BioOne COMPLETE

What makes a tactile forager join mixed-species flocks? A case study with the endangered Crested Ibis (Nipponia nippon)

Authors: Ye, Yuanxing, Jiang, Yiting, Hu, Canshi, Liu, Yao, Qing, Baoping, et al.

Source: The Auk, 134(2) : 421-431

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-16-191.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 134, 2017, pp. 421–431
DOI: 10.1642/AUK-16-191.1

RESEARCH ARTICLE

What makes a tactile forager join mixed-species flocks? A case study with the endangered Crested Ibis (*Nipponia nippon*)

Yuanxing Ye,[1] Yiting Jiang,[1,2] Canshi Hu,[1,3] Yao Liu,[1] Baoping Qing,[4] Chao Wang,[4] Esteban Fernández-Juricic,[5] and Changqing Ding[1]*

[1] School of Nature Conservation, Beijing Forestry University 100083, P. R. China
[2] Ecologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, F-91405 Orsay Cedex, France
[3] College of Life Science, Guizhou University, Guiyang 550025, P. R. China
[4] Shaanxi Hanzhong Crested Ibis National Nature Reserve, Shaanxi 723300, P. R. China
[5] Department of Biological Sciences, Purdue University, West Lafayette, Indiana, USA
* Corresponding author: cqding@bjfu.edu.cn

Submitted September 13, 2016; Accepted January 5, 2017; Published March 22, 2017

ABSTRACT

Visual foragers joining mixed-species flocks can enhance foraging and obtain antipredator benefits. However, relatively little is known about the benefits that tactile foragers may obtain by joining mixed-species groups. We investigated the foraging and antipredator benefits that the Crested Ibis (*Nipponia nippon*), an endangered species, may get while foraging in single-species flocks and in mixed-species flocks with Little Egrets (*Egretta garzetta*) during the nonbreeding season. We found that in single-species flocks ibises decreased the proportion of time spent vigilant and increased that spent foraging as total flock size increased. Flight initiation distance (FID, distance between a threat and the animal when the latter flees) decreased with flock size particularly in single-species flocks and alert distance (AD, distance between a threat and the animal first exhibiting alert behavior) decreased with flock size in both single- and mixed-species flocks, but was greater in mixed-species flocks. Taken together, these findings suggest that Crested Ibises may use risk dilution, but not collective detection, in single-species flocks, but use dilution, collective detection, and early warning in mixed-species flocks. We also found partial support for the resource exploitative competition hypothesis as probing bout duration increased with flock size. This tactile forager may benefit from joining mixed-species flocks with a visual forager by using collective detection and early warning (responding to the antipredator signals of the other species), but also tolerate some intraspecific competition in mixed-species flocks through resource depletion effects. Our findings have management implications that could be applied to the protection of this endangered species.

Keywords: tactile forager, mixed-species flocks, *Nipponia nippon*, foraging, vigilant, dilution and collective detection, early warning

¿Qué hace que un ave forrajera táctil se una a bandadas de especies mixtas? Un estudio de caso con la especie en peligro *Nipponia nippon*

RESUMEN

Los forrajeadores visuales que se unen a bandadas de especies mixtas pueden mejorar el forrajeo y obtener beneficios anti-depredadores. Sin embargo, se sabe relativamente poco sobre los beneficios que pueden obtener los forrajeadores táctiles al unirse a grupos de especies mixtas. Investigamos los beneficios de forrajeo y anti-depredadores que podría obtener *Nipponia nippon*, una especie en peligro, mientras forrajea en bandadas uniespecíficas y en bandadas de especies mixtas junto a *Egretta garzetta* durante la estación no reproductiva. Encontramos que en bandadas uniespecíficas, *N. nippon* disminuye la proporción de tiempo que emplea vigilando y aumenta el que emplea forrajeando, a medida que aumenta el tamaño total de la bandada. La distancia de iniciación de vuelo (distancia entre una amenaza y el animal cuando el éste vuela) disminuye con el tamaño de la bandada, particularmente en bandadas uniespecíficas, y la distancia de alerta (distancia entre una amenaza y la primera exhibición de comportamiento de alerta del animal) disminuyó con el tamaño de la bandada, tanto en bandadas uniespecíficas como de especies mixtas, pero fue más grande en bandadas de especies mixtas. En conjunto, estos hallazgos sugieren que *N. nippon* podría usar la dilución del riesgo, pero no la detección colectiva, en bandadas uniespecíficas, pero usa dilución, detección colectiva y advertencia temprana en bandadas de especies mixtas. También encontramos apoyo parcial para la hipótesis de competencia de explotación del recurso a medida que la duración del sondeo aumentó con el tamaño de la bandada. Este forrajeador táctil podría beneficiarse de unirse a bandadas de especies mixtas con un forrajeador visual mediante el uso de la detección colectiva y la alerta temprana

© 2017 American Ornithological Society. ISSN 0004-8038, electronic ISSN 1938-4254
Direct all requests to reproduce journal content to the Central Ornithology Publication Office at pubs@americanornithology.org

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

(respondiendo a las señales anti-depredador de la otra especie), pero también tolera algunas competencias intra-específicas en bandadas de especies mixtas a través de los efectos del agotamiento de recursos. Nuestros hallazgos tienen implicancias de manejo que podrían ser aplicadas a la protección de esta especie en peligro.

Palabras clave: alerta temprana, bandadas de especies mixtas, dilución y detección colectiva, forrajeador táctil, forrajeo, *Nipponia nippon*, vigilante

INTRODUCTION

Mixed-species flocks (i.e. 2 or more species moving and searching for food together) are a widespread phenomenon, particularly in birds (Morse 1977, Greenberg 2000, Krause and Ruxton 2002, Sridhar et al. 2009). While participating in mixed-species flocks, individuals can obtain 2 major non–mutually exclusive benefits: reduced predation risk and enhanced foraging opportunities (Morse 1977, Jullien and Clobert 2000, Goodale and Kotagama 2005, Beauchamp 2014). On the other hand, joining mixed-species flocks may also increase some costs, such as higher rates of aggressive interactions, competition for resources, and disease transmission (Greenberg 2000, Krause and Ruxton 2002).

