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# Ritualized fights among foraging cattle egrets following Père David's deer in Dafeng Nature Reserve

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## Abstract

The outcome success of animals competing for food resources may be influenced by their differences in resource holding potential and motivation to acquire these resources. This study investigated the naturally occurring aggressive interactions during ritualized fights of the cattle egret (*Bubulcus ibis*) foraging with Père David's deer (*Elaphurus davidianus*). The study was conducted in the first core zone of Dafeng Père David's Deer National Nature Reserve, Jiangsu, China during the summers of 2012 and 2013. The foraging and vigilance variables of resident cattle egrets feeding with a deer with and without intrusion were calculated and compared. Cases of ritualized fights between residents and intruders were recorded in naturally occurring aggressive interactions. The prey capture success rate and the total foraging earnings of resident cattle egrets following a deer with intrusion were significantly higher than those of resident foragers without intrusion. The resident status did not affect the outcomes of the ritualized fights of the cattle egrets, although adult residents or intruders had more cases of winning in contesting ownership of the deer. Thus, age is the major resource holding factor in foraging cattle egrets competing for host ownership.

## Introduction

Animals often engage in aggressive interactions when competing for food, water, shelters and mates, which are necessary for the survival of an individual (Cristol, 1992; Nosil, 2002; Hoem *et al.*, 2007; Sultana, Takaoka & Koga, 2013). Several factors determine the outcome of aggressive interactions; these factors include residency status (Kemp & Wiklund, 2004; Umbers, Osborne & Keogh, 2012), body size (Pratt, McLain & Lathrop, 2003; Briffa, 2008), age (Switzer, 2004; Humphries *et al.*, 2006; Kemp, Wiklund & Gotthard, 2006), sex (Bryant & Newton, 1996) and energy reserves (Marden & Waage, 1990; Plaistow & SivaJothy, 1996), which are collectively termed: resource holding potential (RHP) (Parker, 1974). Resource value (RV) is an important non-strategic variable in aggressive behaviour and may vary among competitions; this variable influences the animal's motivation to fight over a resource (Smith, 1982; Enquist & Leimar, 1987; Sultana *et al.*, 2013). If both competitors could gain information on their opponent's RHP relative to their own, then the one with the lower RHP could eliminate the aggressive interaction immediately, thus reducing the time, energy and risk of injury from engaging in a contest that it would inevitably lose (Arnott & Elwood, 2009).

Resource value can influence the occurrence, intensity and duration of aggressive interactions (Riechert, 1988). Theoretical models predict that the cost incurred by competing for a resource increases with increasing RV (Parker, 1974; Smith & Parker, 1976; Enquist & Leimar, 1987). Thus, intrusion or competition for a resource occurs frequently when the RV is high. In other words, intruders should select a resource with a high RV to invade regardless of the possible increase in time, energy, risk of injury or even death (Briffa & Elwood, 2004).

Many studies have involved resident–intruder situations in which residents usually defeat intruders (Krebs, 1982; Bridge, Elwood & Dick, 2000; Briffa & Elwood, 2004; Kemp & Wiklund, 2004; Kemp *et al.*, 2006; Umbers *et al.*, 2012). Ownership of a resource plays a role in the 'bourgeois' strategy, where the outcome of the aggressive interaction is subjective and purely conventional; that is, residents are respected in the fights rather than challenged simply because they are owners and to avoid numerous consequent fights (Kokko, Lopez-Sepulcre & Morrell, 2006). However, an owner moved to another individual's territory becomes a very unlikely winner or might unwillingly fight (Hardy & Briffa, 2013). 'Prior' ownership of a resource may also provide a strategic advantage for residents because they may have become familiar with the resource and invested effort in maintaining the resource. Previous investments regarding the resource may increase the RHP or the motivation to conserve the resource (Arnott & Elwood, 2008, 2009).

Asymmetries in the quality of the contested resource may also depend on internal factors ('subjective' RV), that is, the hunger level of both contestants (Cristol, 1992; RodriguezGirones, Drummond & Kacelnik, 1996; Nosil, 2002). When hungry, contestants may compete for food resources. A hungry animal would value a food resource higher than a fully satisfied animal, and the former would be more likely to win (Crowley, Gillett & Lawton, 1988; Cristol, 1992; Rodriguez-Girones *et al.*, 1996; Nosil, 2002). From this aspect, intruders should have a higher fighting potential or RHP than residents, who have their own resources and are not hungry at all.

