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Asymmetric antipredator behaviour in a mixed-species colony of two non-mobbing bird species

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Avian species have a variety of antipredator strategies in response to predator threats of different levels. Mobbing behaviour is most common in colonial birds, although the defensive behaviour and interspecific relationships in mixed-species colonies composed of non-mobbing species are still unclear. In a mixed-species colony of Great Cormorants *Phalacrocorax carbo* and Grey Herons *Ardea cinerea*, we investigated defensive responses to potential avian predators and to actual avian predators. Our observations revealed that the birds distinguished between potential predators and reacted to particular predator species that could prey on large birds. Moreover, we found that the two colonial species showed different defensive antipredator behaviours: Herons exhibited aggressively defensive behaviours; whereas Cormorants, though vigilant, remained on the nest. To our knowledge this is the first report to suggest the possibility of commensalism in the Phalacrocoracidae, whereby Great Cormorants benefit from the defensive behaviour of Grey Herons.

Key words: mixed-species colony, defence behaviour, commensalism, Great Cormorant, *Phalacrocorax carbo*, Grey Heron, *Ardea cinerea*

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To avoid predation efficiently, birds distinguish between predatory and non-predatory species by using visual information and adapt their antipredator responses depending on the level of threat posed by predators. Some birds rely on simple predator search images, such as silhouettes (Tinbergen 1948, Schleidt *et al.* 2011). Forest birds, such as Black-capped Chickadees *Poecile atricapillus*, correctly assess the threat levels posed by different raptor predators and elicit longer alarm calls against smaller, more manoeuvrable raptors (which pose a greater threat to them) than against larger, less manoeuvrable raptors (Templeton *et al.* 2005, Courter & Ritchison 2010).

Among colonial birds, mobbing is a common strategy of aggressive antipredator behaviour to drive potential predators away from nesting sites (Clode *et al.* 2000). Curio (1978) describe mobbing as when "birds of one or more species assemble around a stationary or moving predator (potentially dangerous animal), change locations frequently, perform (mostly) stereotyped wing and/or tail movements and emit loud calls usually with a broad frequency spectrum and transients".

Mobbing birds can gain mutual benefits from individuals joining group defence (Lovette & Fitzpatrick 2016). In a single-species gull colony, individuals with neighbours that are aggressive against predators can decrease their predation risk even if they do not participate in defence activities; they consequently avoid the costs associated with defence efforts (Kazama & Watanuki 2010). Even in a mixed-species colony, non-mobbing species can reduce predation by nesting close to an aggressive species that in different circumstances could be their predator or that has a larger body size than them (Quinn *et al.* 2003, Quinn & Ueta 2008, Jones *et al.* 2013). Differences in antipredator responses occur in the context of various interactions in mixed-species colonies, such as mutualism (Burger 1981),

commensalism (Burger 1984) and parasitism (Groom 1992).

In contrast, despite being colonial birds, some species, including herons (Ardeidae), do not exhibit mobbing. Although these birds emit loud calls to potential predators at a colony, they do not perform mobile movements that mobbing birds do; herons are regarded as non-mobbing birds. Herons mainly form mixed-species colonies with related species that never show mobbing. The differences between non-mobbing birds in these mixed-species colonies in response to predators and in their ability to identify predators have not been studied in great detail.

Non-mobbing herons and cormorants often form mixed-species colonies (del Hoyo *et al.* 1992). The Grey Heron *Ardea cinerea* is considered not to be under significant predation pressure to develop mobbing behaviour (van Vessem & Draulans 1986). However, some recent studies have confirmed that predation is the main reason for breeding losses in Grey Herons early in the breeding period (Jakubas 2005, Bishop *et al.* 2018). In the case of the Great Cormorant *Phalacrocorax carbo*, nests at the periphery of the colony are more vulnerable to predation (Andrews & Day 1999). Cormorants and Herons are both susceptible to predation under certain conditions, and they are expected to show antipredator behavioural responses without mobbing.