Interestingly, most of the research on mixed-species flocks has been focused on visual foragers (Sridhar et al. 2009, Beauchamp 2014, 2015), but relatively little on birds that forage using tactile cues such as White Ibis (*Eudocimus albus*; Rojas et al. 1997), Sanderling (*Calidris alba*; Burger et al. 1979), and Dunlin (*C. alpina*; Barbosa 1995). The classic foraging/antipredator behavior trade-off may actually be different in tactile foragers. Presumably both visual and tactile foragers should be less vigilant as group size increases (Beauchamp 2015) because of collective detection (i.e. increased likelihood of detecting a predator in larger groups; Pulliam 1973) and the dilution of risk (i.e. reduced probability of being captured in larger groups; Hamilton 1971). Blick (1980) predicted that tactile foragers should invest more time in vigilance than visual foragers because they have to spend longer in head-down foraging bouts sweeping the substrate. However, Young (1989) found that in mixed-species flocks, the tactile-foraging Long-billed Dowitcher (*Limnodromus scolopaceus*) was less vigilant than the visual-foraging Lesser Yellowlegs (*Tringa flavipes*), likely because of the tactile foragers' narrower binocular fields and wider monocular visual coverage capable of detecting predators even when head-down foraging (Martin 2007). Goss-Custard (2002) proposed that interference would be less pronounced in tactile shorebirds because each prey item can only be detected by the bird touching it, whereas multiple visual foragers can theoretically spot the same prey and interfere with one another. However, Barbosa (2002) showed that in tactile foragers vigilance increased with flock size, possibly because of more scans targeted to flock mates to minimize interference and/or aggression. Furthermore, Myers (1984) proposed that tactile-foraging shorebirds should form large and cohesive flocks to benefit from prey flushing, but visual-foraging shorebirds should forage solitarily or in small loose flocks to avoid competition. Additionally, some studies of the visual-foragers (e.g., Snowy Egret [*Egretta thula*]) have shown them to be good at locating resources that were attractive to other bird species (Caldwell 1981, Master et al. 1993, Smith 1995), but other studies have found them to follow tactile-foragers that disturb prey as they move (Courser and Dinsmore 1975, Erwin 1983). Overall, the benefits that tactile-foragers obtain when joining mixed-species flocks are still not well understood.

To address this gap, we studied both the foraging and antipredator behavior of Crested Ibis (*Nipponia nippon*) while foraging during the nonbreeding season in single-species and mixed-species flocks with Little Egret (*E. garzetta*). Using an observational approach, we tested hypotheses related to antipredator (collective detection, risk dilution, early warning) and foraging (flushing prey, resource exploitative competition, prey interference competition) benefits from the perspective of the Crested Ibis (Table 1). Both species are commonly seen foraging in open habitats, such as riverbanks (gently sloping banks or exposed bed of a river) and winter-flooded rice paddies (i.e. farmers in the area maintain water within the rice) in our study area (Zhang and Ding 2008, Ding 2010). The Crested Ibis is primarily a nonvisual, tactile forager, which uses its long, curved bill for probing in search of loaches, eels, crabs, crayfish, and aquatic insects in winter-flooded rice paddies and estuarine muds (Ding 2004). The Little Egret is a visual forager that feeds on fishes, insects, and crustaceans (Hancock and Kushlan 2010). The Crested Ibis is a species of conservation concern as it was deemed extinct in the wild a few decades ago. However, in 1981, 7 birds were rediscovered in a remote village in China (Liu 1981, Ding 2004). Because of multiple conservation efforts, the population increased to ~1,100–1,200 birds in 2012 (Wang et al. 2014). Currently, the Crested Ibis is categorized as endangered in the IUCN Red List (BirdLife International 2013) and is listed in Appendix I of CITES.

Both the collective detection and risk dilution hypotheses predict that individuals would decrease the proportion of time vigilant and increase the proportion of time foraging (i.e. more time available for food searching) as flock size increases (Table 1). Both hypotheses also predict that flight initiation distance (FID, distance between a threat and the animal at which the latter escapes) would be

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 1. Summary of antipredator and foraging hypotheses and predictions.

Hypotheses	Predictions	References
Collective detection and risk dilution	Proportion time spent on foraging/vigilance of ibises increases/decreases as flock size increases	Hamilton (1971), Pulliam (1973)
	Proportion time spent on foraging/vigilance of ibises decreases/increases with nearest-neighbor distance	Roberts (1996), Fernández-Juricic et al. (2007)
	Flight initiation distance decreases as flock size increases	Matson et al. (2005), Stankowich (2008), Beauchamp (2015)
Early warning	Alert distance increases as flock size increases	Ydenberg and Dill (1986), Fernández-Juricic et al. (2001)
Flushing prey	Moving rate and intake rate increase as flock size increase	Uetz (1989), Davis and Jackson (2007)
Resource exploitative competition	Probing bout duration/intake rates of ibises increases/decreases as flock size increases	Sutherland (1996), Beauchamp (2005)
Prey interference competition	Probing bout duration and foraging success of ibises decrease as flock size increases	Goss-Custard (2002), Vahl et al. (2005)

lower in larger flocks because individuals would be more tolerant to the approach of predators as a result of lower perceived risk (Matson et al. 2005, Stankowich 2008, Beauchamp 2015; Table 1). Additionally, the early-warning hypothesis predicts that alert distance (AD, distance between a threat and the animal first exhibiting alert behavior) should be higher in larger flocks because individuals would have personal as well as social information available to quickly detect a threat (collective detection) and consequently show signs of alertness sooner (Ydenberg and Dill 1986, Fernández-Juricic et al. 2001; Table 1).

From an antipredator perspective, both the collective detection and risk dilution hypotheses make similar predictions, so it is difficult to disentangle their individual contributions (Roberts 1996) despite some previous attempts (Delm 1990, Bednekoff and Lima 1998, Fairbanks and Dobson 2007, Beauchamp and Ruxton 2008, Rieucau and Martin 2008). One approach to tease these hypotheses apart focuses on assessing the results of vigilance behavior, FID, and AD all together (Roberts 1996, Fernández-Juricic and Schroeder 2003). If both collective detection and risk dilution are at play in flocks, we expect that individuals should have (1) a lower proportion of time spent vigilant (Hamilton 1971, Pulliam 1973), (2) lower FIDs (Recarte et al. 1998), and (3) higher ADs in larger flocks (Fernández-Juricic et al. 2001, 2002). However, if individuals show (1) and (2), but lower ADs in larger flocks, it would suggest that individuals may not pay attention to the level of vigilance of other flock members whether conspecifics or heterospecifics (no collective detection benefits), which would indicate the lack of information transfer about predation risk in larger groups of conspecifics or heterospecifics (Lima and Zollner 1996, Beauchamp 2002), and suggest that only risk dilution may be at play (Roberts 1996, Fernández-Juricic and Schroeder 2003).

From a foraging perspective, individuals can benefit from flock mates moving and flushing prey (flushing prey hypothesis), which might lead to an increase in moving rate (i.e. walking) and intake rate (i.e. number of food items swallowed per unit time) in larger flocks because of the increase in prey availability (Uetz 1989, Davis and Jackson 2007; Table 1). The resource exploitative competition hypothesis proposes that food depletes more quickly when larger flocks exploit a foraging patch, which would increase probing bout duration (i.e. period of time the animal is head down searching for food) and reduce intake rates in larger flocks (Sutherland 1996, Beauchamp 2005; Table 1). The prey interference competition hypothesis proposes that behavioral interactions between individuals (i.e. aggressive interactions, food stealing) would have a negative effect on foraging effort, leading to a decrease in probing bout duration and foraging success (i.e. rate of capture of food items per probing attempt) in larger flocks (Goss-Custard 2002, Vahl et al. 2005; Table 1).