Cattle egrets are successful foragers when following Père David's deer, by moving with them and picking up insects disturbed by the movements of the deer (Fernandez *et al.*, 2014). In addition, cattle egrets defend their host against intruding cattle egrets. This study aims to explore whether RV affects the outcome of the aggressive interactions and whether 'residents always win' applies. This study proposes two hypotheses: (1) If RV affects aggressive interactions, then ritualized fights are likely to occur when RV or foraging benefits (such as capture success rate, total foraging earnings, etc.) are high, which means intruder egrets would select residents with higher foraging benefits to invade; (2) If 'residents always win' applies, then residents are likely to win more than intruders because they have acquired enough information on the established possession of the host.

## Materials and methods

### Study area

The study of the foraging variables and aggressive interactions of cattle egrets in association with Père David's deer was carried out in Dafeng Père David's Deer National Nature Reserve (32°59′–33°03′ N, 120°47′–120°53′ E) in Yancheng City, Jiangsu Province, China during the summers of 2012 and 2013. The reserve was founded in 1986 and is located on the Yellow Sea coast in eastern China, 2–4 m above sea level. The nature reserve is composed of three core protected zones, and the vegetation is dominated by Chinese Pennisetum *Pennisetum alopecuroides*, cogon grass *Imperata cylindrica*, Canadian Populus *Populus*, *canadensis* and locust *Robinia pseudoacacia* (Yu & He, 2011). The annual average temperature is 14.1°C, with an average temperature of 0.8°C in January and 27.0°C in July. The average precipitation is 1068 mm with rain falling mostly between June and September.

### Behavioural observation

Data were collected from semi-free-ranging herds of Père David's deer associated with cattle egrets in the isolated semi-natural ecosystem of the reserve using a telescope (Celestron® Ultima80ed, Model 52251 20–60 × 80 mm) or binoculars (80 × 42 mm) in the two summers of 2012 and 2013. Focal observations of the foraging cattle egrets with Père David's deer were confined at a distance not less than 120 m to avoid interference of the observers (Li *et al.*, 2007). The cattle egrets were considered to be associated with the deer if they were within approximately 2 m of the grazing deer. Young cattle egrets can be distinguished from the adults in terms of bill and plumage. Adults mainly exhibit white plumage, yellow bills, dark brown to yellow legs and black toes. Young birds lack coloured plumes and have black bill and black legs.

Behavioural observations on foraging cattle egrets in association with Père David's deer were randomly observed within 10 min, and the average observation duration of foraging was 4.23 ± 0.06 min. Cattle egrets foraged with Père David's deer by moving with them and picking up insects disturbed by the movements of the deer. The number of head-jerk swallow and the number of steps per minute of the foraging cattle egrets were counted and used to determine their capture success rate. The number of scans in the environment (standing upright and holding its neck erect) was used as an index of vigilance. The term pecking frequency was used to indicate the number of attempts of capturing food items that were obtained per minute. The total foraging earnings were obtained by determining the number of successful captures per minute. The expenditure per capture was obtained by dividing the steps/capture by the captures $min^{-1}$. This parameter gives a relative foraging efficiency ratio, a low ratio indicating a high capture rate with few steps (Dinsmore, 1973).

The number of cases of ritualized fights between residents' cattle egrets and intruders was recorded in naturally occurring contests. The aggressive interactions of cattle egrets (residents and intruders) were easy to observe in the field continuously, and the outcomes of the interactions (lose, win and draw) were noted in each event. The event was recorded 'draw' when both contestants did not gain or retain the host and both stayed or flew from the host.

The population of Pere David's deer, the host of the cattle egrets, was about 1500 in the first core zone of Dafeng National Nature Reserve in 2015. A specific survey on the population of cattle egrets was not performed, but at least several hundreds were present in the nature reserve (Liu *et al.*, 2012). Although the animals were unmarked, the same individuals were unlikely sampled more than once on a given day because of the large numbers of deer and cattle egrets. Therefore, the possibility of pseudoreplication should be extremely low and exerts minimal effect on the reliability of our results.

