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Intraspecific host selection of Père David's deer by cattle egrets in Dafeng, China

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ABSTRACT

Studies have focused on foraging ecology of cattle egrets (*Bubulcus ibis*) and their selection of ungulate host species. However, few studies have been conducted at intraspecific levels, such as the sex/age class of a specific ungulate. In this study, the foraging behavior and intraspecific host selection of cattle egrets associated with Père David's deer (*Elaphurus davidianus*) were investigated at the Dafeng National Nature Reserve, China in summer 2011 and 2012. Egret-deer pairing status was analyzed and intraspecific host selection index was calculated. Cattle egrets preferred to feed with female deer compared with male deer and fawns. In contrast to solitary birds, cattle egrets following a deer benefited from a relatively low vigilance output, high foraging success, low energy expenditure, and high total foraging yields. These egrets also maximized benefits when they followed female deer compared with male deer and fawns. Our results further indicated that egrets likely preferred females because of the appropriate moving speed that allowed these egrets to follow and forage sufficiently and effectively. The males of Père David's deer were possibly more aggressive than the females during the rutting season, causing egrets to experience difficulty in accompaniment and feeding. Fawns were not preferred because they were usually motionless and insufficiently large to stir more insects. We did not find any behavioral differences in vigilance and feeding between juveniles and adults. Our results suggested that cattle egrets could obtain significant benefits from their association with Père David's deer, and these benefits were maximized when they followed female deer.

This article is part of a Special Issue entitled: insert SI title.

1. Introduction

Mixed-species groups are common in the animal world; they range from closely related species, such as the mixed groups of Przewalski's gazelle (*Procapra przewalskii*) and Tibetan gazelle (*Procapra picticaudata*) (Li et al., 2010), to species of different classes, such as cleaner birds and their corresponding mammal partners (Swash and Still, 2006; King and Cowlishaw, 2009). Theoretical and empirical studies have focused on the advantages experienced by animals living in mixed-species groups that are usually derived from improved foraging and/or predator avoidance (Powell, 1985; Valone, 1989; Hodge and Uetz, 1996). Group-living animals maximize the success of foraging and minimize the risk of predation by applying personal information or by pooling social information from other group members (King and Cowlishaw, 2007).

Cattle egret (*Bubulcus ibis*) is the only species of heron that mainly feeds on insects. This species is globally distributed in various habitats. Cattle egrets also live alongside herbivores, such as cattle, zebras, water buffalos, bison, and other large mammals (Rice, 1954; Caldwell, 1956; Burger and Gochfeld, 1989; Seedikkoya et al., 2005). Studies on the foraging behavior of cattle egrets associated with ungulates support their commensalistic relationship, in which cattle egrets gain feeding benefits, but ungulates slightly benefit from this relationship (Dinsmore, 1973; Thompson et al., 1982; Wahungu et al., 2003; Seedikkoya et al., 2005; Kamler et al., 2008). Studies have further demonstrated that cattle egrets foraging with ungulates obtain more food items and require fewer steps than those foraging alone in the same habitat (Dinsmore, 1973; Burger and Gochfeld, 1993; Seedikkoya et al., 2005).

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Many decisions should be made when cattle egrets follow a foraging ungulate. These important decisions may include one of the following: time at which cattle egrets seek hosts; specific host species; sex/age class; and time at which cattle egrets should choose a new individual or host species. Studies have been conducted to compare foraging behaviors when different host species are followed (Thompson et al., 1982; Burger and Gochfeld, 1993; Kour and Sahi, 2012). These studies have revealed that the moving speed of hosts may be an important factor influencing host selection (Burger and Gochfeld, 1982, 1993). However, studies have been rarely conducted to investigate host selection at intraspecific levels. Many ungulates are sexually dimorphic and segregated (Ruckstuhl, 2007). Thus, the sex/age of hosts likely affects the mechanism by which cattle egrets select hosts.

Age-related foraging differences have been extensively studied in various species, particularly wetland birds (Li et al., 2013). In many avian species, older birds commonly expend less effort to capture preys than younger birds. Age-related differences in foraging efficiency may be the result of differences in foraging skill, patch usage, or both (Brandt, 1984). In this case, adult egrets likely gain more benefits than young birds when similar hosts are followed.