For many of the aforementioned hypotheses, individuals are assumed to use social cues from other species, whether flock mates, predators, or prey, to make antipredator and foraging decisions. However, the question is to what degree a given species relies on social information from different species within a mixed-species flock. For example, Barnard and Stephens (1983) found that Fieldfares (*Turdus pilaris*) can use the information from Redwings (*T. iliacus*) about the whereabouts of prey more than the information available from conspecifics. Depending on how Crested Ibises perceive conspecific social cues relative to heterospecific social cues, we envision 3 different scenarios. First, if ibises valued information from egrets in the same way as from conspecifics, we expected that behavioral changes with flock size would not differ between single-species versus mixed-species flocks. Second, if ibises placed more value on social cues from egrets than from conspecifics, we

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

expected that the behavioral changes with flock size would be more pronounced in mixed- than in single-species flocks. Third, if ibises placed less value on social cues from egrets than from conspecifics, we expected that the behavioral changes with flock size would be less pronounced in mixed-species than in single-species flocks.

METHODS

Study Area

We conducted the study in Yang County (33°06′N to 33°36′N, 107°17′E to 108°02′E) in the southwest of Shaanxi Province, China. The study area is on the south slope of the Qinling Mountains, and ranged in elevation from 400 to 800 m. The study was carried out on sunny days from December 2, 2011, to January 15, 2012, and December 30, 2012, to January 26, 2013. The mean temperature during the study season was 2°C (range: –10.1 to 11.0°C). Local vegetation is dominated by *Pinus massonianna*, *Platycladus orientalis*, *Quercus acutissima*, *Q. variabilis*, *Castanea mollissima*, and *Cyclobalanopsis glauca*, scattered within an agricultural landscape that includes extensive riverbanks and winter-flooded rice paddies where the birds feed (Ding 2004).

Behavioral Observations

We used focal sampling to measure the behavior of ibises. We defined a flock as a group of individuals occurring within 20 m of each other (i.e. ibises often did not respond to changes in the behavior of conspecifics when they were positioned more than 20 m away). We recorded birds with a digital video camera (VIXIA HF S20, Full HD Camcorder, Canon, Tokyo, Japan) with 10× optical zoom lens. Before data collection, we estimated the alert distance of Crested Ibis (40–60 m) and Little Egret (60–90 m) in pre-experiments. We positioned ourselves ~80 m away to record the video to minimize human disturbance. We recorded focal samples in 5 min duration. In total, we acquired 112 foraging and vigilance behavior samples (65 samples of Crested Ibis in single-species flocks and 47 samples in mixed-species flocks). After recording foraging and vigilance behaviors, we attempted to measure alert distance (AD) and flight initiation distance (FID) of the focal individuals; however, we were not always successful. We acquired 84 AD and FID samples (61 samples of Crested Ibis in single-species flocks and 23 samples in mixed-species flocks). Additionally, we measured only AD and FID from 26 individuals (16 single-species flocks and 10 mixed-species flocks).

We defined vigilance behavior as the behavioral patterns birds showed (number of times vigilance bouts ocurred per unit time, bout time duration) when birds were in the head-up position scanning (i.e. bill parallel to the ground). We defined alert behavior as a specific point at the beginning of a vigilance bout in which the animal exhibited alert behaviors toward the threat (i.e. raising its head, stretching its neck, and changing its head position in relation to the observer approaching). We defined flight initiation behavior as an individual walking away or taking flight in response to the threat (i.e. observer approaching). An observer approached the focal individual at a steady speed (1 step per second) in open areas because of the easy access and visibility. We recorded start distance (SD, the distance between the observer and the focal bird at the initiation of the approach), AD, and FID of animals using a laser rangefinder (Yardage Pro Elite 1500, Bushnell, Overland Park, Kansas, USA). The observer always wore light jeans and a camouflage coat to minimize differential responses from ibises. Because habitat type can influence antipredator behavior (Fernández-Juricic et al. 2001, Stankowich and Blumstein 2005, Li et al. 2013), we also recorded the habitat in which the ibises were foraging (riverbanks or winter-flooded rice paddies). Additionally, we recorded flock type (single or mixed-species flock), flock size, and ambient temperature (range: 2–14°C).

To minimize the chances of sampling the same individual more than once, we used the following methods: (1) Crested Ibises were identified by their leg bands (24 individuals of 252 birds, 9.5%); (2) for those birds without bands, we identified individuals by other characteristics (e.g., size of red tip at the end of bill, size and shape of red facial skin, bill length); (3) collecting samples in different transects on the same day; and (4) selecting focal individuals at random. We recorded one sample per individual per sampling period (even if in a flock) to reduce the chances of pseudoreplication.

We used the Observer XT 12 (Noldus Information Technology, Wageningen, The Netherlands) for video analysis. We scored the number and duration of the following variables from the videos: (1) probing events: food searching by probing the foraging substrate with their beak, head down below the horizontal; (2) intake events: swallowing after capturing a food item; (3) vigilance events: birds stopped foraging to scan the surroundings, with their head up above the horizontal; and (4) moving events: walking. After coding, we analyzed the proportion of time foraging (i.e. including time spent on probing and food swallowing over the total sampling time) and in vigilance (i.e. time spent on vigilance over the total sampling time), intake rate (i.e. intake events per min), probing bout duration (i.e. average amount of time spent head down probing, recorded in s), foraging success (i.e. number of food items swallowed per probing attempt), and moving rate (i.e. number of steps walked per min).

We also estimated neighbor distance (i.e. distance from the focal individual to its to nearest neighbor) as a potential confounding factor. Both the collective detection and risk dilution hypotheses predict an increase in

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

vigilance with increasing nearest-neighbor distance because social information is anticipated to be more difficult to obtain at greater distances (Roberts 1996, Fernández-Juricic et al. 2007) and because the probability of a predator singling out an individual when farther away from neighbors may be higher (Hamilton 1971). To estimate neighbor distance, we captured 5 random frames on each video, measured the body length of a Crested Ibis (from breast to tail) and then the distance to the nearest individual with a ruler. Finally, we calculated the relative magnitude of the measured distance between 2 individuals and the length of the ibis as an estimate of nearest-neighbor distance.

Statistical Analyses

We used the independent-sample *t*-test to compare total flock size of birds between single-species and mixed-species flocks. We used paired *t*-test to compare the number of Crested Ibises vs. those of Little Egrets in mixed-species flocks. We analyzed different behaviors (proportion of time spent in foraging and vigilant, probing bout duration, intake rate, foraging success, moving rate, AD, FID) with general linear models. We used flock type (single-species flock, mixed-species flock) and habitat type (riverbanks, winter-flooded rice paddies) as categorical factors, and total flock size (including ibises and egrets) as a continuous factor. We considered the interaction between flock type and total flock size to determine whether the changes in behavioral parameters were more or less pronounced depending on whether individuals were in single-species or mixed-species flocks. We also ran general linear models to test the effects of the ratio of egrets to ibises in mixed-species flocks on the aforementioned dependent variables. We assessed the relationship between ADs and FIDs of Crested Ibises, and ADs and FIDs of egrets, using Pearson's correlation coefficient in mixed-species flocks. We also investigated whether the time released from vigilance (i.e. proportion of time spent vigilant) would increase the investment in foraging (i.e. probing bout duration) using Pearson's correlation.

Originally, we included ambient temperature, distance to the nearest ibis, distance to the nearest egret, and the interaction between habitat type and flock type in all models, but they turned out to be nonsignificant (model results available upon request). Therefore, we removed these factors from the analyses to increase the statistical power of the tests.