### Data analysis

General linear models were used to address the effects of intrusion status (with, without), host type/deer's sex and age (male, female and fawn) and cattle egret's age (adult and young) on foraging variables (vigilance rate, number of steps made, pecking frequency, expenditure per capture, capture success rate and total foraging earnings). All foraging variables were normally distributed. Non-significant interactions were not retained in the final model. Thus, we only used the intrusion status, cattle egret's age and host type in the final analyses as well as the observation duration as covariate. A multinomial logistic regression was used to examine the factors that influence the outcomes (lose, win or draw) of the

aggressive interactions of ritualized fights of the foraging cattle egrets competing for ownership of the host (Hardy & Field, 1998). Resident's age, intruder's age and their interaction were firstly, included in the logistic model, but the interaction exerted no effect ($\chi^2 = 4.195$, d.f. = 2, $P = 0.123$) and was removed from the final model. All data were analysed using SPSS version 18.0. (PASW Statistics for Windows, SPSS Inc., Chicago, IL, USA). The variables were considered significant at $P < 0.05$.

## Results

A total of 322 behavioural observations of foraging cattle egrets were performed in association with Père David's deer. Of the 322 behavioural observations, 260 and 62 focused on foraging cattle egrets following a deer without and with intrusion respectively. The foraging variables of the resident cattle egrets with and without intrusion were compared as shown in Table 1. No significant difference was found in the vigilance rate ($F_{1,314} = 0.467$, $P = 0.496$), the number of steps made ($F_{1,341} = 1.545$, $P = 0.215$), the pecking frequency ($F_{1,341} = 1.788$, $P = 0.182$) and the expenditure per capture ($F_{1,314} = 0.056$, $P = 0.813$) between resident foragers with and without intrusion. However, the foraging capture success rate ($F_{1,314} = 3.583$, $P = 0.043$) and the total foraging earnings ($F_{1,314} = 4.289$, $P = 0.039$) of resident foragers with intrusion were significantly higher than those of the residents without intrusion.

**Table 1** Foraging variables (estimated marginals with GLM) between resident cattle egrets without intrusion and resident foragers with intrusion

| | Resident foraging cattle egrets | |
|---|---|---|
| | Without intrusion | With intrusion |
| | Mean ± SE | Mean ± SE |
| Dependent variables | ($N = 260$) | ($N = 62$) |
| Vigilance frequency | 0.07 ± 0.01a | 0.05 ± 0.02a |
| Capture success rate | 0.15 ± 0.01a | 0.19 ± 0.02b |
| No. of steps/attempt | 4.00 ± 0.30a | 3.23 ± 0.53a |
| Pecking frequency | 2.82 ± 0.14a | 3.17 ± 0.26a |
| Total foraging earnings | 1.10 ± 0.06a | 1.35 ± 0.12b |
| Expenditure per capture | 13.65 ± 3.50a | 12.07 ± 6.62a |

Different letters in the same line indicate significance at $P < 0.05$.

For other factors, host type significantly affected the capture success rate ($F_{2,314} = 5.731$, $P = 0.001$; Table 2), pecking frequency ($F_{2,314} = 3.290$, $P = 0.039$), total foraging earnings ($F_{2,314} = 8.701$, $P < 0.001$) and vigilance frequency ($F_{2,314} = 14.833$, $P < 0.001$); the age of the egrets also influenced the capture success rate ($F_{1,314} = 25.496$, $P < 0.001$; Table 3), pecking frequency ($F_{1,314} = 23.238$, $P < 0.001$) and vigilance frequency ($F_{1,314} = 11.725$, $P < 0.001$).

A total of 148 cases of aggressive interactions were observed in the cattle egrets defending their hosts. The cattle egrets aggressively defended their hosts against different age classes of intruders; 89 and 59 cases involved adult and young egrets as residents respectively. The model provided a good fit ($\chi^2 = 16.514$, d.f. = 4, $P = 0.002$) and indicated a significant effect of intruder's age ($\chi^2 = 13.840$, d.f. = 2, $P = 0.001$) and a non-significant effect of resident's age ($\chi^2 = 4.618$, d.f. = 2, $P = 0.099$). Adult residents had more cases of winning against young intruders, whereas young residents had more cases of losing the ownership when facing adult intruders (Fig. 1). However, resident status showed no effect ($\chi^2 = 1.245$, d.f. = 2, $P = 0.537$).

