Effects of foraging mode and group pattern on vigilance behavior in water birds: a case study of mallard and black-winged stilt

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ABSTRACT. Vigilance behavior is affected by many factors including foraging mode and group pattern which we attempted to understand through a case study of mallard *Anas platyrhynchos* and black-winged stilt *Himantopus himantopus* in the Hengshui Lake National Nature Reserve, China. Mallard, a swimming bird, forages in irregular and loose circular groups in open water and its foraging mode (with its head underwater looking for food) does not allow for simultaneous monitoring of potential threats above the water surface, which is why its foraging is called "blind period of foraging". In contrast, black-winged stilt is a wading bird and forages along riversides in long linear foraging groups. Its long beak, neck and legs enable it to scan around while foraging without any obviously blind period. We used the focal sampling method and measured vigilance behavior by the time spent vigilant, vigilance frequency, average duration of vigilance, alert distance and flee distance for the two species. We predicted higher levels of vigilance and longer alert and flee distance in mallard with long blind periods of foraging. Our results indicated significant differences ($p<0.05$) in vigilance behavior between the two species. The effects of group size and gender on vigilance were also checked but showed no significant differences. Higher-level vigilance in mallard was mainly due to its foraging mode with long 'blind periods' and circular foraging group pattern. We suggested that buffer zones be established in ecotourism regions in order to protect birds from human interference.

KEYWORDS: alert distance, *Anas platyrhynchos*, blind period of foraging, flee distance, *Himantopus himantopus*

INTRODUCTION

Vigilance behavior plays an important role in ensuring the fitness of animals and their offspring (Treves, 2000; Beauchamp, 2001). If animals monitor their surroundings and detect threats earlier, they may have a better chance to survive. However, high-level vigilance is often at the expense of other activities crucial for their maintenance (Inger et al., 2006). Therefore, animals should balance the tradeoff between vigilance and other activities, especially feeding and resting (Bachman, 1993; Illius & Fitzgibbon, 1994; Gauthier-Clerc et al., 2000; Inger et al., 2006; Benhaiem et al., 2008).

Many factors affect vigilance pattern and how animals balance the tradeoff (Gauthier-Clerc et al., 2000; Boysen et al., 2001; Rolando et al., 2001; Childress & Lung, 2003; Lazarus, 2003; Li & Jiang, 2008). Investigation of the effects of foraging posture (or body posture) has received the attention of a number of researchers (Krause & Godin, 1996; Kaby & Lind, 2003; Makowska & Kramer, 2007). Animals with different foraging postures differ in their efficiency of detecting predation risk during feeding known as low-quality vigilance and high-quality vigilance suggested by Lima & Bednekoff (1999). During foraging, the visual field is, to some extent, obstructed (Metcalfe,

1984) resulting in lower-quality vigilance. Compared with foraging posture, more emphasis should be put on foraging mode, which has more obvious influence on vigilance pattern. Group geometry is another important factor influencing vigilance behavior. Individual position and distance-to-neighbor have been found to affect vigilance behavior (Lazarus, 2003; Dias, 2006; Proctor et al., 2006; Fernández-Juricic et al., 2007; Öst et al., 2007). In addition, group pattern (or group shape) is also a potential factor of concern. Birds foraging in linear foraging group are more vigilant and change their heads and body positions more often than do those foraging in a circular group (Bekoff, 1995; Bahr & Bekoff, 1999).

Along with percentage time, frequency and duration of vigilance, alert and flee distance are also indices for vigilance level in animals (Walther, 1969; Li et al., 2007) and reflect tolerance to intrusions (Erwin, 1989; Fernández-Juricic et al., 2002). Alert distance was defined as the minimum distance between an animal and the approaching threat when the animal started to be alert toward the threat (Cooper, 2008). Flee distance is referred to as the minimum distance when the animal can not tolerate the approaching threat and flees away (Fernández-Juricic et al., 2002).

Mallard *Anas platyrhynchos* Linnaeus, 1758 and black-winged stilt *Himantopus himantopus* Linnaeus, 1758 differ in both foraging mode and group pattern, which makes them ideal models for investigating the effects of these two factors on vigilance behavior. Mallard is a swimming bird, that forages in irregular and loose circular groups in open water. During foraging, it keeps its head underwater looking for food. This kind of foraging mode blindfolds its eyes from monitoring potential threats above the water surface, which is why this foraging behavior is called "blind period of foraging". In contrast, black-winged stilt has a long beak, neck and legs, which are all typical characteristics of a wading bird. This species forages in linear foraging groups at the waterfront along the riverside. The morphological characteristics and foraging behavior enable black-winged stilts to scan the surroundings while foraging without any evident blind period.