Here, we investigated the presence of defensive responses to multiple avian predators, including raptors and crows, presenting varying degrees of threat in a mixed-species colony of Great Cormorants and Grey Herons, both non-mobbing species. Our findings also describe behavioural interactions between the two species and differences in their defence behaviour against major predators.

METHODS

Study site

We studied a mixed-species colony of Great Cormorant (105 nests) and Grey Heron (126 nests) beside Hiyamizu marsh (40°48'42.3"N, 140°16'17.2"E) in Aomori, Japan. The colony was situated in a mixed forest of Japanese Red Pine *Pinus densiflora* and Black Locust *Robinia pseudoacacia* at the north side of the marsh. The study was conducted for a total of 68 non-consecutive days (a total of 215 h), in the breeding period from 5 March to 13 August 2016. The observation point was set at the distance of c. 200 m from the colony across the marsh.

Responses to potential avian predators

We observed raptors and crows as potential aerial predators that could prey on eggs, chicks or adult Cormorants and Herons using 8 × 42 binoculars and a 30× spotting scope. When potential predators appeared within 5 m of the colony, we recorded the species, the presence or absence of predation by the potential predators, and the presence or absence of reaction by the Cormorants and Herons. The behavioural responses of colonial birds were classified into the following five categories: escape (flying away from a nest or a perch to the sky or water surface; strong negative response), vigilance (stretching the neck and looking around; non-aggressive response), alarm call (emitting an alarm call; moderately aggressive response), intimidation (sticking the bill out and making a loud call at a predator without moving from the current place; the most aggressive response) and no response (acting other than the above, e.g. preening, courtship display). If more than half of the individuals in the colony responded by escape, vigilance, alarm calling or intimidation, we considered it to constitute a reaction. To identify behavioural responses and response rate, the reactions were recorded on video using a digital camera (Canon EOS 7D), by recording an overview of the entire colony.

Responses to actual avian predators

We defined birds as predators when they successfully predated nests (eggs, chicks or adult birds). When we encountered the predation scene, we recorded the number of predation occurrences, the victim (Cormorant or Heron) and the prey item (egg, chick or adult).

Statistical analysis

A Mountain Hawk-eagle *Nisaetus nipalensis* appeared intermittently in the colony over a 20-day period (from 5 to 24 April) during the incubation period (from late March to early May). On most days, extreme panic responses among the colonial birds as a group or multiple behavioural responses by individual birds made quantitative observations impossible. Quantitative behavioural observations could be made on the last day that the eagle was observed (day 20, i.e. 24 April, all herons and cormorants were in the incubation period, with a maximum clutch age of 20 days). Therefore, for the data of 24 April, we used chi-squared tests (significance level = 0.05) to determine whether the positions and behavioural responses were comparable between Cormorants and Herons. Here we distinguished their positions when a Hawk-eagle appeared as

Mixed-species colony of Great Cormorants and Grey Herons at the study site in Aomori, Japan (19 April 2016).

'staying on nest' (a bird perched on its own nest or on a branch near the nest) or 'approaching the predator' (a bird left its own nest and perched on a branch near the predator). In addition, we considered alarm call and intimidation as aggressive behaviours. For the analysis, we used all birds that were within a 5-m radius of the predator when the predator appeared.

RESULTS

Responses to potential avian predators

Twelve raptor species and two crow species appeared at the colony (Table 1). All raptors appeared alone, while crows appeared alone or in pairs. The frequency of appearance varied depending on the species. The most frequent visitors were a pair of Large-billed Crows *Corvus macrorhynchos* nesting in the forest, approximately 10 m away from the colony. Conversely, the least frequent visitors were Crested Honey Buzzard *Pernis ptilorhynchus* and Eurasian Sparrowhawk *Accipiter nisus*. Six species of raptors always elicited a behavioural response from both the Cormorants and the Herons, i.e. White-tailed Eagle *Haliaeetus albicilla*, Steller's Sea Eagle *Haliaeetus pelagicus*, Eurasian Sparrowhawk, Northern Goshawk *Accipiter gentilis*, Mountain Hawk-eagle and Peregrine Falcon *Falco peregrinus*. There was little response when the remaining eight species visited (Grey Herons responded only once when a Black Kite *Milvus migrans* appeared; Table 1).

