VIGILANCE BEHAVIOUR OF PREENING BLACK-TAILED GODWIT *LIMOSA LIMOSA* IN ROOSTING FLOCKS

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SUMMARY.—*Vigilance behaviour of preening black-tailed godwit* Limosa limosa *in roosting flocks.*
Aims: The vigilance behaviour of preening black-tailed godwits *Limosa limosa* was studied during postbreeding migration.
Location: Salt pans situated in the Parque Natural de las Marismas del Odiel (ría de Huelva, Spain).
Methods: Actively preening birds were arbitrarily selected. Each bird was observed for 2 minutes using a 20-60 x 60 telescope. For each focal bird air temperature, windspeed (using an anemometer), distance to the nearest conspecific at the start of monitoring, number of individual godwits and other waders and gulls in a radius of 10 m of the sampled bird and godwit position (central or peripheral) were recorded. Dependent variables recorded were vigilance time, scanning rate and scan duration.
Results and Conclusions: Vigilance time and scanning rate were higher in peripheral godwits than in central godwits, while mean scan duration did not differ significantly between both groups. Using as predictors godwit position (central *vs* peripheral), presence or absence of black-headed gull and air temperature the best model to explain vigilance time (Akaike weight, $w_i = 0.248$) and scanning rate ($w_i = 0.427$) included in both cases the godwit position, presence of black-headed gulls and air temperature. Godwit position was a consequential predictor with a negative effect of the central sites in the vigilance time and scanning rate. Black-headed gull presence and air temperature were two consequential predictors that influenced the increase of the vigilance time and scanning rate in roosting godwits. Birds may make postural changes to alter heat loss and we suggest that to increase heat loss the head may be more frequently raised after preening bout. In accordance with this hypothesis, in high temperatures the head rising in preening godwits could have antipredatory and thermoregulatory functions.
Key words: black-tailed godwit, *Limosa limosa*, preening, vigilance.

RESUMEN.—*Vigilancia de agujas colinegras* Limosa limosa *atusándose en bandos en reposo.*
Objetivos: Durante la migración posnupcial se estudió el comportamiento de vigilancia de agujas colinegras atusándose.
Localidad: Salinas situadas en el Parque Natural de las Marismas del Odiel (ría de Huelva, España).
Métodos: Se seleccionaron arbitrariamente agujas atusándose activamente. Cada ejemplar fue seguido durante 2 minutos utilizando telescopio 20 - 60 x 60. Para cada ejemplar muestreado se registraron al inicio temperatura del aire, velocidad del viento, distancia al conespecífico más próximo, conespecíficos y láridos 10 m alrededor del ejemplar y posición en el bando (central o periférica). Las variables dependientes fueron tiempo de vigilancia, número de actitudes de vigilancia y duración de las actitudes de vigilancia.
Resultados y Conclusiones: El tiempo de vigilancia y número de actitudes de vigilancia fueron mayores en aves periféricas que centrales, pero la duración media de las actitudes no difirió entre ambos gru-

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pos. Empleando como predictores la posición del ejemplar (central *vs* periférica), presencia/ausencia de gaviotas reidoras y temperatura ambiente, los modelos más parsimoniosos para explicar el tiempo de vigilancia (peso de Akaike, $w_i = 0.248$) y número de actitudes ($w_i = 0.427$) incluyeron en ambos casos los tres predictores. La posición de la aguja fue un predictor consecuencial, con efecto negativo de la posición central sobre el tiempo de vigilancia y número de actitudes de vigilancia. La presencia de gaviotas reidoras y la temperatura ambiente fueron dos predictores consecuenciales con efecto positivo sobre ambas variables dependientes. Las aves pueden realizar movimientos para modificar la pérdida de calor y sugerimos que para incrementar dicha pérdida la cabeza podría ser erguida más frecuentemente. De acuerdo con esta hipótesis, a temperatura ambiente elevada el alzamiento de la cabeza en agujas atusándose podría tener funciones antipredadora y termoreguladora.

Palabras clave: Aguja colinegra, atusamiento, *Limosa limosa*, vigilancia.