In the present study, we hypothesized that foraging mode and group pattern influence vigilance behavior in mallard and black-winged stilt. We predicted that mallard with long "blind period of foraging" would have a higher vigilance level, a longer alert distance and a larger fleeing distance.

MATERIALS AND METHODS

Study site and animals

We conducted our field work in the Hengshui Lake National Nature Reserve (37°31′40″-37°41′56″N, 115°27′50″-115°42′51″E), Hebei Province, China. The climate in the reserve is characterized as a temperate continental monsoon climate. The nature reserve is composed of a mixed landscape with lakes, rivers, swamps, mudflats, meadows, field crops and woodlands. Hengshui Lake is a crucial foraging and resting site for migratory birds. For observation of black-winged stilt, we selected a foraging site along a riverside in the northern part of the reserve. An open lake about 4 000m^2 was selected to observe the mallard's behavior. The lake is surrounded by wetlands and several ponds, and separated from the selected foraging site of black-winged stilt by a dam. Mallard and black-winged stilt, focal species in our study, were the dominant species at the two sites. Other sympatric birds included spotbill duck *Anas poecilorhyncha* Forster, 1781, little grebe *Tachybaptus ruficollis* Pallas, 1764, white-eyed pochard *Aythya nyroca* Güldenstädt, 1770, common moorhen *Gallinula chloropus* Linnaeus, 1758, common snipe *Gallinago gallinago* Linnaeus, 1758 and long-toed stint *Calidris subminuta* Middendorff, 1853. Predators of mallard or black-winged stilt were rarely seen at the study site. Occasionally, there were human intrusions but the activities of the birds were rarely disturbed.

Behavior observation

We used the focal sampling method (ALTMANN, 1974) to observe and record behaviors of mallard and black-winged stilt from sunrise to sunset during sunny days between April 12 and May 13, 2007. Observations were conducted over all daylight hours equally to avoid the probable effect of time period on vigilance during daytime (ELGAR, 1989; LI & JIANG, 2008). In order to avoid disturbing the normal behavior of the focal individual, we hid behind bushes or reeds about 100m away on the bank and conducted observations of birds with a pair of binoculars (8-16×40) a few minutes after a group of birds entered into the observation area.

We defined a focal group as a flock of individuals of a single species with a visually estimated distance between intra-group members being shorter than ten meters. Due to the difficulties of individual identification, we numbered group members from left to right, randomly selected focal individuals according to their sequence number and kept eyesight focused on the focal individuals through each observation session. This random selection process resulted in focal individuals with random spatial locations in groups, which avoided the effects of distance-to-neighbour and position in group on vigilance behavior (ROLANDO et al., 2001; LAZARUS, 2003; PROCTOR et al., 2006; FERNÁNDEZ-JURICIC et al., 2007). We randomly selected one but never more than two individuals in a single focal group as focal observation to lower the probability of repeated observation. Each focal individual was observed for ten minutes unless it ran out of sight or the focal group composition changed. Observations shorter than ten minutes were discarded.

For each observation, we recorded date, time, location, gender, and group size. When one behavior state occurred, we immediately recorded the behavior and the time. The observation and recording tasks were carried out by the same person. For both mallard and black-winged stilt, we recorded 13 different types of behavior states, which were then categorized into four types: feeding, resting, vigilance and others (see details in Table 1). No juveniles of either species was observed during our field work, thus all the data were of adult birds. During the field work, we adhered to the “Guidelines for the use of animals in research” published in *Animal Behaviour* (1991), and also adhered to the Wildlife Protection Law of People’s Republic of China.

TABLE 1

Behavior definition for mallard (*Anas platyrhynchos*) and black-winged stilt (*Himantopus himantopus*).