Responses to actual avian predators

We observed predation events by the Large-billed Crow (12 times), Steller's Sea Eagle (once) and Mountain Hawk-eagle (once) and Northern Goshawks were observed twice attacking unsuccessfully (Table 1).

Cormorants and Herons varied in their responses depending on the predator species. The Large-billed Crows preyed on eggs or chicks of Cormorants and Herons throughout the breeding season. However, neither Cormorants nor Herons responded to the Large-billed Crows until they intruded into the nest, and even neighbours of an invaded nest did not respond. A Steller's Sea Eagle appeared twice during the incubation period and preyed on a Cormorant's eggs. When the eagle came to the colony, the Cormorants fled into the air or to the marsh, and the Herons flew away from the colony into the air. Northern Goshawks attacked adult Cormorants twice during the incubation period. When the Goshawks came to the colony, most of the

Cormorants and Herons showed vigilance, and the targeted Cormorant and the surrounding individuals fled. A Mountain Hawk-eagle appeared in the colony intermittently over a 20-day period during the whole observation period. On day 20, The Hawk-eagle grabbed an adult Heron that flew up from the colony and dragged it down to the ground to eat. Thereafter it did not reappear. The responses of the Cormorants and Herons to the Mountain Hawk-eagle changed from day to day (Table 2). When the predator was in the colony on day 20, the Herons flew from nest to tree crown and walked closer to the predator, but Cormorants did not; the Herons were significantly more likely than the Cormorants to approach the predator (Figure 1; $\chi^2 = 68.926$, $P < 0.001$). On that occasion, the Herons showed vigilance, emitted calls or showed intimidating behaviour, whereas the Cormorants simply showed vigilance; the herons behaved significantly more aggressively than the Cormorants ($\chi^2 = 65.164$, $P < 0.01$).

Table 1. List of the potential predators that were observed and responses of Great Cormorants and Grey Heron in a mixed-species colony. 'Number of appearances' indicates the number of observation days on which the potential predators appeared. 'Number of reactions' indicates the number of times the colony birds reacted. Data on body size and wingspan are from del Hoyo *et al.* (1994, 2009).

Species	Length (wingspan)	Number of appearances	Number of reactions		Predation	Prey item	Number of successful predations (Number of attempted predation)
			P. carbo	*A. cinerea*			
Pandionidae							
Western Osprey *Pandion haliaetus*	55–58 cm (145–170 cm)	3	0	0	–	–	0 (0)
Accipitridae							
Crested Honey Buzzard *Pernis ptilorhynchus*	52–68 cm (135–150 cm)	1	0	0	–	–	0 (0)
Black Kite *Milvus migrans*	55–60 cm (135–155 cm)	27	0	1	–	–	0 (0)
White-tailed Eagle *Haliaeetus albicilla*	69–92 cm (200–245 cm)	5	5	5	–	–	0 (0)
Steller's Sea Eagle *Haliaeetus pelagicus*	85–94 cm	3	3	3	Cormorant	eggs	1 (2)
Eastern Marsh Harrier *Circus spilonotus*	47–55 cm	8	0	0	–	–	0 (0)
Eurasian Sparrowhawk *Accipiter nisus*	28–38 cm (60–75 cm)	1	1	1	–	–	0 (0)
Northern Goshawk *Accipiter gentilis*	48–68.5 cm (96–127 cm)	4	4	4	–		0 (2)
Eastern Buzzard *Buteo Japonicus*	50–57 cm (113–128 cm)	29	0	0	–	–	0 (0)
Mountain Hawk-eagle *Nisaetus nipalensis*	67–86 cm (130–165c m)	7	7	7	Heron	adult	1 (1)
Falconidae							
Eurasian Hobby *Falco subbuteo*	28–36 cm (69–84 cm)	2	0	0	–	–	0 (0)
Peregrine Falcon *Falco peregrinus*	34–50 cm (80–120 cm)	1	1	1	–		0 (0)
Corvidae							
Carrion Crow *Corvus corone*	48–53 cm	3	0	0	–	–	0 (0)
Large-billed Crow *Corvus macrorhynchos*	46–59 cm	60	0	0	Cormorant	eggs, chicks	12 (12)

Table 2. Responses of Great Cormorants and Grey Herons to visits by a Mountain Hawk-eagle over a 20-day period (5 to 24 April). Note that these are the average behaviour of individuals in the colony.