We checked the data for normality. Variables whose residuals were not normally distributed were arcsine square-root or log transformed before the analyses (see Results). Statistical analyses were carried out with R 3.1.3 (R Core Team 2015), and the statistical significance level was set at 0.05. We present the results with means ± SE.

TABLE 2. Effects of total flock size (including ibises and egrets), flock type (single-species, mixed-species), and habitat type (winter-flooded rice paddies, riverbanks) on the proportion of time spent vigilant, proportion of time spent foraging, probing bout duration, intake rate, foraging success, and moving rate of Crested Ibises. Significant results at probability <0.05 are marked in bold.

	df	*F*	*P*
(log) The proportion of time spent vigilant			
(log) Total flock size	1,107	8.288	**0.005**
Flock type	1,107	0.297	0.587
Habitat type	1,107	6.146	**0.015**
Flock type * (log) total flock size	1,107	5.746	**0.018**
(arcsin-sqrt) The proportion of time spent foraging			
(log) Total flock size	1,107	7.077	**0.009**
Flock type	1,107	0.971	0.327
Habitat type	1,107	7.882	**0.006**
Flock type * (log) total flock size	1,107	5.299	**0.023**
(log) Probing bout duration (s)			
(log) Total flock size	1,107	43.671	<**0.001**
Flock type	1,107	1.050	0.308
Habitat type	1,107	0.368	0.546
Flock type * (log) total flock size	1,107	0.072	0.788
(log) Intake rate			
(log) Total flock size	1,107	0.011	0.921
Flock type	1,107	0.652	0.424
Habitat type	1,107	13.973	<**0.001**
Flock type * (log) total flock size	1,107	1.530	0.220
(log) Foraging success			
(log) Total flock size	1,107	2.472	0.119
Flock type	1,107	1.431	0.234
Habitat type	1,107	13.502	<**0.001**
Flock type * (log) total flock size	1,107	2.842	0.095
(log) Moving rate			
(log) Total flock size	1,107	1.396	0.240
Flock type	1,107	4.976	**0.028**
Habitat type	1,107	2.712	0.103
Flock type * (log) total flock size	1,107	3.365	0.069

RESULTS

The average total flock size birds in single-species flocks (only ibises, 2.47 ± 1.48, range: 1–12) was significantly lower than in mixed-species flocks (including ibises and egrets, 5.35 ± 2.32, range: 2–24, $t = -4.330$, df = 137, $P < 0.001$). However, in mixed-species flocks, Crested Ibis flock size (2.03 ± 1.22, range: 1–8) was not significantly different from that of Little Egrets (3.33 ± 2.16, range: 1–19, $t = -1.939$, df = 113, $P = 0.055$).

The proportion of time spent vigilant ranged from 0.04 to 0.48. As total flock size increased, the proportion of time spent vigilant decreased significantly (Table 2). We found a significant interaction effect between flock type and total flock size (Table 2, Figure 1A), such that the proportion of time spent in vigilance decreased with total flock size in single-species flocks ($\beta = -0.045 \pm 0.013$, $P = 0.001$; Figure 1A), but did not vary significantly with total flock size in mixed-species flocks ($\beta = -0.000 \pm 0.007$, $P = 0.980$;

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

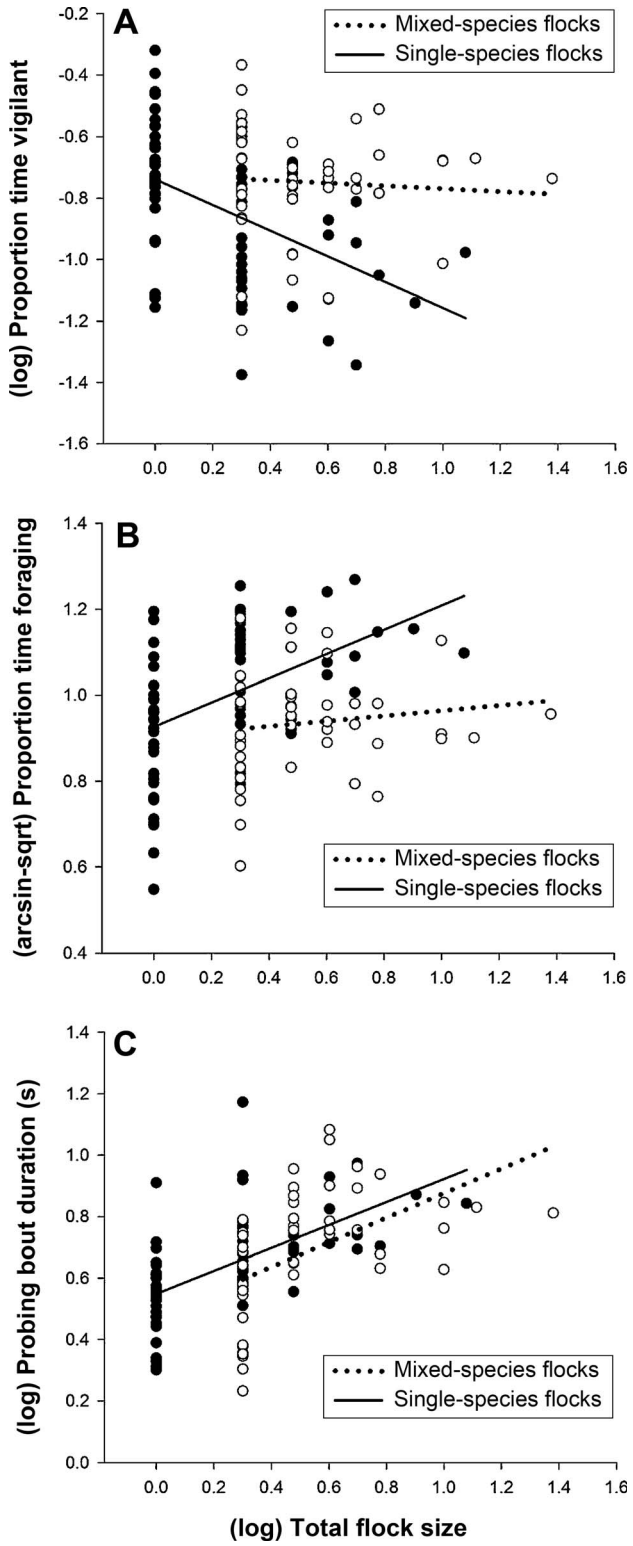


FIGURE 1. Effects of total flock size (including ibises and egrets) on the (**A**) proportion of time spent vigilant, (**B**) proportion of time spent foraging, and (**C**) probing bout duration of Crested Ibises in single-species flocks (black circle) and mixed-species flocks (white circles).

Figure 1A). Time spent vigilant was significantly higher when the birds foraged along riverbanks (0.20 ± 0.03) than in winter-flooded rice paddies (0.15 ± 0.03; Table 2).

The proportion of time spent foraging ranged from 0.52 to 0.95, and significantly increased with total flock size (Table 2). However, we found a significant interaction effect between flock type and total flock size (Table 2), by which the proportion of time spent foraging increased significantly with flock size in single-species flocks ($\beta = 0.030 \pm 0.009$, $P = 0.001$; Figure 1B), but did not vary significantly with flock size in mixed-species flocks ($\beta = 0.002 \pm 0.005$, $P = 0.751$; Figure 1B). The time spent foraging was significantly higher in winter-flooded rice paddies (0.85 ± 0.29) than on riverbanks (0.80 ± 0.29; Table 2).