INTRODUCTION

Vigilance and visual scanning of the surroundings beyond the immediate vicinity (Treves, 2000), is a crucial activity need to assure the individual survival. This activity may be use to detect approaching predators, but also to monitor conspecifics, mainly when there is scramble competition (Beauchamp and Ruxton, 2003; Randler, 2005a). Flocking is a common antipredatory strategy of many birds and mammals, and flock size is habitually related with a decrease in the individual vigilance (Roberts, 1996; Treves, 2000), although in both mammals and birds there are species where this negative relationship between flock size and vigilance of feeding individuals apparently did not exist (Keys and Dugatkin, 1990; Treves, 2000; Beauchamp, 2001; Barbosa, 2002; Domínguez, 2002a). It was argued that predation-related factors and scramble competition represent equally viable explanations for the group-size effect (Beauchamp and Ruxton, 2003), and for that reason studies of preening and sleeping birds can be useful to elucidate the relationship between group size and vigilance (Roberts, 2003). Preening birds are useful to show that the edge effect may indeed related to predation, because during feeding birds at the edge of a flock may either experience a higher predation or a better food supply.

Preening, the arrangement, cleaning, and general maintenance of the plumage using the bill (Campbell and Lack, 1985), is an important activity for the survival of birds, representing a mean of 9 % in the daily budget of birds (Cotgreave and Clayton, 1994). In the post-breeding period, the comfort behaviour of the waders oscillates between 2 and 31% of daily budget (Puttick, 1984; Young, 1989; Domínguez, 1990; Fasola and Biddau, 1997; Ntiamoa-Baidu *et al.*, 1998), and is longer for the species with long bills (Barbosa, 1996). In these birds preening occurs at low tide, in feeding flocks with the birds searching for their prey and stopping temporarily to preen the feathers for few minutes, and at high tide, in compact and static roosting flocks, with alternating sleeping and preening periods.

Many biotic and abiotic variables can potentially affect vigilance behaviour (Elgar, 1989; Quenette, 1990), including the type of activity alternating with vigilance. During preening, birds can have decreased vision caused by feathers covering their eyes (Redpath, 1988), and this could cause an increase in the predation risk because individuals with visual obstructions are less likely to detect a predator and/or the alarm flight of other birds (Harkin *et al.*, 2000).

Modelling has shown its utility in analysis where many independent variables can affect the variable studied (Anderson *et al.*, 2000), although it has been questioned as a useful methodology to explain the vigilance behaviour (Lazarus, 2003; Treves, 2003). However,

it has been used or considered useful to understand the causes of changes in vigilance with group size and to predict quantitatively the nature of such changes (Ward and Low, 1997; Burger *et al.*, 2000; Boysen *et al.*, 2001; Beauchamp, 2003). Thus, the black-tailed godwit *Limosa limosa*, a very gregarious wader in feeding and roosting periods was selected and an attempt was made to model the godwit vigilance behaviour in preening birds located in roosting flocks. As predictors the air temperature, godwit position (peripheral or central) and presence or absence of black-headed gulls were used. Flock size and nearest neighbour distance were not used as predictors. The first because godwits sampled were in compact flocks greater than 100 birds and several studies have shown that the decrease in the individual vigilance with the flock size was asymptotic with densities of 7 - 10 birds (Abramson, 1979; Redpath, 1988; Quenette, 1990). Distance to the nearest neighbour was not used because the studied flocks were extremely compact and the variation in the nearest distances was very small.

In relation to edge effect it is known that individual vigilance effort varies according to its position in the group, with peripheral birds vigilant more than central birds (Petit and Bildstein, 1987; Burger and Gochfeld, 1991a; Desholm *et al.*, 1999; Randler, 2005b), including sleeping godwits in roosting flocks (Domínguez, 2003). In this case it was predicted that the position of birds in roosting flocks would affect the vigilance behaviour, the more peripheral godwits scanning more than centrally preening birds.