	Response	
Day	Cormorant	Heron
1	escape	escape
2	escape	escape
4	escape	escape
5	escape	escape
6	escape, vigilance	escape, vigilance, alarm call
12	escape, vigilance	escape, vigilance, alarm call
20*	vigilance	vigilance, alarm call, intimidation

*an adult Heron was preyed on by the Hawk-eagle after the recording

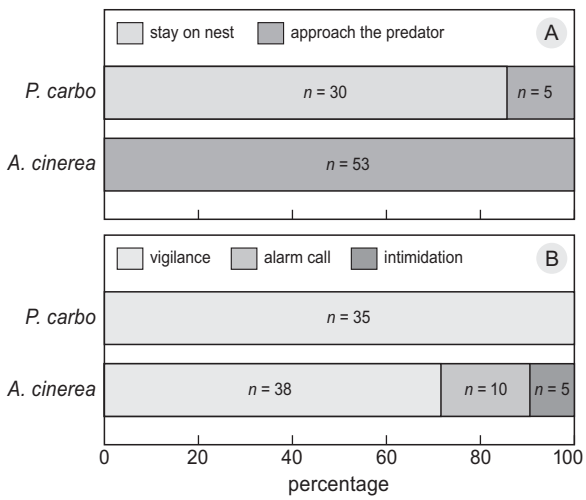

Figure 1. (A) Positions and (B) responses of Great Cormorants and Grey Herons during a visit to the colony by a Mountain Hawk-eagle on observation day 20 (24 April). On that day, an adult Heron was preyed on by a Hawk-eagle after the recording.

DISCUSSION

By escaping, emitting alarm calls, showing vigilance or intimidation, Cormorants and Herons both responded to six out of 14 potential predator species that appeared in the colony. The potential predators to which they responded had different features in terms of body size and wingspan, while five species of them shared the ability to prey on adult Cormorants and Herons. However, they did not respond to predators preying on eggs or chicks, such as Large-billed Crows. These results show that the birds' responses to potential predators were not intended as a defence for their broods but rather for themselves. In general, species with high adult survival and longevity respond more strongly to risks that impact their survival than the survival of their nestlings (Ghalambor & Martin 2001, Schneider & Griesser 2014). Adult Cormorants and Herons have high longevity and a high survival rate (del Hoyo 1992, Wasser & Sherman 2010, Kushlan 2018). Therefore, Cormorants and Herons are likely to distinguish between high-risk and non-risk predatory species and respond to predators that are of high-risk to adults. Exceptionally, they responded to a Eurasian Sparrowhawk that does not prey on the adults, which may be due to confusing the Sparrowhawk with a Northern Goshawk, which is a predator of the adults. These two raptors have similar silhouettes and plumage (Brazil 2009), and we found that Cormorants and Herons responded to the Goshawk at all four visits.

The Great Cormorants and Grey Herons ignored the Large-billed Crows until they intruded into their nests, although this species was the main predator of their eggs and chicks. The Large-billed Crow has been found in other studies to be a general predator of the eggs or chicks of cormorants (Siegel-Causey & Hunt 1981, Andrews & Day 1999) and herons (Bellinato & Bogliani 1995, Kelly *et al.* 2007). It is likely that the adults did not show defensive behaviour because they were not, themselves, being attacked by the crows. In contrast, they responded to Steller's Sea Eagle by escaping. To adult Cormorants and Herons, Steller's Sea Eagles are dangerous predators; if such a predator succeeds in an attack, it is very likely to kill adult birds (Utekhina *et al.* 2000, Vennesland & Butler 2004). However, we observed that Steller's Sea Eagles are also predators of eggs. Responses to the Mountain Hawk-eagle changed from day to day, from fleeing behaviour to relatively aggressive behaviour (i.e. intimidation). These changes in responses could have been caused by progress of the breeding stage and habituation. Parental investment may increase with clutch age, as parents respond to the increased likelihood of offspring surviving as they age (Ackerman & Eadie 2003). During the 20-day period when the Hawk-eagle appeared, all Herons and Cormorants were in the incubation period, and clutch age increased up to a maximum of 20 days. The incubation period is 27–31 days for the Cormorant and 25–26 days for the Heron (del Hoyo *et al.* 1992). Both study species may have behaved more boldly in the late-incubation period than the early-incubation period to protect their eggs, because they are more likely to hatch. Habituation to