Probing bout duration ranged from 1.7 to 14.9 s, and increased significantly with total flock size (Table 2), yet we did not find a significant interaction effect between flock type and total flock size (Table 2). Probing bout duration increased with total flock size both in single-species ($\beta = 0.341 \pm 0.038$, $P < 0.001$; Figure 1C) and mixed-species flocks ($\beta = 0.397 \pm 0.090$, $P < 0.001$; Figure 1C). We found that probing bout duration of Crested Ibises was significantly and negatively correlated with the proportion of time spent vigilant both in single-species ($r = -0.760$, $P < 0.001$) and mixed-species ($r = -0.601$, $P < 0.001$) flocks.

Intake rate and foraging success were not significantly affected by flock size and flock type (Table 2). However, we found intake rate to be significantly higher in winter-flooded rice paddies (2.43 ± 1.42 events min^{-1}) than in riverbanks (0.95 ± 1.18 events min^{-1}; Table 2), and foraging success to be significantly higher on winter-flooded rice paddies (0.21 ± 0.18) than in riverbanks (0.09 ± 0.15; Table 2) as well. None of the studied factors influenced moving rate significantly (Table 2).

Alert distance (AD) ranged from 39 to 77 m, and decreased significantly with total flock size (Table 3; Figure 2A). Additionally, AD was significantly higher in mixed-species (61.61 ± 2.63 m) than in single-species (53.34 ± 2.78 m) flocks (Table 3; Figure 2A). AD increased significantly with start distance (Table 3). The interaction between flock type and total flock size was not significant (Table 3). Moreover, we found the AD of Crested Ibises were positively and significantly correlated with the AD ($r = 0.625$, $P < 0.001$) and the FID ($r = 0.435$, $P = 0.011$) of egrets in mixed-species flocks.

FID ranged from 20 to 64 m. FID decreased significantly with larger total flock sizes (Table 3). However, we found a significant interaction effect between flock type and total flock size (Table 3, Figure 2B) whereby FID decreased significantly with total flock size in single-species flocks ($\beta = -0.014 \pm 0.005$, $P = 0.013$; Figure 2B), but it did not vary significantly with total flock size in mixed-species flocks ($\beta = 0.001 \pm 0.003$, $P = 0.791$; Figure 2B). We found that the

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 3. Effects of total flock size (including ibises and egrets), flock type (single-species, mixed-species), habitat type (winter-flooded rice paddies, riverbanks), and starting distance on alert and flight initiation distances of Crested Ibises. Significant results at probability <0.05 are marked in bold.

	df	*F*	*P*
Alert distance			
Total flock size	1,104	7.771	**0.006**
Flock type	1,104	8.732	**0.004**
Habitat type	1,104	3.281	0.073
Flock type * Total flock size	1,104	2.032	0.157
Start distance	1,104	14.080	**<0.001**
(log) Flight initiation distance			
Total flock size	1,104	4.362	**0.039**
Flock type	1,104	0.010	0.922
Habitat type	1,104	3.390	0.069
Flock type * Total flock size	1,104	5.218	**0.024**
Start distance	1,104	10.522	**0.002**

FID of Crested Ibises was not correlated with the AD ($r = 0.193$, $P = 0.283$) or the FID ($r = 0.325$, $P = 0.065$) of egrets in mixed-species flocks. FID increased significantly with start distance (Table 3).

We found that the ratio of egrets to ibises did not affect the proportion of time spent vigilant and foraging, probing bout duration, intake rate, foraging success, moving rate, and alert distance of Crested Ibises (Table 4 and 5). However, FID increased significantly with the ratio of egrets to ibises ($\beta = 0.691 \pm 0.238$, $P = 0.007$, Table 5).

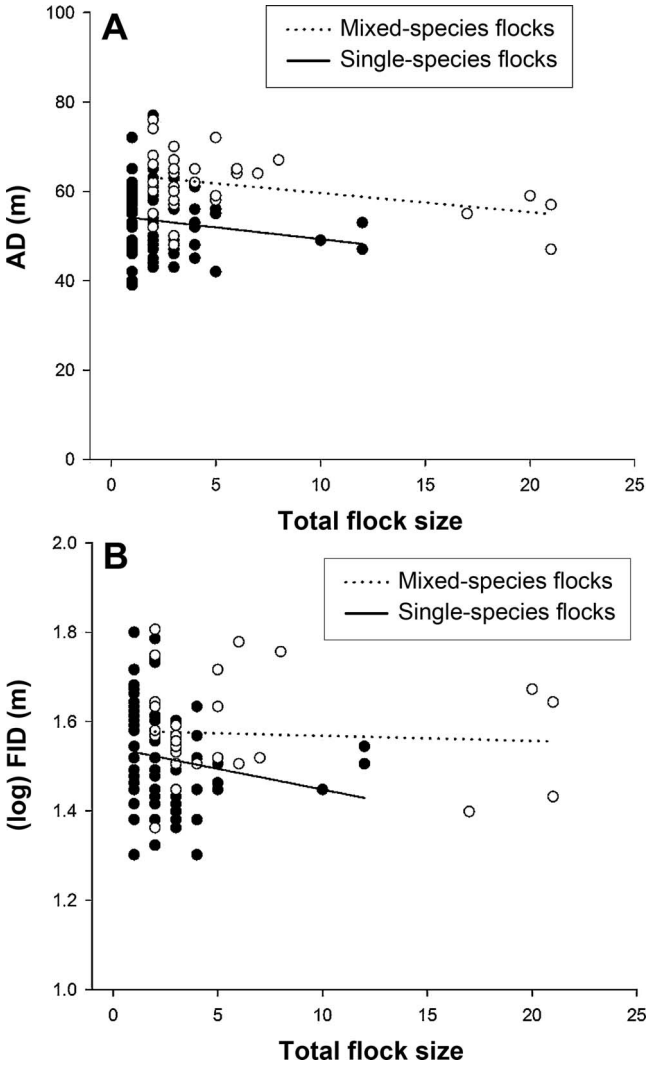


FIGURE 2. Effects of total flock size (including ibises and egrets) on the (**A**) alert distance (AD) and (**B**) flight initiation distance (FID) of Crested Ibises in single-species flocks (black circles) and mixed-species flocks (white circles).

DISCUSSION

Our results show that Crested Ibises decreased the proportion of time spent vigilant and increased the time spent foraging as flock size increased, and this effect was most pronounced in single-species flocks. Additionally, FID decreased with flock size particularly in single-species flocks. Although these results are consistent with the predictions of both the collective detection, early warning, and dilution hypotheses, we found that AD actually decreased (rather than increased) with flock size and that AD was higher in mixed-species compared with single-species flocks. Taken together, these findings suggest that Crested Ibises may use risk dilution, but not necessarily collective detection, in single-species flocks, but use both dilution and collective detection in mixed-species flocks. From a foraging viewpoint, we did not find support for the flushing prey and prey interference competition hypotheses, but we found partial support for the resource exploitative competition hypothesis as probing bout duration increased with flock size both in single-species and mixed-species flocks.