Black-headed gulls habitually share feeding and roosting areas with godwits in Palearctic wetlands. The effect of this gull in the godwit vigilance behaviour apparently depended on the wader activity. Gull presence increased the vigilance rates of feeding godwits, probably because its kleptoparasitic activity (Amat and Aguilera, 1990; Domínguez, 2002a, 2002b), but did not seem to influence the vigilance behaviour of sleeping godwits (Domínguez, 2003). In other feeding waders there was a positive relationship between gull numbers and vigilance effort (Metcalfe, 1984; Barnard and Thompson, 1985), while there is no information about this topic in preening birds. Agonistic encounters between nonfeeding waders and gulls are not frequent (Cramp and Simmons, 1982; Ferns, 1992), and it has been suggested that black-headed gulls may act as one form of protector species in mixed flocks with lapwings *Vanellus vanellus* and golden plovers *Pluvialis apricaria* (Barnard and Thompson, 1985). Here, the effect of gull presence in the vigilance behaviour is explored.

Abiotic factors as air temperature and wind speed were investigated less, especially in areas characterized by high temperatures. Postbreeding waders migrate and they winter along warm areas of the south of Europe and Africa. This climate could cause them thermal stress (Klaassen, 1990) and this suggests its possible influence in the bird behaviour. The patterns between temperatures, scanning and flock size seem contradictory. Several studies in foraging birds found a positive relationship between vigilance rate and air temperature (Caraco, 1979; Pravosudov and Grubb, 1995, 1998), but other studies showed a negative relationship (Ward and Low, 1997) or showed no relationship at all (Boysen *et al.*, 2001). In cold climates, the increase of temperature was related with the increase in the peeking rate of sleeping waders (Ferns, 1992). The combination of high temperatures and moderate winds could influence the vigilance behaviour of godwits, for example, influencing the bird position in the roosting flock and, thus, its vigilance effort (Domínguez, 2003). Here the influence of air temperature in the vigilance behaviour of godwits is investigated.

MATERIALS AND METHODS

Observations took place on salt pans situated in the Parque Natural de las Marismas del

Odiel (ría de Huelva, Spain) (37° 12' N - 06° 58' W). This habitat was characterized by the absence of objects that could limit the visual field of resident birds. Observations were carried out in four days between 28 August to 19 September 1991, each day between two hours before and after the peak of high tide. Mean ± SD air temperature surveying roosting flocks was 25.8 ± 2.43 (range 22-32 °C) and windspeed was 2.8 ± 0.23 m/s (range 1 - 8 m/s).

Actively preening birds were selected arbitrarily, trying not to repeat monitoring of the same bird in the same period of the tidal cycle. Godwits were not marked but during work the local godwit population was greater than 1,000 birds, made it highly unlikely that the same individual was sampled twice. Preening behaviour was defined as the arrangement, cleaning and general maintenance of the plumage using the bill (Campbell and Lack, 1985), anywhere that the body area was treated. Each bird was observed for 2 minutes using a 20 - 60x telescope. Age and sex were not noted, because many adults had moulted and it was difficult to specify sex and age of the godwits in compact flocks. Birds were surveyed whose only behaviour during the 2 minutes period was preening. Finally, 64 observations in roosting flocks were obtained. For each focal bird the following variables were recorded using a tape-recorder at the start of monitoring: air temperature, windspeed (using an anemometer), distance to the nearest conspecific at the start of monitoring and number of individual godwits and other waders and gulls in a radius of 10 m of the sampled bird and godwit position (central or peripheral). Those birds defined as central were all surrounded by other godwits and as peripheral the outermost godwits of the flock, always at distances of less than 1 m from other conspecifics. In roosting flocks, the black-headed gull was a common species and the lesser black-backed gull *Larus fuscus* was present sporadically. Dependent variables recorded were vigilance time (time with its head raised to at least the horizontal position),

scanning rate (number of scans per two minutes preening) and scan duration (vigilance time / scanning rate).

Statistical analysis

The data were inspected for normality and homoscedasticity, and were transformed with $\log_{10}$ to satisfy the assumptions of statistical analyses when necessary.

A candidate set of 7 *a priori* models was developed to analyze the effect of independent variables on vigilance time and scanning rate of preening birds. The godwit position (central or peripheral), presence/absence of black-headed gull in 10 m around the focal godwit and air temperature were used as predictors. Wind velocity was not used as a predictor because it was very variable even in a 2 minutes period.

