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McBlain, Meaghan; Jones, Katherine; Shannon, Graeme

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Sleeping Eurasian oystercatchers adjust their vigilance in response to the behaviour of neighbours, human disturbance and environmental conditions

M. McBlain, K. A. Jones & G. Shannon [ID]

School of Natural Sciences, Bangor University, Bangor, UK

Abstract

Vigilance is a costly behaviour but it enables animals to detect and avoid threats of predation and intraspecific competition. To compensate for the increased risk while sleeping, many bird species have evolved eye-blinking strategies called peeking, which allows vigilance to persist in a sleep-like state. However, the drivers of vigilance behaviour during sleep have rarely been explored. We investigated how social factors, anthropogenic disturbance and environmental conditions affected the sleep-vigilance trade-off in the Eurasian oystercatcher (*Haematopus ostralegus*). Data were collected on the frequency, total duration and average duration of peeking at two locations on the Menai Strait, North Wales. Our results reveal that exposure to anthropogenic disturbance, particularly the presence of people exercising dogs, led to an increase in vigilance duration and reduced time sleeping, while increasing boat traffic resulted in elevated levels of peek frequency, but the overall duration of vigilance was in fact reduced. Furthermore, oystercatchers adjust their vigilance behaviour according to social context, with reduced levels of individual vigilance when a greater number of animals were present. However, if surrounding neighbours were awake – then the observed animal was more likely to be alert, demonstrating the importance of monitoring the behaviour of conspecifics. Likewise, the temperature and wind speed influenced vigilance with elevated levels of peek frequency observed in warmer and windier conditions. Oystercatchers are able to make fine-scale adjustments to their vigilance behaviour while asleep, which reduces the risk of external threats such as predators. Nevertheless, they are making these decisions against the backdrop of a finely balanced energy budget, particularly during the winter months. Increased levels of human activity and disturbance may elevate the costs of vigilance and ultimately have fitness implications for this species.

Introduction

Vigilance enables animals to mediate risk by actively monitoring their surroundings and detecting an approaching threat (Beauchamp, 2015). However, vigilance is costly as it can interfere with other key fitness-enhancing behaviours, such as foraging (Fortin *et al*., 2004), reproduction (Rasa, 1989) and sleep (Lima *et al*., 2005). Therefore, maximizing survival and reproductive success ultimately depends on an animal's ability to balance the time engaged in the acquisition of resources against monitoring the threat posed by predators and competitors (Beauchamp, 2019). Furthermore, these assessments of risk and reward are made in dynamic environments where conditions are rarely static for long.

Among gregarious species, group size has been shown to have an important influence on vigilance behaviour, whereby increasing numbers of animals within a group results in the reduction of an individual's investment in vigilance (Beauchamp, 2008). This is due to a greater level of collective threat detection (many eyes hypothesis: Pulliam, 1973; Lima, 1995), a reduced probability that a single animal will be targeted (dilution effect: Dehn, 1990) and the greater challenge of a predator singling out a specific individual in a rapidly moving group (confusion effect: Landeau & Terborgh, 1986; Olson *et al*., 2013). However, there is also considerable variability in predation risk experienced by animals within the same group (Eshel, Sansone & Shaked, 2011), which is a function of location (i.e. greater risk at the edge of the group: Rattenborg *et al*., 1999a; Hirsch & Morrell, 2011), age, body size and dominance (Pravosudov & Grubb, 1998; Pravosudov & Grubb, 1999).

The daily decisions and trade-offs animals make are not limited to balancing resource acquisition against the risk of predation and competition, but they are also influenced by environmental conditions and human activity (Beauchamp, 2015). For example, stronger wind speeds may result in the

elevated vigilance of prey animals as it has been shown to negatively affect their ability to detect and evade predators (Cherry & Barton, 2017), while animals which rely on flight to flee predators often show lower levels of responsiveness with increasing wind speed (Carr & Lima, 2010), possibly because it is more physically demanding and riskier to take-off in strong winds. Likewise, trade-offs have been demonstrated between the physiological costs of thermoregulation and vigilance, suggesting that vigilance is more energetically costly at lower temperatures (Pravosudov & Grubb, 1995). Meanwhile, disturbance from human activity presents a growing threat to wildlife populations and even when it is unintentional (e.g. recreation) it can cause animals to increase time spent vigilant instead of searching for food or resting (Frid & Dill, 2002), which can ultimately have implications for individual fitness (West *et al.*, 2002; Arlettaz *et al.*, 2015).