Mixed-species association is observed between cattle egrets and Père David's deer at the Dafeng Nature Reserve, China. Père David's deer, which is sexually dimorphic and segregated (Jiang et al., 2000), is probably the only host of cattle egrets in the Jiangsu coastlines of China. In the rutting season from May to August, males compete with other males, hold harems, and mate (Jiang et al., 2000, 2004; Zheng et al., 2013); as such, males probably move faster than females. This condition indicates that foraging cattle egrets experience difficulty when they follow males. By contrast, fawns are smaller (Li, 2013) and move less than adults (Zeng et al., 2004); therefore, fawns may rouse insects at a lesser extent than adult deer. Thus, cattle egrets should likely prefer female Père David's deer rather than males and fawns. We further investigated the foraging benefits of cattle egrets from their specific hosts. In our hypothesis, cattle egrets possibly obtain more food easily when they forage with female deer. We also examined the difference in the foraging success of adult cattle egrets from that of juvenile cattle egrets foraging with the same hosts.

2. Methods

2.1. Study site

This study was carried out at the Dafeng Père David's Deer National Nature Reserve (32°59′N to 33°03′N, 120°47′E to 120°53′E) in Jiangsu Province, China from July to August 2011 and 2012. The reserve was founded in 1986 and is located along the Yellow Sea coast in eastern China (2 m to 4 m above the sea level). The reserve's vegetation is dominated by Chinese Pennisetum (*Pennisetum alopecuroides*), cogongrass (*Imperata cylindrical*), Canadian Populus (*Populus canadensis*), and locust (*Robinia pseudoacacia*) (Yu et al., 1996).

2.2. Host selection

Data were collected from the semi-free ranging herds of Père David's deer associated with cattle egrets in the reserve by using a telescope (Celestron® Ultima80ed, Model 52251 20–60 × 80 mm). The foraging behavior of cattle egrets with Père David's deer was focally observed on a 39 m high tower or at a distance >120 m to avoid the interference of observers (Li et al., 2007). This tower is located in the east district of the first core zone of the nature reserve, where the overall situation of mixed-species groups can easily be monitored and observed. Père David's deer is the only grazing animal in the vicinity where cattle egrets can forage with. In this study, cattle egrets were considered to be associated with deer if they were within the range of approximately 3 m of the grazing deer.

Deer-egret pairing status was scanned observed at an interval of 1 h to determine the host preferences of egrets. This one-hour interval was considered because the pairs were usually separated within 30 min. After 1 h, pairing status should be different from the initial status. Each pair was classified into six types: adult egret-male deer; adult egret-female deer; adult egret-fawn; juvenile egret-male deer; juvenile egret-female deer; and juvenile egret-fawn. The deer groups were also classified into three types: male-only group; female-only group; and mixed-sex group. In each scan, the pairing status and the deer group composition were recorded. Approximately 82 scans were performed in 46 groups. However, only the mixed-sex deer group (55 scans on 32 groups) was used as targets to calculate host preference index. Host preference index was defined on the basis of the habitat selection index expressed as $w_i = o_i/\pi_i$ (Boyce and McDonald, 1999). w_i is calculated as the proportion of used host units of category i from available units. o_i is the proportion of used host units of category i; $\pi_i = a_i/a_+$, where a_+ is the population of available host units and a_i is the population in category i.

2.3. Behavioral observation

Behavioral observations on foraging adult and juvenile cattle egrets were randomly selected and recorded for 10 min. The samples selected in less than 2 min were deleted, and the average observation duration of the remaining samples was 3.85 ± 0.07 min. Juvenile cattle egrets can be distinguished from the adults in terms of bill and plumage. Adults mainly exhibit white plumage, a yellow bill, dark brown to yellow legs, and black toes. Juvenile birds lack colored plumes and have a black bill and black legs. The number of the head-jerk swallow and the number of steps per minute by adult and juvenile cattle egrets were counted to determine the capture success rate. The number of scans on the environment (i.e., standing upright, holding its neck erect) was used as an index of vigilance. Pecking frequency was used as the number of attempts to capture food items per minute. Total foraging earnings were obtained by determining the number of successful captures per minute. Expenditure per capture was determined by dividing the steps/capture by the captures/min. This value provides a relative foraging efficiency ratio, which is a low ratio indicating a high capture rate with few steps (Dinsmore, 1973).

Considering that the animals did not move remarkably during foraging, we selected the samples from different parts of the deer group to avoid sampling the same individual on the same day. We also randomly selected 33 solitary egrets and counted the same parameters for comparison.