The best parsimonious model was selected using the Akaike criteria (AIC; Sakamoto *et al.*, 1986), being

$$\text{AIC}_c = n \log_e (\text{RSS/n}) + 2K + \frac{2K\,(K+1)}{(n\text{-}K\text{-}1)}$$

(Anderson *et al.*, 2000), where RSS = residual sum of squares, n = sample size and K = number of parameters estimated. We used a modified criterion of AIC, called AICc, because n/K < 40. Also, AIC values were rescaled using the model with the minimum AIC_c, as Δ_i = AIC_i – minAIC_c. Generally, models with Δ_i values ≤ 2 have strong support, whereas those with values > 10 have little support (Burnham and Anderson, 1998). Akaike weights were obtained as (Anderson *et al.*, 2000):

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum\limits_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta_r\right)} .$$

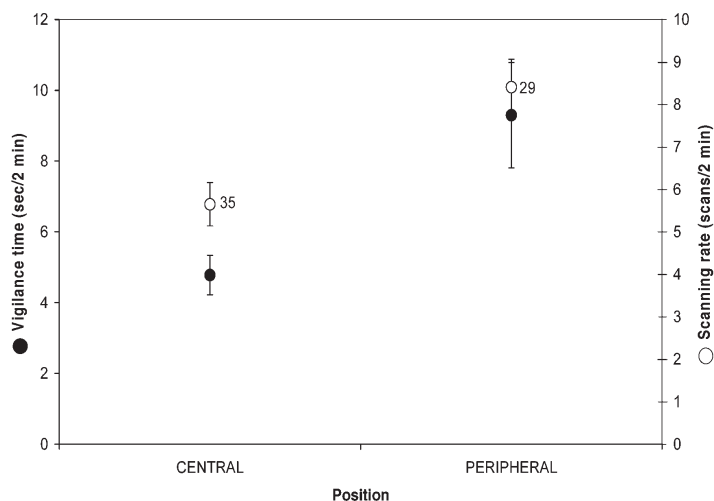Evidence for the importance of each predictor was obtained summing of Akaike weights

FIG. 1.—Mean ± SE of vigilance time and scanning rate of peripheral and central preening godwits in roosting flocks. Sample sizes are shown.
[Media ± se del tiempo y número de actitudes de vigilancia de agujas colinegras centrales y periféricas atusándose en bandos en reposo. Se indican los tamaños de muestra.]

(Σ wi) over models in which the variable occurred (Burnham and Anderson, 1998). Importance values were considered consequentials when Σ wi > 0.5 (Taylor and Knight, 2003).

Mean scan duration and other variables that could not be normalized were analysed with nonparametric tests (Siegel and Castellan, 1988). Throughout the paper mean ± SE are given. Statistical analyses were made with SPSS 11.1 package.

RESULTS

The number of conspecifics in a radius of 10 m of the focal preening godwits was 70.3 ± 3.20 and flocks were compact and static (mean 182 ± 18, range 110-200 birds). The distance (m) to the nearest conspecific was 0.57 ± 0.19 ($n = 64$).

Vigilance time and scanning rate were greater in peripheral than in central godwits (Fig. 1). The best model to explain the vigilance time included godwit position, presence of gulls and air temperature, but other three models had $\Delta_i < 2$ (Table 1). All included the godwit position in the flock with sum of Akaike weights smaller for the other variables (Table 2). The best model using scanning rate included all predictors and other model including godwit position and air temperature had $\Delta_i < 2$ (Table 1). In this case the sum of Akaike weights of godwit position was highest, but the others predictors were consequentials (Table 2). All predictors had a positive relationship with vigilance time and scanning rate. Mean scan duration did not differ significantly between central and peripheral godwits (Mann Whitney test, $U_{29,35} = 456$, $P > 0.05$).

DISCUSSION

One prediction supported by these results was that in roosting flocks peripheral preening godwits spent more vigilance effort than central ones.