The drivers of vigilance have been well-studied across a range of taxa – particularly during active behaviours, such as foraging, movement and social interaction (for review see Beauchamp, 2015). However, our understanding of the factors involved in the modulation of vigilance during inactive behaviours such as sleeping has been explored to a much lesser extent (but see Gauthier-Clerc & Tamisier, 2000; Dominguez, 2003; Beauchamp, 2009), despite the vulnerability of resting animals to external threats, such as predators, competitors and changing environmental conditions (Lendrem, 1983; Rattenborg *et al.*, 1999b). A key reason that quantifying vigilance during sleep is very challenging, is that the traditional method of measuring 'head ups' or 'scanning' is no longer applicable. Indeed, during sleep the internal physiological activities slow down and the body becomes temporarily inactive (Lima *et al.*, 2005; Siegel, 2008).

Many bird species engage in unihemispheric slow-wave sleep, which results in one of the cerebral hemispheres remaining awake during sleep (Rattenborg *et al.*, 1999a, 2016, 2019). This in turn, enables the bird to employ eye-blinking strategies using either one or both eyes to maintain a level of vigilance during sleep and therefore decrease predation risk, which is particularly important given the vulnerability associated with sleep when most animals are immobile and unaware of the environment around them (Lima *et al.*, 2005). These vigilance behaviours are defined by eye closure with short bouts of eye opening, often called 'peeks' or 'peeking' (Lendrem, 1983). During peeking the eyelid' opens to expose the pupil and allows the bird to monitor their surroundings.

Electrophysiological studies of the eye-blinking states have been conducted to understand sleep in birds (Rattenborg *et al.*, 2019). Like mammals, birds exhibit two types of sleep, rapid eye movement (REM) sleep and non-REM (NREM) sleep. During NREM sleep, one or both eyes can be closed. When only one eye is open, the opposite cerebral hemisphere is partially or fully awake. In contrast to NREM sleep, REM sleep always occurs with both eyes closed (Rattenborg et al., 2017). When the eye is open, the birds enter a transitional state of sleep between quiet sleep and wakefulness. Therefore, eye-blinking strategies can be used in situ to measure vigilance in bird populations (Lendrem, 1983; Rattenborg *et al.*, 1999a,b; Lima *et al.*, 2005; Beauchamp, 2009). Interestingly, research

on roosting gulls demonstrated that although birds in larger groups spent more time sleeping (in line with group size predictions), this was strongly dependent on the activity of their nearest neighbours. With sleep significantly reduced when neighbouring birds were awake and alert – suggesting that the monitoring of conspecifics behaviour is key to mediate risk from predation and competition (Beauchamp, 2009). Indeed, exploring vigilance during sleep enables researchers to exclude confounding factors such as foraging and competition for resources, which allows greater focus on quantifying the perception of individuals and groups of animals to external threats. Furthermore, peeking behaviour provides the opportunity to assess the time spent vigilant as a function of the duration and frequency of peeks. For example, fewer longer scans versus a greater number of short scans contribute the same overall time to vigilance behaviour, but can have very different outcomes for the detection of threats in the environment (Sirot & Pays, 2011; Beauchamp & Ruxton, 2016); however, this has rarely been explored with data from field studies (Beauchamp, 2015).

Our study focused on the Eurasian oystercatcher (*Haematopus ostralegus*), a bird of British, European and international importance. Oystercatchers provide an excellent study species for exploring the social, environmental and anthropogenic drivers of vigilance during sleep, as they exhibit pronounced peeking behaviour and roost during daylight hours in groups of varying sizes on exposed shoreline habitats. Moreover, starvation is often a leading cause of mortality during severe winter weather and preserving energy is therefore a priority (Duriez *et al.*, 2012; Schwemmer *et al.*, 2014), while a number of studies have shown that shorebirds, such as oystercatchers are vulnerable to human disturbance (Yasué, 2005; Martin *et al.*, 2015). Indeed, modelling-based research has indicated that human presence can actually increase the mortality of oystercatchers during the winter when competition for food is high and the weather conditions are particularly unfavourable (West *et al.*, 2002).