2.4. Data analysis

One-sample t-test was used to examine the host preference index. In this test, if $w_i > 1$, a cattle egret prefers its host class; if $w_i = 1$, a cattle egret has no specific host preference; and if $w_i < 1$, a cattle egret does not prefer its host class. For foraging and vigilance data, a general linear model was used to address the possible effects of the age of egrets (i.e., adult, juvenile), host status (i.e., male deer, female deer, fawns, and without deer), and interaction. Observation duration was also included in the model as a continuous co-variable to minimize the possible effect of the observation length on these variables. For multiple comparisons, LSD for post-hoc tests was used. All of the data were analyzed with SPSS and significance levels were set at $p < 0.05$.

Table 1
Foraging variables (estimated marginals with GLM) of cattle egrets in selecting a specific host in Dafeng National Nature Reserve.

Dependent variables	Egrets with male deer Mean ± SE (N = 92)	Egrets with female deer Mean ± SE (N = 99)	Egrets with fawn Mean ± SE (N = 19)	Solitary foragers Mean ± SE (N = 33)
Vigilance frequency (no./min)	0.15 ± 0.04a	0.23 ± 0.04ab	0.38 ± 0.11b	0.67 ± 0.07c
Capture success rate	0.58 ± 0.02a	0.57 ± 0.02a	0.46 ± 0.06ab	0.32 ± 0.04b
No. of steps/attempt	10.96 ± 0.79a	9.93 ± 0.82a	11.67 ± 2.32a	11.10 ± 1.60a
Pecking frequency (no./min)	2.69 ± 0.20a	3.01 ± 0.21a	2.31 ± 0.60a	2.89 ± 0.41a
Total foraging earnings (successful captures/min)	1.44 ± 0.10ab	1.64 ± 0.10a	0.94 ± 0.28bc	0.82 ± 0.19c
Expenditure per capture (steps/capture)	13.07 ± 2.48ab	8.98 ± 2.58a	26.97 ± 7.28b	21.64 ± 5.02b

The same letters in the same line indicate insignificant at $p < 0.05$.

Table 2
Foraging variables (estimated marginals with GLM) between juvenile and adult foraging cattle egrets in Dafeng National Nature Reserve.

Dependent variables	Juveniles with deer Mean ± SE (N = 167)	Adults with deer Mean ± SE (N = 76)
Vigilance frequency (no./min)	0.30 ± 0.03a	0.41 ± 0.06a
Capture success rate	0.51 ± 0.02a	0.46 ± 0.04a
No. of steps/attempt	12.17 ± 0.67a	9.66 ± 1.35a
Pecking frequency (no./min)	2.78 ± 0.17a	2.67 ± 0.35a
Total foraging earnings (successful captures/min)	1.21 ± 0.08a	1.21 ± 0.16a
Expenditure per capture (steps/capture)	20.15 ± 2.12a	15.18 ± 4.25a

The same letters in the same line indicate insignificant at $p < 0.05$.

3. Results

Using the 55 scans on host selection, we calculated w_i. Cattle egrets preferred to forage or follow the female deer at $w_f = 1.32 \pm 0.15$, which is significantly greater than 1 ($t_{54} = 2.152$, $p = 0.036$); by contrast, no significant preference for the male deer ($w_m = 1.12 \pm 0.11$, $t_{54} = 1.142$, $p = 0.259$) or fawns ($w_f = 0.93 \pm 0.15$, $t_{48} = 1.142$, $p = 0.622$) was observed.

A total of 243 observations of foraging cattle egrets were recorded during the two summers. Among these observations, 167 were juvenile egrets, whereas 76 were adult egrets; 92 cases were associated with male deer, 99 cases were associated with female deer, 19 cases were associated with fawns, and 33 cases were associated without a deer. The foraging cattle egrets following male Père David's deer (Table 1) exhibited the lowest mean time spent vigilant; egrets with female deer and fawns showed higher mean vigilance time than foraging cattle egrets. Solitary egrets exhibited the highest mean time vigilance ($F_{3,234} = 13.909$, $p < 0.001$). The capture success rate decreased significantly from egrets with male deer, with female deer, and with fawns to solitary egrets ($F_{3,234} = 10.931$, $p < 0.001$). No significant difference was observed in the attempts to capture a prey ($F_{3,234} = 0.397$, $p = 0.756$) and in pecking frequency ($F_{3,234} = 0.661$, $p = 0.577$) when egrets followed deer of different sex and age classes. However, cattle egrets foraging with female deer exhibited the highest mean earnings per minute, followed by egrets with male deer, fawns, and solitary foragers exhibited the lowest total foraging earnings ($F_{3,234} = 5.76$, $p = 0.001$). The energy spent to capture food items decreased significantly in foraging egrets with female deer, egrets with male deer, solitary egrets, and egrets with fawns ($F_{3,234} = 3.031$, $p = 0.030$).