## Discussion

Many studies indicated that RV is an important factor influencing intruders' selection (Arnott & Elwood, 2007, 2008; Doake & Elwood, 2011). To gain foraging benefits, intruders should select their targets with higher RVs. As expected, foraging cattle egrets following a deer with intrusion had significantly higher capture success rates and total foraging earnings than foragers without intrusion. This result indicates that Père David's deer stimulating many insects represents a better resource for foraging cattle egrets. This result also indicates that intruders first gather resident's information on how much food a resident was able to obtain by observing resident frequency, capture success rate and number of steps in capturing the food items. Despite individual differences in foraging skills, selecting an owner with higher foraging earnings is a good strategy for intruders because they could possibly earn similarly as the residents if they can invade successfully.

Residents are positioned more advantageously than intruders in resident–intruder contests because residents have more knowledge on the cost and value of the resource that may be unavailable to the intruders (Arnott & Elwood, 2009; Doake &

**Table 2** Foraging variables (estimated marginals with GLM) of cattle egrets following specific host deer

| | Cattle egrets following | | |
|---|---|---|---|
| | Male ($N = 129$) | Female ($N = 156$) | Fawn ($N = 37$) |
| Dependent variables | Mean ± SE | Mean ± SE | Mean ± SE |
| Vigilance frequency | 0.14 ± 0.02b | 0.05 ± 0.02a | 0.01 ± 0.03a |
| Capture success rate | 0.16 ± 0.01b | 0.20 ± 0.01a | 0.15 ± 0.02b |
| No. of steps/attempt | 3.77 ± 0.38a | 3.76 ± 0.33a | 3.16 ± 0.73a |
| Pecking frequency | 3.18 ± 0.19b | 3.37 ± 0.16a | 2.42 ± 0.36b |
| Total foraging earnings | 1.25 ± 0.09a | 1.53 ± 0.07a | 0.89 ± 0.16b |
| Expenditure per capture | 14.50 ± 4.69a | 11.01 ± 4.08a | 13.06 ± 9.05a |

The same letters in the same line indicate insignificance at $P < 0.05$.

**Table 3** Foraging variables (estimated marginals with GLM) between adult and young cattle egrets following Père David's deer

| | Foraging cattle egrets | |
|---|---|---|
| | Adult ($N$ = 171) | Young ($N$ = 151) |
| Dependent variables | Mean ± SE | Mean ± SE |
| Vigilance frequency | 0.02 ± 0.02a | 0.10 ± 0.02b |
| Capture success rate | 0.22 ± 0.02a | 0.13 ± 0.01b |
| No. of steps/attempt | 3.59 ± 0.48a | 3.53 ± 0.37a |
| Pecking frequency | 2.35 ± 0.23a | 3.63 ± 0.18b |
| Total foraging earnings | 1.26 ± 0.11a | 1.18 ± 0.08a |
| Expenditure per capture | 12.37 ± 5.93a | 13.35 ± 4.63a |

The same letters in the same line indicate insignificance at $P < 0.05$.

Elwood, 2011; Umbers *et al.*, 2012). In the classic residency system, the residents/owners of the host are more likely to win in aggressive interactions even when they are smaller or younger because residents are well informed on the value of the resource, whereas intruders lack the opportunity to gather such information (Gherardi, 2006; Arnott & Elwood, 2008). However, in the mixed-species association system of cattle egrets and Père David's deer, cattle egrets are secondary and need to follow the deer to obtain foraging resources. As 'prior' owners of the deer, foraging residents may have already obtained enough food from the host, and keeping their host for a long time might be too costly for them. The willingness of the intruders to win the aggressive interactions was also assumed because they were hungrier and were motivated to win the aggressive interactions. Moreover, residents spent their time feeding and probably had no time to gather information about their opponent, whereas intruders might have evaluated the RHP of their opponent as well as the RV before deciding to obtain ownership of the Père David's deer; both are important factors determining the intensity and the outcome of aggressive interactions (Arnott & Elwood, 2007, 2008).