TABLE 1

Summary of model selection results for vigilance time and scanning rate of preening godwits in roosting flocks. Models with $\Delta_i < 2$ are showed and ranked by descending Akaike weights (w_i). Predictors: 1, godwit position; 2, black-headed gull presence; 3, Air temperature.
[Resumen de los modelos para tiempo de vigilancia y número de actitudes de vigilancia de agujas colinegras atusándose en bandos en reposo. Se muestran los modelos con $\Delta_i < 2$ ordenados en orden descendente de sus pesos de Akaike (w_i). Predictores: 1, posición de la aguja; 2, presencia de gaviota reidora; 3, temperatura ambiente.]

Dependent variable	Model	R^2	K	AICc	Δ_i	w_i
Vigilance time	{123}	0.110	5	-149.00	0	0.248
	{12}	0.110	4	-148.99	0.01	0.246
	{13}	0.110	4	-148.98	0.02	0.245
	{1}	0.109	3	-148.95	0.05	0.242
Scanning rate	{123}	0.176	5	-194.05	0	0.427
	{13}	0.172	4	-193.69	0.36	0.356

TABLE 2

Importance values (as calculated by summing Akaike weights across all possible models) and direction of effects of predictors used to model vigilance behaviour in roosting flocks. Categorical variables: Godwit position (0 value = central position; 1 value = peripheral position); black-headed gull presence (0 value = no gulls; 1 value = presence of gulls).
[Valores de importancia (calculados como suma de los pesos de Akaike de todos los modelos) y dirección del efecto de los predictores empleados para modelizar el comportamiento de vigilancia de agujas colinegras atusándose en bandos en reposo. Variables categóricas: Posición de la aguja (0 = central; 1 = periférica); presencia de gaviotas reidoras (0 = sin gaviotas; 1 = con gaviotas).]

	Predictors		
Dependent variable	Godwit position	B-h gull presence	Air temperature
Vigilance time	0.981 +	0.507 +	0.505 +
Scanning rate	0.995 +	0.562 +	0.787 +

The same result was obtained in many studies with feeding birds, where peripheral birds were more vigilant (Jennings and Evans, 1980; Petit and Bildstein, 1987; Keys and Dugatkin, 1990; Burger and Gochfeld, 1991b; Desholm *et al.*, 1999) although there were birds and mammals where that difference did not exist (Quenette, 1990; Pöysä, 1994). However, a small number of work has only shown this result in preening (Randler, 2005b) or sleeping birds (Domínguez, 2003). The centre-edge effect could be interpreted in terms of predation risk as centred birds experience greater safety. Other variables with influence in the vigilance behaviour such as

flock size and nearest neighbour distance showed a very small variation in this study and probably did not influence in the results.

Mean scan duration did not differ significantly between peripheral and central birds. This result suggests that with the increase in the risk perception, the godwit strategy involved interspersing more scan postures and not increasing the scan duration. Similar results have been described in preening sanderlings *Calidris alba* (Roberts, 1995).

The presence of black-headed gulls in roosting flocks was treated as a categorical predictor, which was consequential to explain an increase of the vigilance time and scanning rate. The interpretation of this result remains unclear since agonistic encounters between nonfeeding waders and gulls are not frequent (Cramp and Simmons, 1982; Ferns, 1992) and no aggressions were seen during the focal sessions. Moreover, when sleeping the position of the godwit in the flock had a significant effect on peeking rates, but not the presence of blackheaded gulls and not the interaction between position in the flock and presence of gulls (Domínguez, 2003). These facts suggest that godwits would modulate their vigilance behaviour depending on their main activity and the presence of gulls.

Air temperature was a consequential predictor that influenced the increase of the vigilance time and scanning rate in roosting flocks. It was hypothesized that this influence could be related with the thermal stress associated to high temperatures, during which the bird would need to insert more sequences of head risings to improve the thermoregulation. Moderate wind as those registered during the sampling could improve the thermoregulatory effect. Birds may make postural changes to alter heat loss, for example to reduce heat loss the face may be hidden under the scapulars (Campbell and Lack, 1985) and, as is suggested here, to increase heat loss the head may be more frequently raised after a preening bout. In accordance with this hypothesis, in high temperatures the head raising in preening godwits could have antipredatory and thermoregulatory functions.

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