Several studies have documented the reduction in vigilance effort and increase in foraging effort with increasing flock size (reviewed in Beauchamp 1998, 2001, 2008). We found this to be the case in single-species flocks. This is likely the result of lower perception of risk in larger flocks (Fairbanks and Dobson 2007, Beauchamp and Ruxton 2008, Wang et al. 2011), which can ultimately lead to an increase in the probability of finding food (Beauchamp 2014). In our study, this vigilance effect was prevalent when Crested Ibises were flocking with conspecifics, but not with heterospecifics. Every now and then, we would see egrets flying directly to ibises and attempting to steal their food, suggesting some form of interference, although foraging success did not decrease significantly with flock size in mixed-species flocks. Nevertheless, if ibises perceived heterospecifics as potential food competitors, they may have responded to mixed-species flocks in 2 ways: decreasing the time scanning the surroundings but

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 4. Effects of total flock size (including ibises and egrets), habitat type (winter-flooded rice paddies, riverbanks), and ratio of egrets to ibises on the proportion of time spent vigilant, proportion of time spent foraging, probing bout duration, intake rate, foraging success, and moving rate of Crested Ibises in mixed-species flocks. Significant results at probability <0.05 are marked in bold.

	df	*F*	*P*
(log) The proportion of time spent vigilant			
(log) Total flock size	1,43	1.113	0.297
Habitat type	1,43	0.578	0.451
Ratio of egrets to ibises	1,43	2.178	0.147
(arcsin-sqrt) The proportion of time spent foraging			
(log) Total flock size	1,43	1.856	0.180
Habitat type	1,43	0.858	0.359
Ratio of egrets to ibises	1,43	2.109	0.154
(log) Probing bout duration (s)			
(log) Total flock size	1,43	15.252	**<0.001**
Habitat type	1,43	0.729	0.399
Ratio of egrets to ibises	1,43	1.192	0.283
(log) Intake rate			
(log) Total flock size	1,43	0.024	0.877
Habitat type	1,43	3.197	0.083
Ratio of egrets to ibises	1,43	1.321	0.259
(log) Foraging success			
(log) Total flock size	1,43	0.114	0.737
Habitat type	1,43	2.278	0.139
Ratio of egrets to ibises	1,43	0.688	0.412
(log) Moving rate			
(log) Total flock size	1,43	3.264	0.078
Habitat type	1,43	2.798	0.102
Ratio of egrets to ibises	1,43	0.199	0.658

TABLE 5. Effects of total flock size (including ibises and egrets), habitat type (winter-flooded rice paddies, riverbanks), ratio of egrets to ibises, and starting distance on alert and flight initiation distances of Crested Ibises in mixed-species flocks. Significant results at probability <0.05 are marked in bold.

	df	*F*	*P*
Alert distance			
Total flock size	1,28	0.897	0.352
Habitat type	1,28	0.942	0.340
Ratio of egrets to ibises	1,28	0.170	0.683
Start distance	1,28	5.933	**0.021**
(log) Flight initiation distance			
Total flock size	1,28	3.949	0.057
Habitat type	1,28	0.031	0.861
Ratio of egrets to ibises	1,28	5.218	**0.007**
Start distance	1,28	0.531	0.472

increasing the time monitoring egrets in larger flocks. Although we did not quantify these 2 mechanisms, they could explain the lack of a significant relationship between time allocated to vigilance and flock size in mixed-species flocks (Favreau et al. 2010, Pays et al. 2014). In addition, Crested Ibis FID decreased with flock size predominantly in single-species flocks, which could be explained by individuals being more tolerant to threats as a result of lower perceived risk in larger groups (Ydenberg and Dill 1986, Cooper and Blumstein 2015). However, Crested Ibis FID increased with a higher ratio of egrets to ibises in mixed-species flocks, possibly suggesting a cumulative impact on the flushing of proportionally more egrets.

Interestingly, we found AD to be lower in larger single-species and mixed-species flocks. Previous studies indicated that AD could be a proxy of detection distance (Roberts 1996, Lima and Bednekoff 1999, Fernández-Juricic and Schroeder 2003), which suggests that detection was reduced in larger groups. A similar negative relationship between AD and flock size has been found in alpine marmots (*Marmota marmota*; Louis and Le Beere 2000). In principle, this suggests that individuals may not pay as much attention to the vigilance behavior of conspecifics in larger flocks, potentially relying more on dilution effects. This effect was similar in both single-species and mixed-species flocks, although in the latter, the targets of vigilance may have shifted to ibises to prevent food stealing from heterospecifics, as explained before. This may account for the higher AD of ibises in mixed-species flocks compared to that in single-species flocks. We found that ibis ADs were positively correlated with the egret ADs in mixed-species flocks. Therefore, ibises may have paid attention to both the alert behaviors of egrets when in mixed-species flocks, indicating the use of heterospecific social cues, but this effect seemed related to the presence, rather than the number, of heterospecifics. The implication is that ibises may place a higher value on the antipredator behavior of heterospecifics than that of conspecifics (Pays et al. 2014) because the former detect and flush earlier in response to threats. Overall, Crested Ibises may benefit from the early alert of egrets, suggesting that collective detection between species may lead to an early warning effect. Other studies have also documented early warning benefits in mixed-species flocks (Thompson and Barnard 1983, Thompson and Thompson 1985, Semeniuk and Dill 2006).

Our results partially support the resource exploitative competition hypothesis as probing bout duration increased with flock size (but no effect was documented on intake rate), which may be related to the depletion of food resources when more individuals are exploiting a patch (Sutherland 1996). Previous studies found similar effects in other species (Beauchamp 2005). In our study, probing bout duration increased with flock size in both flock types, which may be related to the greater overlap in food preference and foraging strategies among conspecifics and heterospecifics. The implication is that ibises may tolerate some level of competition when joining both single-species and mixed-species flocks as a trade-off for other advantages (i.e. antipredator benefit) of flocking (Krebs 1973, Terborgh 1990). Alternatively, the increase in probing bout

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

duration with flock size in ibises may simply be the result of a release of time from vigilance.

We did not find significant effects of flock size on intake rate, foraging success, or moving rate, indicating that flushing prey and interference competition may not be very strong in these flocks. Nevertheless, we did find a habitat effect on foraging behavior: intake rate and foraging success were higher in winter-flooded rice paddies than on riverbanks. One possible reason is that farmers in our area keep rice paddies flooded with water during winter to conserve the aquatic fauna (Ding 2004), thereby they may incidentally increase winter food availability for ibises. Additionally, most of the winter-flooded rice paddies we studied were located in middle-lower mountain regions (600–1,000 m elevation), whereas the riverbanks were located in open areas at lower elevations (390–600 m) (Ding 2004, Sun et al. 2014). One of the major predators of ibises is the Common Buzzard (*Buteo buteo*), which is common in open and lower-elevation areas in winter (Shi and Cao 2001, Wikar 2008). The potentially higher abundance of these predators might have been a factor influencing the perceived predation risk, hence increasing vigilance efforts in riverbanks.