The variables of juvenile cattle egrets were compared with those of adult cattle egrets (Table 2), but no significant difference was observed (i.e., vigilance, $F_{1,234} = 2.461$, $p = 0.118$; capture success rate, $F_{1,234} = 1.571$, $p = 0.211$; attempts, $F_{1,234} = 2.785$, $p = 0.096$; pecking frequency, $F_{1,234} = 0.073$, $p = 0.788$; total foraging earnings, $F_{1,234} < 0.001$, $p = 0.991$; and expenditure benefit, $F_{1,234} = 1.098$, $p = 0.296$).

4. Discussion

On the basis of these results, we found that the cattle egrets gained feeding and vigilance advantages when they followed grazing Père David's deer. The egrets associated with a deer spend less vigilance time than solitary egrets, indicating a shelter effect from deer and a potential to feed longer. The egrets associated with deer gained the following significant feeding benefits: higher capture success rate; lower energy spent; and higher foraging earnings. These results were also found in other studies, such as between egrets and cattle, zebras, water buffalos, bison, and ostriches (Rice, 1954; Dinsmore, 1973; Thompson et al., 1982; Burger and Gochfeld, 1989; Wahungu et al., 2003; Kamler et al., 2008).

As expected, cattle egrets spread themselves among Père David's Deer, choosing females as their favorite hosts. Burger and Gochfeld (1982) as well as Kour and Sahi (2012) revealed that cattle egrets prefer hosts with moderate speed and bulky body size. These hosts are easy to follow and provide egrets with the ability to search for sufficient insects or other food items; as a result, capture success is improved. Considering that host age classes differ in terms of several characteristics (i.e., size, weight, movement speed, and tolerance of egrets), Burger and Gochfeld (1993) found that egrets can avoid or leave hosts that move extremely slowly or extremely fast and remain with or join hosts that move at optimal speed. In the rutting season, male Père David's deer fight with one another to obtain a higher rank. These males also monitor a harem group to find the right females that are in estrus to obtain mating rights. All of these conditions cause males to move at a higher rate than females (Jiang et al., 2004; Li et al., 2004; Zheng et al., 2013); as such, cattle egrets do not prefer to follow males as often as females. Males are also vigilant and aggressive (Thompson et al., 1982; Li et al., 2010). In some instances, males even chase and drive away nearby egrets. Females are less aggressive and spend more time feeding at a slow walking speed; therefore, these females are probably easier for egrets to follow than males. By comparison, fawns are playful but sometimes stand motionless to avoid predators or human disturbance (Zeng et al., 2004). Hence, fawns provide less feeding opportunities to egrets because fewer insects are roused because of their smaller body sizes and less locomotion than adult deer. Although previous studies reported the host selection of egrets at interspecific levels and showed that cattle, cows, or other ungulates are the most effective host species of commensal cattle egrets in various habitats (Thompson et al., 1982; Burger and Gochfeld, 1993; Kour and Sahi, 2012), our study is the first to describe host selection at an intraspecific level.

In foraging, adult birds are more successful foragers than juveniles when these birds are associated with several host species (Espin et al., 1983; Stevens, 1985; Cezilly and Boy, 1988; Burger and Gochfeld, 1989). However, no significant difference between the two ages was observed in this study. Considering that all of the juveniles were at least one year old and have spent more than half a year in a southern temperate area to feed with cattle or other host species (BirdLife International, 2013), we hypothesize that juveniles have learned adequate food-catching skills following other host species. Therefore, juveniles have likely learned sufficient feeding skills and strategies to search for resources by the time they visited Dafeng in spring and summer.

In general, the study showed the significant benefits that cattle egrets derived from feeding in association with Pere David's deer, although egrets showed selection preference for different sex and age classes of deer. Cattle egrets selected female Père David's deer as the best host class probably based on the greater food availability for the egrets, and this preference was likely related to the moderate movements of female deer compared with male deer and fawns. Further studies should be conducted on several specific factors, such as the moving rate and active status of deer, because these factors affect the host selection and foraging behavior of cattle egrets associated with Père David's deer at the Dafeng National Natural Reserve. Furthermore, we found that egrets usually defend their hosts against other egrets. Hence, further studies should be conducted to determine whether or not host defense is related to the age of egrets or sex/age of deer.

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