predators results in reduced responses and shorter flight initiation distances (Stankowich & Blumstein 2005). Habituation may have caused a decrease in escape behaviour as observed in this study.

The responses to the Mountain Hawk-eagle also differed between the two studied species. The data was recorded before an adult Heron was killed, so the responses were unaffected by that successful predation event. Herons responded to the predator with collectively aggressive behaviours, such as alarm calls or intimidation, while Cormorants did not participate in these aggressive behaviours. The difference may have been cause by mobility in trees. In contrast to Cormorants, Herons can walk in trees by which they can approach predators sitting close by. Their high mobility in trees may enable various behaviours. Other species can eavesdrop on the alarm calls emitted by aggressive species (Fallow & Magrath 2010); birds hearing these calls can thereby notice the predator and initiate defensive behaviour themselves, thereby increasing their own breeding success (Burger 1984). Furthermore, some colonial birds achieve their colonial defence commensally from more aggressive species by nesting near them in mixed-species colonies (Blomqvist & Elander 1987). In such studies, the species that did not behave aggressively depended on the other species for their entire aggressive defence; we observed the same behaviours in the Great Cormorants. In addition, colonial species that benefit from the aggression used by other species follow them and join their colonies (Groom 1992). Similarly, in mixed-species colonies in this study area, including the Hiyamizu marsh, Cormorants actively join established Heron colonies (Honda unpubl. data). Our results, therefore, suggest that the interaction between Great Cormorants and Grey Heron is commensal. To our knowledge this is the first report of this potential behaviour in the Phalacrocoracidae family.

Our study shows that non-mobbing birds, such as cormorants and herons, can distinguish between predators and non-predators; one species engaged in aggressive defensive behaviour, whereas the other did not. These differences in behaviour can indicate commensalism in mixed-species colonies. However, in our study, we were not able to determine how much the Great Cormorants profit from the behaviour of Grey Herons. To show this interspecific relationship in more detail, additional research, on e.g. reproductive success and rates of predation, is required, in more colonies. Our findings may help to explain the formation of mixed-species colonies composed of non-mobbing birds.

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SAMENVATTING

Vogels hebben verschillende manieren om op bedreigingen van predatoren te reageren. Bij koloniebroeders komt pesten ('mobbing') van potentiële roofvijanden het meest voor. Hoe soorten in gemengde broedkolonies op predatoren reageren, is nauwelijks onderzocht. De auteurs van dit artikel hebben in een gemengde broedkolonie van Blauwe Reigers *Ardea cinerea* en Aalscholvers *Phalacrocorax carbo* gekeken of er verdedigingsgedrag naar potentiële predatoren optrad en, zo ja, hoe de twee soorten dan reageerden. Uit het onderzoek blijkt dat de vogels onderscheid kunnen maken tussen verschillende predatoren. Bovendien was hun gedrag verschillend in de richting van de predatoren. De Blauwe Reigers vertoonden agressief gedrag naar de predatoren toe, terwijl de Aalscholvers oplettend kijkend op hun nesten bleven zitten. De Aalscholvers waren voor hun verdediging geheel afhankelijk van de reigers. Dit zou de eerste keer zijn dat is aangetoond dat Aalscholvers in gemengde kolonies bij de verdediging van hun broedsel profijt trekken van het agressieve gedrag van Blauwe Reigers naar predatoren.

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