theory of Combat" predicts, if all individuals are equally vulnerable to attack, a large number of subordinate individuals are better than a few dominant ones (Franks and Partridge 1993). The group size effect appeared to be prominent in large birds such as the Spotted-necked Dove, but seemed less apparent for the smaller Tree Sparrow. Lanchester's "Theory of Combat" was applied to behavioral studies (Franks and Partridge 1993, McGlynn 2000, Shelley et al. 2004), in ant wars (Whitehouse and Jaffe 1996, McGlynn 2000), and interspecific dominance matrix in birds (Shelley et al. 2004). We suggest that further studies apply Lanchester's laws and incorporate multiple factors, including body size, group size, and social interactions to formulate a more-realistic dominance ranking.

ACKNOWLEDGEMENTS

We thank the man that provided us the chance to observe those birds he has been feeding for more than 5 yr. We are also indebted to HL Chen and SP Lai for their help during the study.

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