Crested Ibises allocated about 17% of their time to vigilance in single-species flocks, and 20% in mixed-species flocks. These values are higher than those reported previously for visual foragers, such as Lesser Yellowlegs (9%), Semipalmated Sandpiper (*C. pusilla*; 3%), Little Stint (*C. minuta*; 1%), Ruddy Turnstone (*Arenaria interpres*; 6%), Black-winged Stilt (*Himantopus himantopus*; 4%), and Eurasian Oystercatcher (*Haematopus ostralegus*; 9%) (Barbosa 1995, Young 1989). This supports Blick's (1980) idea that tactile foragers should spend more time vigilant than visual foragers to compensate for the longer head-down foraging bouts sweeping or probing the substrate. Crested Ibises in single-species flocks decreased time spent in vigilance as group size increased, which did not agree with Barbosa's (2002) findings on tactile foragers where vigilance increased with flock size. This mismatch may be explained by the fact that tactile foragers may also benefit from dilution and collective detection, as visual foragers do.

Overall, our results suggest that Crested Ibises benefit from joining mixed-species flocks with Little Egrets by using collective detection and early warning and may tolerate some intraspecific competition through depletion effects. Our results have implications for the management of this endangered species. First, developing habitat conditions that favor mixed-species flocks may reduce the perception of risk by ibises due to the early warning effects of egrets, particularly in habitats with high levels of predation and/or disturbance. Second, creating suitable conditions for ibises in winter-flooded rice paddies is of foremost importance because the higher food resource availability can positively affect their foraging behavior. Third, because Crested Ibis distribution has expanded to lowland areas, riverbank habitats are also important in winter as they can provide additional foraging habitat (Hu et al. 2016).

ACKNOWLEDGMENTS

We would like to thank the staff of the Crested Ibis Nature Reserve for their generous support. We are grateful to Geoffrey W. H. Davison for his constructive comments on the manuscript.

Funding statement: This work was supported by National Natural Science Foundation of China (No.31372218) and the first author was supported by a scholarship from China Scholarship Council (CSC) No. 201406510017.

Ethics statement: All our study procedures were approved by the ethics committees of China State Forestry Administration (Beijing, China, 2011). We also obtained permission to work on the Crested Ibises from Shaanxi Hanzhong Crested Ibis National Nature Reserve.

Author contributions: Y. Y. conceived and designed the experiments, performed the experiments, analyzed the data, and wrote the paper; Y. J., H. C., and Y. L. designed and performed the experiments and contributed data analysis; B. Q. and C. W. contributed substantial materials and resources; E. F. contributed data analysis, wrote the paper, and reviewed drafts of the paper; C. D. conceived and designed the experiments, wrote the paper and reviewed drafts of the paper, and all authors approved the submission.

LITERATURE CITED

Barbosa, A. (1995). Foraging strategies and their influence on scanning and flocking behaviour of waders. Journal of Avian Biology 26:182–186.

Barbosa, A. (2002). Does vigilance always covary negatively with group size? Effects of foraging strategy. Acta Ethologica 5:51–55.

Barnard, C. J., and H. Stephens (1983). Costs and benefits of single and mixed species flocking in Fieldfares (*Turdus pilaris*) and Redwings (*T. iliacus*). Behaviour 84:91–123.

Beauchamp, G. (1998). The effect of group size on mean food intake rate in birds. Biological Reviews 73:449–472.

Beauchamp, G. (2001). Should vigilance always decrease with group size? Behavioral Ecology and Sociobiology 51:47–52.

Beauchamp, G. (2002). Little evidence for visual monitoring of vigilance in Zebra Finches. Canadian Journal of Zoology 80: 1634–1637.

Beauchamp, G. (2005). Does group foraging promote efficient exploitation of resources? Oikos 111:403–407.

Beauchamp, G. (2008). What is the magnitude of the group-size effect on vigilance? Behavioral Ecology 19:1361–1368.

Beauchamp, G. (2014). Social Predation: How Group Living Benefits Predators and Prey. Elsevier, Amsterdam, The Netherlands.

Beauchamp, G. (2015). Animal Vigilance: Monitoring Predators and Competitors. Academic Press, London, UK.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Beauchamp, G., and G. D. Ruxton (2008). Disentangling risk dilution and collective detection in the antipredator vigilance of Semipalmated Sandpipers in flocks. Animal Behaviour 75: 1837–1842.

Bednekoff, P. A., and S. L. Lima (1998). Re-examining safety in numbers: Interactions between risk dilution and collective detection depend upon predator targeting behaviour. Proceedings of the Royal Society of London B: Biological Sciences 265:2021–2026.

BirdLife International (2013). *Nipponia nippon*. In The IUCN Red List of Threatened Species (Version 2013.1). http://www.iucnredlist.org.

Blick, D. J. (1980). Advantages of flocking in some wintering shorebirds. Ph.D. dissertation, University of Michigan, Ann Arbor, MI, USA.

Burger, J., D. C. Hahn, and J. Chase (1979). Aggressive interactions in mixed-species flocks of migrating shorebirds. Animal Behaviour 27:459–469.

Caldwell, G. S. (1981). Attraction to tropical mixed-species heron flocks: Proximate mechanism and consequences. Behavioral Ecology and Sociobiology 8:99–103.

Cooper W. E., Jr, and D. T. Blumstein (2015). Escaping from Predators: An Integrative View of Escape Decisions. Cambridge University Press, Cambridge, UK.

Courser, W. D., and J. J. Dinsmore (1975). Foraging associates of White Ibis. The Auk 92:599–601.

Davis W. E., Jr, and J. A. Jackson (2007). Willets kleptoparasitize and use White Ibis as "beaters." The Wilson Journal of Ornithology 119:758–760.

Delm, M. M. (1990). Vigilance for predators: Detection and dilution effects. Behavioral Ecology and Sociobiology 26:337–342.

Ding, C. (2004). Research on the Crested Ibis. Shanghai Scientific and Technological Education Publishing House, Shanghai, P. R. China.

Ding, C. (2010). Crested Ibis. Chinese Birds 1:156–162.

Erwin, R. M. (1983). Feeding habitats of nesting wading birds: Spatial use and social influences. The Auk 100:960–970.

Fairbanks, B., and F. S. Dobson (2007). Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: Dilution versus detection. Animal Behaviour 73:115–123.

Favreau, F. R., A. W. Goldizen, and O. Pays (2010). Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. Proceedings of the Royal Society of London B: Biological Sciences 277:2089–2095.

Fernández-Juricic, E., G. Beauchamp, and B. Bastain (2007). Group-size and distance-to-neighbour effects on feeding and vigilance in Brown-headed Cowbirds. Animal Behaviour 73: 771–778.

Fernández-Juricic, E., M. D. Jimenez, and E. Lucas (2001). Alert distance as an alternative measure of bird tolerance to human disturbance: Implications for park design. Environmental Conservation 28:263–269.

Fernández-Juricic, E., M. D. Jimenez, and E. Lucas (2002). Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. Canadian Journal of Zoology 80:1212–1220.

Fernández-Juricic, E., and N. Schroeder (2003). Do variations in scanning behavior affect tolerance to human disturbance? Applied Animal Behaviour Science 84:219–234.

Goodale, E., and S. W. Kotagama (2005). Alarm calling in Sri Lankan mixed-species bird flocks. The Auk 122:108–120.