Behavior Category	Behavior Definition
Feeding	Mallard: drilling its head into deep water or exploring with its beak in shallow water Black-winged stilt: searching and foraging along the riverside wetland during a foraging session with its head down
Resting	Standing still on one leg, lying down and preening feathers
Vigilance	Scanning around with head up, alarm calling and flushing
Others	Twitter, flying, bathing, swimming, fighting, and chasing

Alert and flee distance measurement

To measure the alert and flee distance, one observer approached the focal group slowly (always in the same clothes and at approximately the same speed, c. one kilometer per hour) and recorded the focal group size and the distance data measured by a laser range finder (WCJ-2, Leiyuan Electronic Industry Co., Ltd, China, guaranteed range: 30-4,000m, accuracy: ±1m). We defined alert distance as the minimum distance when approximately 50% individuals in the focal group became alert toward the observer, and flee distance as the minimum distance when approximately 50% individuals in the focal group fled away (ERWIN, 1989). When the distance was shorter than the detection range of the range finder, we measured distance with tapelines after focal individuals fled away. We measured the alert and flee distances in mallard and black-winged stilt on two successive days at the same time of day: early morning and late afternoon when birds were most active.

Statistical treatment

We assembled the following data for both mallard and black-winged stilt: time spent vigilant, vigilance frequency, average duration of vigilance, alert distance and flee distance. Time spent vigilant in each observation session was calculated and expressed as percentage of the total time being vigilant to the entire duration of the observation session. Vigilance frequency was defined as the number of vigilance behaviors per minute. Average duration of one vigilant bout was calculated by dividing the time spent vigilant by the corresponding number of vigilance states.

Data were first tested for normality with a one-sample Shapiro-Wilk test. Linear regression analysis was used to test the correlation between

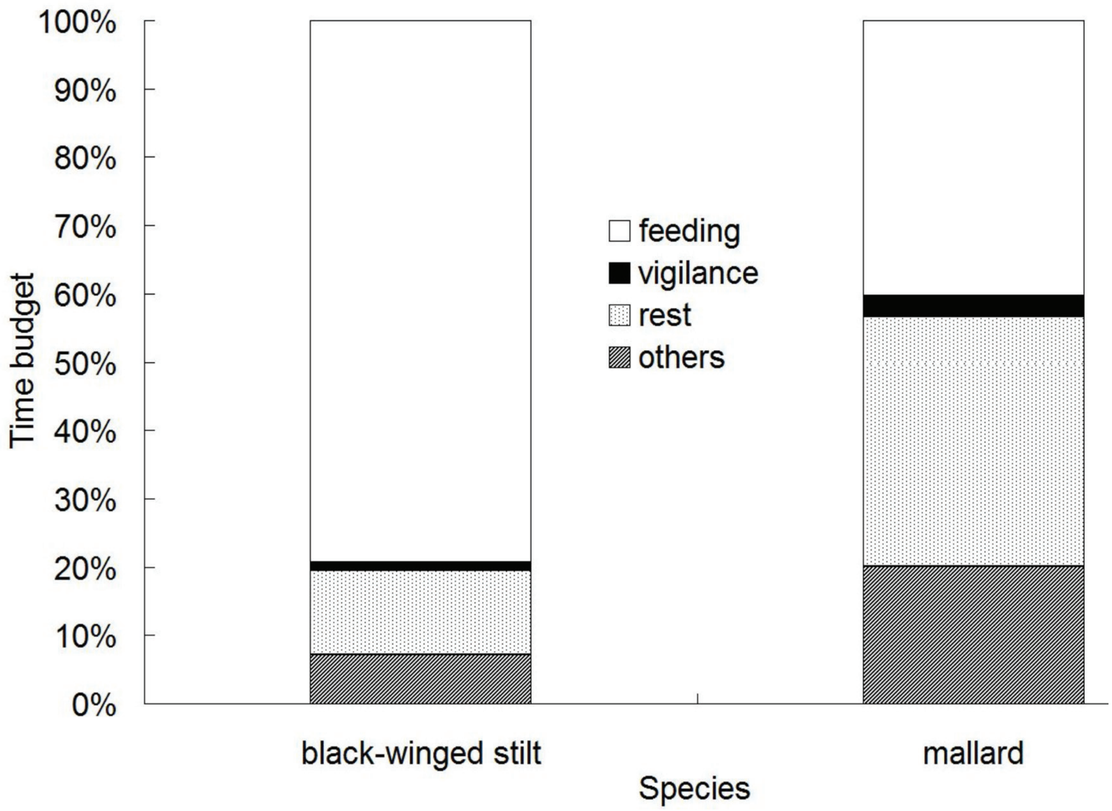

Fig. 1. – Percentage time spent being vigilant in mallard (*Anas platyrhynchos*) and black-winged stilt (*Himantopus himantopus*).