The motivation of residents in defending their hosts also reflects the outcome of the interactions. A high motivation to maintain ownership of the hosts exists when the food resource value is high. The findings that the residents of cattle egrets did not win more may be because residents already acquired enough food from foraging prior to the invasion of the intruders. In theory, the outcome of the aggressive interactions of animals reflects the contestants' expected payoffs as well as their relative fighting ability (Fromhage & Schneider, 2005; Hoem *et al.*, 2007). The residency status is also not evident in fighting interactions observed in the non-reproductive season of mud crabs (*Ilyoplax pusilla*; Sultana *et al.*, 2013). The reason may be that residents value the burrow more highly in the reproductive season and fight harder to retain it because the loss of a burrow in the reproductive season would have severe consequences for their mating success and fitness (Sultana *et al.*, 2013).

Meanwhile, the age of cattle egrets affected the outcome of the ritualized fights in defending the host deer. Regardless of being a resident or an intruder, an adult egret wins more than a young one. Age in cattle egrets equals to body size, that is, adults are larger than young (Hancock, 1999); age also indicates experience, that is, adults are more experienced in both feeding and fighting skills (Burger & Gochfeld, 1989; Li, Wang & Ge, 2013). The effect of age on aggressive interactions has been observed in different animals, including

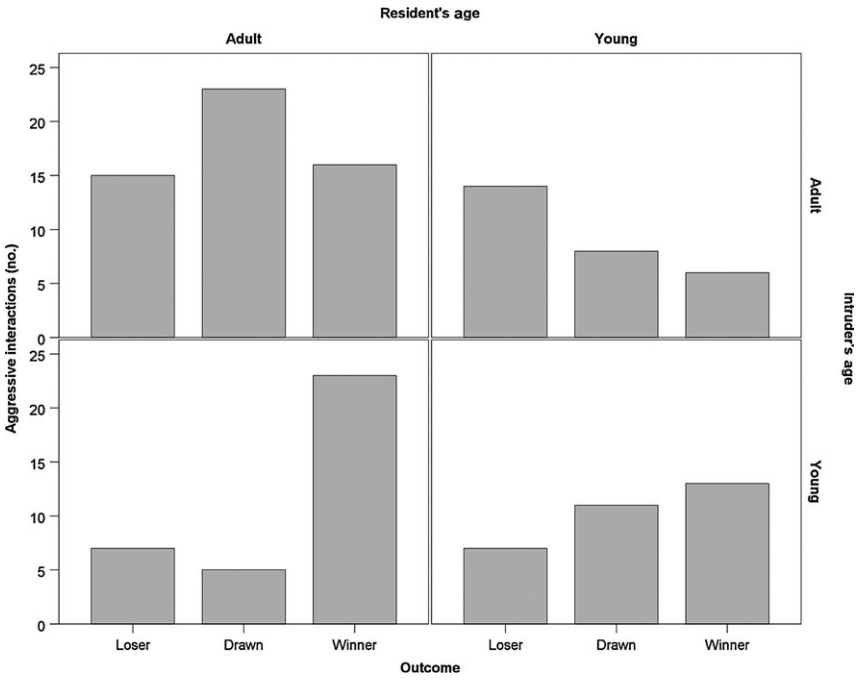


**Figure 1** Effects of age and resident's status on aggressive interactions between cattle egrets in host defence and intrusion.

domestic goats *Capra hircus* (Barroso, Alados & Boza, 2000), water strider *Metrocoris histrio* (Koga & Hayashi, 1993) and Weidemeyer's admiral butterfly *Limenitis weidemeyerii* (Rosenberg & Enquist, 1991). This study also confirmed that age is the major determinant of aggressive interactions in cattle egrets.

Notably, the resource (Père David's deer) used by the competing foraging cattle egrets is a 'moving' animal and not a fixed target. Similar to previous studies, this study demonstrated that higher RV is an important factor influencing host intrusion. 'Residents always win' was inapplicable in this study, but the age affected the outcome of the aggressive interactions probably because spending a long time defending a moving and temporal deer host–resource is costly and may not be necessary because they have already gathered enough food prior to the intrusion. Further studies should focus on the detailed hosting process, such as the active status and moving speed of Père David's deer, and whether the duration of following a deer influences the aggressive interactions of the cattle egrets.

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