Goss-Custard, J. D. (2002). Competition for food and interference among waders. Ardea 68:31–52.

Greenberg, R. (2000). Birds of many feathers: The formation and structure of mixed-species flocks of forest birds. In On the Move: How and Why Animals Travel in Groups (S. Boinski and P. A. Garber, Editors). University of Chicago Press, IL, USA.

Hamilton, W. D. (1971). Geometry for the selfish herd. Journal of Theoretical Biology 31:295–311.

Hancock, J., and J. A. Kushlan (2010). The Herons Handbook. Christopher Helm Publishers, Bloomsbury, UK.

Hu, C., X. Song, C. Ding, Y. Ye, B. Qing, and C. Wang (2016). The size of winter-flooded paddy fields no longer limits the foraging habitat use of the endangered Crested Ibis (*Nipponia nippon*) in winter. Zoological Science 33:345–351.

Jullien, M., and J. Clobert (2000). The survival value of flocking in Neotropical birds: Reality or fiction? Ecology 81:3416–3430.

Krause, J., and G. D. Ruxton (2002). Living in Groups. Oxford University Press, Oxford, UK.

Krebs, J. R. (1973). Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). Canadian Journal of Zoology 51:1275–1288.

Li, Z., Z. Wang, and C. Ge (2013). Time budgets of wintering Red-Crowned Cranes: Effects of habitat, age and family size. Wetlands 33:227–232.

Lima, S. L., and P. A. Bednekoff (1999). Back to the basics of antipredatory vigilance: Can nonvigilant animals detect attack? Animal Behaviour 58:537–543.

Lima, S. L., and A. P. Zollner (1996). Anti-predatory vigilance and the limits to collective detection: Visual and spatial separation between foragers. Behavioral Ecology and Sociobiology 38:355–363.

Liu, Y. (1981). Rediscovery of the Crested Ibis in Qin Mountain. Acta Zoologica Sinica 27:273.

Louis, S., and M. Le Beere (2000). Adjustment in flight distance from humans by *Marmota marmota*. Canadian Journal of Zoology 78:556–563.

Martin, G. R. (2007). Visual fields and their functions in birds. Journal of Ornithology 148:547–562.

Master, T. L., M. Frankel, and M. Russell (1993). Benefits of foraging in mixed-species wader aggregations in a southern New Jersey saltmarsh. Colonial Waterbirds 16:149–157.

Matson, T. K., A. W. Goldizen, and D. A. Putland (2005). Factors affecting the vigilance and flight behaviour of impalas. South African Journal of Wildlife Research 35:1–11.

Morse, D. H. (1977). Feeding behavior and predator avoidance in heterospecific groups. BioScience 27:332–339.

Myers, J. (1984). Spacing behavior of nonbreeding shorebirds. In Shorebirds: Migration and Foraging Behavior (J. Burger and B. L. Olla, Editors). Plenum Press, New York, USA.

Pays, O., A. Ekori, and H. Fritz (2014). On the advantages of mixed-species groups: Impalas adjust their vigilance when associated with larger prey herbivores. Ethology 120:1207–1216.

Pulliam, H. R. (1973). On the advantages of flocking. Journal of Theoretical Biology 38:419–422.

R Core Team (2015). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Recarte, J. M., J. P. Vincent, and A. J. M. Hewison (1998). Flight responses of park fallow deer to the human observer. Behavioural Processes 44:65–72.

Rieucau, G., and J. G. A. Martin (2008). Many eyes or many ewes: Vigilance tactics in female bighorn sheep *Ovis canadensis* vary according to reproductive status. Oikos 117:501–506.

Roberts, G. (1996). Why individual vigilance declines as group size increases. Animal Behaviour 51:1077–1086.

Rojas, L. M., R. McNeil, T. Cabana, and P. Lachapelle (1997). Diurnal and nocturnal visual function in two tactile foraging waterbirds: The American White Ibis and the Black Skimmer. The Condor 99:191–200.

Semeniuk, C. A., and L. M. Dill (2006). Anti-predator benefits of mixed-species groups of cowtail stingrays (*Pastinachus sephen*) and whiprays (*Himantura uarnak*) at rest. Ethology 112:33–43.

Shi, D., and Y. Cao (2001). The Crested Ibis of China. China Forestry Publishing House, Beijing, P. R. China.

Smith, J. P. (1995). Foraging sociability of nesting wading birds (Ciconiiformes) at Lake Okeechobee, Florida. The Wilson Bulletin 107:437–451.

Sridhar, H., G. Beauchamp, and K. Shanker (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. Animal Behaviour 78:337–347.

Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation 141:2159–2173.

Stankowich, T., and D. T. Blumstein (2005). Fear in animals: A meta-analysis and review of risk assessment. Proceedings of the Royal Society of London B: Biological Sciences 272:2627–2634.

Sutherland, W. J. (1996). From Individual Behaviour to Population Ecology. Oxford University Press, Oxford, UK.

Sun, Y., A. K. Skidmore, T. Wang, H. A. M. J. van Gils, Q. Wang, B. Qing, and C. Ding (2014). Reduced dependence of Crested Ibis on winter-flooded rice fields: Implications for their conservation. PLOS One 9:e98690. doi:10.1371/journal.pone.0098690.

Terborgh, J. (1990). Mixed flocks and polyspecific associations: Costs and benefits of mixed groups to birds and monkeys. American Journal of Primatology 21:87–100.

Thompson, D., and M. Thompson (1985). Early warning and mixed species association: The 'Plover's Page' revisited. Ibis 127:559–562.

Thompson, D. B. A., and C. J. Barnard (1983). Anti-predator responses in mixed-species associations of Lapwings, Golden Plovers and Black-headed Gulls. Animal Behaviour 31:585–593.

Uetz, G. W. (1989). The "ricochet effect" and prey capture in colonial spiders. Oecologia 81:154–159.

Vahl, W. K., J. van der Meer, F. J. Weissing, D. van Dullemen, and T. Piersma (2005). The mechanisms of interference competition: Two experiments on foraging waders. Behavioral Ecology 16:845–855.

Wang, C., D. Liu, B. Qing, H. Ding, Y. Cui, Y. Ye, J. Lu, L. Yan, L. Ke, and C. Ding (2014). The current population and distribution of wild Crested Ibis *Nipponia nippon*. Chinese Journal of Zoology 49:666–671.

Wang, Z., Z. Li, G. Beauchamp, and Z. Jiang (2011). Flock size and human disturbance affect vigilance of endangered Red-crowned Cranes (*Grus japonensis*). Biological Conservation 144:101–105.

Wikar, D., M. Ciach, M. Bylicka, and M. Bylicka (2008). Changes in habitat use by the Common Buzzard (*Buteo buteo* L.) during non-breeding season in relation to winter conditions. Polish Journal of Ecology 56:119.

Ydenberg, R. C., and L. M. Dill (1986). The economics of fleeing from predators. Advances in the Study of Behavior 16:229–249.

Young, A. D. (1989). Spacing behavior of visual- and tactile-feeding shorebirds in mixed-species groups. Canadian Journal of Zoology 67:2026–2028.

Zhang, Z., and C. Ding (2008). The in-situ conservation of Crested Ibis and relate research progress. Science and Technology Review 26:48–53.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use