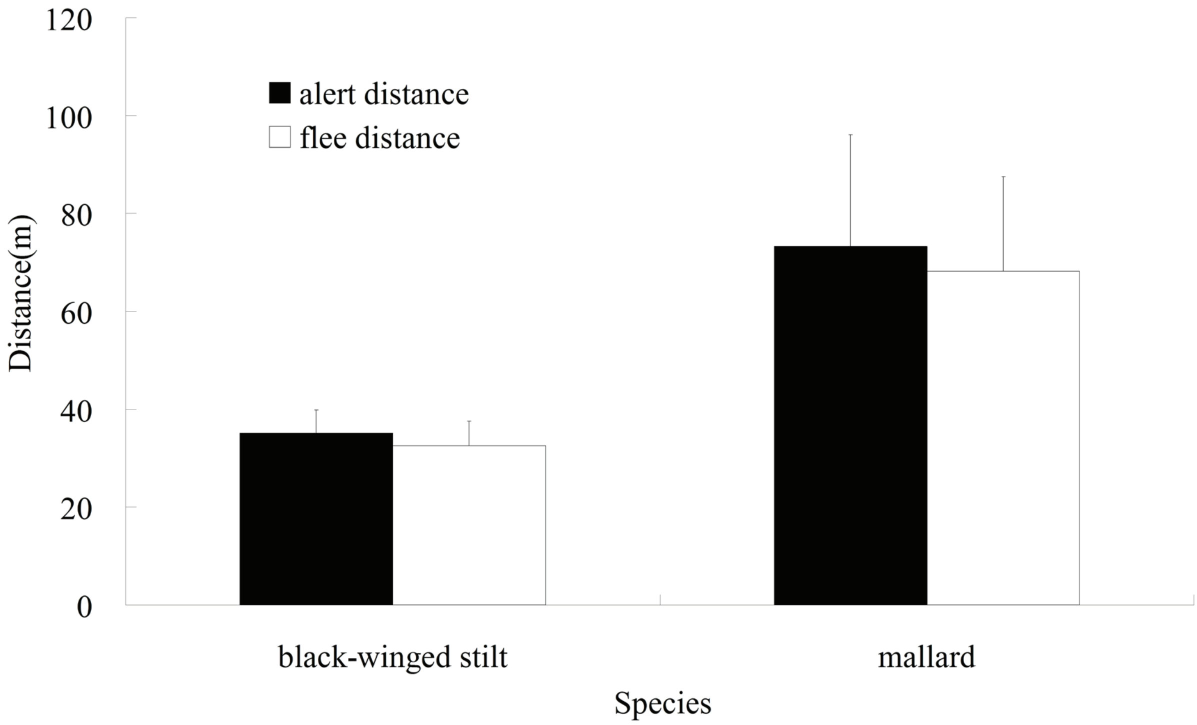

Fig. 2. – Alert and flee distances of mallard (*Anas platyrhynchos*) and black-winged stilt (*Himantopus himantopus*).

alert and flee distance, $\log_{10}$ transformed average duration of vigilance and group size (continuous factor) or gender (discrete factor). Because these tests gave no significant results (p>0.05 for all), we removed the effects of gender and group size in the subsequent analyses. The interaction between alert distance and flee distance was also tested using the linear regression analysis. Then we performed the General Linear Model (GLM) to test the effect of the blind period (two level, 1 for black-winged stilt and 2 for mallard) on average duration of vigilance. GLM was also used to test the effect of the blind period on alert and flee distances. Time spent vigilant and vigilance frequency were tested with nonparametric tests because they failed to fit normal distribution even after transformations. Statistical analyses were carried out with SAS 8.1 (Cary, NC, USA). All significant differences were set at p=0.05.

RESULTS

In total, we conducted 163 (1,630min) and 72 (720min) focal observations (each observation session lasted ten minutes) after discarding those less than ten minutes for black-winged stilt and mallard, respectively. Twenty-nine sets of alert distance and flee distances were measured for each of the two species. The focal group size of black-winged stilt and mallard ranged from 13 to 53 (37 ± 8, mean ± SE) and from 8 to 33 (17 ± 7), respectively. Alert distance, flee distance and $\log_{10}$ transformed average duration of vigilance were normally distributed (p>0.05).

Duration of each vigilant bout averaged 17.9 ± 15.6s ranging from 0 to 65s for black-winged stilt and 23.4 ± 16.0s ranging from 0 to 72s for mallard. The GLM process gave a significant result indicating that average vigilance duration of black-winged stilt was significantly shorter than that of mallard ($F_{1, 85}$=3.04, p=0.0349<0.05). Vigilance frequency in each observation session of mallard ranged from 0 to 0.4min^{-1} and averaged 0.06min^{-1}. Percentage of time spent vigilant in the entire duration time of each observation session for mallard ranged from 0 to 48% and was 2.95% on average, with two-thirds of observations less than the average. Vigilance of black-winged stilt was less frequent, i.e. 0.04min^{-1} on average and ranging from 0 to 0.3min^{-1}. Black-winged stilt spent 1.22% on average of total observation time on vigilance ranging from 0 to 22% with three-quarter observations less than the average (Fig. 1). Nonparametric tests showed that differences in both time spent vigilant and vigilance frequency between the two species were significant (p=0.0098<0.05 and p=0.0276<0.05, respectively). Black-winged stilt spent 79.3% of the total time feeding while mallard spent 40.2% on this activity (p<0.0001). In contrast, mallard spent nearly three times as much time resting as black-winged stilt: 36.6% and 12.3%, respectively (p<0.0001).

Alert distance and flee distance of black-winged stilt ranged from 24m to 44m with an average of 35.1 ± 4.8m and from 23m to 43m with an average of 32.6 ± 5.0m, respectively. Mallard had longer alert and flee distances: 73.3 ± 22.8m of alert distance ranging from 27m to 128m and 68.3 ± 19.2m of flee distance ranging from 25m to 103m (Fig. 2). The GLM analysis for the alert and flee distances between the two species also indicated both distances were significantly longer for mallard ($F_{1, 57}$=78.38, p<0.001 for alert distances and $F_{1, 57}$=93.51, p<0.001 for flee distances). Differences between alert distance and flee distance ranged from 1m to 13m with an average of 2.52 ± 2.46m for black-winged stilt and from 1m to 33m with an average of 5.21 ± 6.52m for mallard. Flee distance was linearly correlated with alert distance (β=-0.83 ± 0.09, p<0.001 and β=-1.14 ± 0.06, p<0.001, respectively).

DISCUSSION

Cost of vigilance behavior and blind period of foraging

Vigilance behavior plays a crucial role in maintenance and offspring protection in animals, but it is often costly and conflicts with energy intake and preservation (Bachman, 1993; Gauthier-Clerc et al., 2000; Lazarus, 2003; Inger et al., 2006). Almost no prey animals can successfully detect approaching threats in its surroundings while concentrating on foraging or resting (Beauchamp & Livoreil, 1997; Jones, 1998). However, vigilance behavior is not completely incompatible with other activities for many animals (Lima & Bednekoff, 1999). For instance, ungulates are able to chew cud with their heads up scanning around (Frid, 1997; Treves, 2000). In practice, however, it is often difficult to determine whether the focal animal is vigilant or not while foraging. In a previous study, the view field of dairy cattle was manually restricted so that they could not feed and scan simultaneously (Welp et al., 2004). Obviously this is not feasible when studying wild animals in the field.

Mallard is a dabbling duck that usually feeds by pulling and tearing underwater plants (Guillemain et al., 2000). When a mallard has a blind period of foraging, it must spend time after each feeding dive to carefully scan its surroundings above water surface. In contrast, black-winged stilt is a typical wading bird with long beak, long neck and long legs. It mainly forages in waterfronts along riversides (Zhang et al, 2003). These morphological and ecological characteristics enable black-winged stilt to scan its surroundings more conveniently while it forages. Black-winged stilt neglect mild disturbances that are often misjudged as serious risks and given undue attention by mallard. This advantage results from foraging mode. Compared with mallard, black-winged stilt have a reduced cost of vigilance and are able to spend more time engaged in other crucial behaviors such as foraging and resting.

We found that mallard were significantly more vigilant than black-winged stilt. Mallard spent more time (p=0.0098<0.05) on vigilance behavior (2.95% of the total time) than did black-winged stilt (1.22%). In addition, mallard scanned more often (p=0.0276<0.05) (0.06min^{-1} versus 0.04min^{-1}). The frequent interruption to foraging sessions could cost extra energy because of the stop and start nature. The process of switching between the two activities was much longer for mallard than black-winged stilt, which easily switched from scanning to feeding with simple changes to their head position.

Furthermore, mallard were forced to stay alert longer after they perceived any approaching threat. This was apparent by the fact that the mean vigilance duration of mallard (23.4 ± 16.0s) was significantly ($F_{1, 85}$=3.04, p=0.0349<0.05) longer than that of black-winged stilt (17.9 ± 15.6s). These results revealed that cost of vigilance was not equal among different species. Animals with long blind periods of foraging may allocate more energy in vigilance and the cost of vigilance behavior may be higher than in the case of animals without blind periods. Thus, blind periods of foraging contribute substantially to the higher level of vigilance of mallard.

Group pattern and vigilance behavior

Group geometry is another promising area to be investigated (ARENZ, 2003). Many studies have shown that position in the group (LAZARUS, 2003; PROCTOR et al., 2006) and the distance-to-neighbor (ROLANDO et al., 2001; FERNÁNDEZ-JURICIC et al., 2007) affect vigilance pattern. These findings may be more applicable to species that feed in a circular group such as mallard. Individuals arranged in a circular pattern are closer to each other. This pattern allows individuals to receive signals given by alert neighbors and thus guarantees the rapid transmission of social information (TREVES, 2000; BEKOFF, 2003; FERNÁNDEZ-JURICIC et al., 2007). As for the species foraging in linear arrays such as black-winged stilt, individuals in a group do not have more than two neighbors (BAHR & BEKOFF, 1999). In this case, signal transfer will be frustrated and individuals foraging in this kind of group pattern may rely more on their own detection rather than on associates (TREVES, 2000). BEKOFF (1995) found that, compared with those foraging in a circle, evening grosbeaks *Coccothraustes vespertinus* Cooper 1825 in a linear array reacted to changes in group size more slowly, showed less coordination in head movements and more variability in all measures. Social information transfer inefficiency in linear group pattern hinders the synchronization of behavior among group members, resulting in unreliability of collective detection (SIROT, 2006).

The two species we studied represent two distinct foraging group patterns (GUILLEMAIN et al., 2000; ZHANG et al, 2003). Comparison between these two species provided some valuable insights that, in fact, group pattern and foraging mode can independently as well as jointly affect vigilance behavior. We found in this study that longer blind periods of foraging increased the vigilance level of mallard, but the group pattern of a circle shape palliated the effect of blind period. However, the mixed effects of foraging mode and group pattern cannot be easily differentiated without robust evidence from laboratory experiments.

Alert distance and flee distance

Trade-off between vigilance behavior and other activities is also reflected by alert and flee distance (WALTHER, 1969; LI et al., 2007). Animals will not immediately flee upon detection of an approaching predator or other threat. Rather they will stare at or listen to the approaching threat for a short time, which is called the detectability period (GUTZWILLER et al., 1998). If they flee at once, they will waste time and energy and may miss a feeding chance. Continuing to forage will save them some energy, but at the risk of being captured by a predator. When the potential prey can no longer tolerate the approaching predator, they will flee. Difference between alert and flee distance reflects the tolerance of prey animals to predation pressure (WANG et al., 2004; HOLMES et al., 2005).

The tolerance to approaching threats differs among species and reflects biological, ecological and even historical characteristics of the species. Like the other aspects of vigilance behavior, alert and flee distances are affected by many factors, such as seasonal reproductive status (White & Berger, 2001; Wolff & Van Horn, 2003) and nutritional status, habitat type, experience of the specific animal to threats (Treves, 2003), body size, and time of the day (Taylor & Knight, 2003). In the present study, we found that in mallards the longer alert and flee distances coincided with higher vigilance levels. The results were due to differences in foraging mode and group pattern of the two species but not to group size effects (Erwin, 1989).

Management implications

Animals express higher levels of vigilance where predation risk or intrusion is frequent (Creel et al., 2008). However, higher vigilance level is at the expense of feeding or resting time (Inger et al., 2006). Efficient and convenient vigilance behavior saves time for other activities resulting in increased fitness. Management measures should be taken to protect animals from intense intrusions and especially from human interference. Analysis of vigilance behavior for animals is one of the necessary steps when formulating efficient management measures. The results of our present study on mallard and black-winged stilt could be generalized for other taxa. Based on our findings, we suggest the establishment of a buffer zone around feeding sites of wild animals. As for the protection of Anatidae and shorebirds in ecotourism regions, we suggest buffer zones being 100m and 50m wide, respectively.

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