The aim of the study was to identify the relative effects of sociality, anthropogenic disturbance and environmental conditions on the trade-off between sleep and vigilance. Three hypotheses were tested. (1) Individual birds are predicted to reduce their vigilance with increasing numbers of surrounding birds, but this will be modulated by the proportion of their immediate neighbours that are awake. (2) Oystercatchers will have a greater investment in vigilance when exposed to elevated levels of anthropogenic disturbance. (3) Environmental conditions (e.g. ambient temperature and wind speed) will affect the sleep-vigilance trade-off as a result of changes in energy demands and acoustical masking – with greater levels of vigilance predicted in higher ambient temperatures and elevated wind speeds (see Ferretti *et al.*, 2019).

Methods

Study sites

Data were collected from November 2016 until March 2017 at two sites where oystercatchers roost over winter in large

numbers at high tide, both sites are located on the Menai Strait, North Wales (Fig. 1).

Beaumaris: This site is located on Anglesey at the eastern entrance of the Menai Strait (53°15'16.1"N 4°06'22.3"W, see Fig. 1). The birds will normally roost on a spit of exposed land or on nearby rocks. Observations were taken from a lay-by and focused on birds located on the rocky habitat. The oystercatchers were ~200 m from a large boat yard and ~10 m from a 2-lane road (A545) carrying cars travelling up to 40 mph. Commercial mussel trawlers and leisure craft are very active along this section of the Menai Straits. This site is a part of the Wales Coast Path; however, access is often only permissible at low tide. Red shanks and turnstones occasionally roosted with the oystercatchers.

Llanfairfechan: This site is located close to the A55 (~380 m) at the Morfa Madryn reserve (53°13'47.0"N 4°02'59.2"W, see Fig. 1). This habitat consists of intertidal sand, salt marsh and mud flats, which are all exposed at low tide. Various wildfowl and shorebirds can be found overwintering at the reserve with mixed-species flocks being common. Observations are taken from a bird hide that faces the roosting birds. The site lies on the Wales Coast Path and is a popular destination for dog walkers (off-lead walking is permitted), with permanent pathways throughout the reserve. The reserve has a double-track trainline within ~130 m and carries mainline trains travelling up to a maximum speed of 90 mph.

Data collection

The study involved 33 individual daily site visits (Beaumaris: *n* = 17 & Llanfairfechan: *n* = 16) with a mean of 9 (±SD 4) observations per visit. A total of 152 birds were observed at Beaumaris (sub-adults *n* = 80, adults *n* = 72) and 142 at Llanfairfechan (sub-adults *n* = 77, adults *n* = 65). Behavioural data from individual birds were recorded on video using an iPhone connected to a 50 x HD RSPB spotting scope for an observation period of three-minute. Birds were selected for observation using a systematic random approach, whereby the group was divided up into four equal quadrants with a maximum of five birds randomly selected from each of these quadrants during a given site visit. If the selected bird was not asleep then another was chosen. Repeated sampling of an individual during a study site visit was assumed not to occur as several hundred birds were present and sleeping simultaneously. For every focal observation, the ambient temperature (°C) was measured using a ClimeMet handheld meter (CM2030). Wind speed (km h^{-1}) was recorded from the nearest weather station from each site (Capel Curig and Mona). Ambient noise (dBA) was measured using an ATP sound level meter (ET-958) at 20-second intervals during observations to provide a mean noise level.

Each focal individual was aged as either sub-adult or adult based on a series of physical characteristics. The adults are distinguished by their black body feathers, orange to pink legs and bright red eyes, while sub-adults are duller and greyer in body coloration with grey to pink legs (Holden & Cleeves, 2014). Sexual dimorphism is not present within the species (Goss-Custard, 1996). The position of the individual within the roost was categorized as either being on the edge or in the middle of the group. The number of birds surrounding the focal individual within a 3-bird length radius was calculated to provide a level of density, rather than absolute values of group size – as this could be difficult to discern due to the number of birds and the shape of the coastline, which meant not all individuals could be readily observed. If birds arrived or left the radius of the focal individual during observations the average number of surrounding birds was taken over the three-minute observation period. The proportion of awake neighbours was calculated for each observation (immediate neighbours awake/total number of immediate neighbours). Birds were classified as asleep when they had their eyes closed and their head turned and tucked under the scapular feathers (Ball & Amlaner, 1983), while an awake immediate neighbour was defined as being in the non-sleeping posture (i.e. head un-tucked
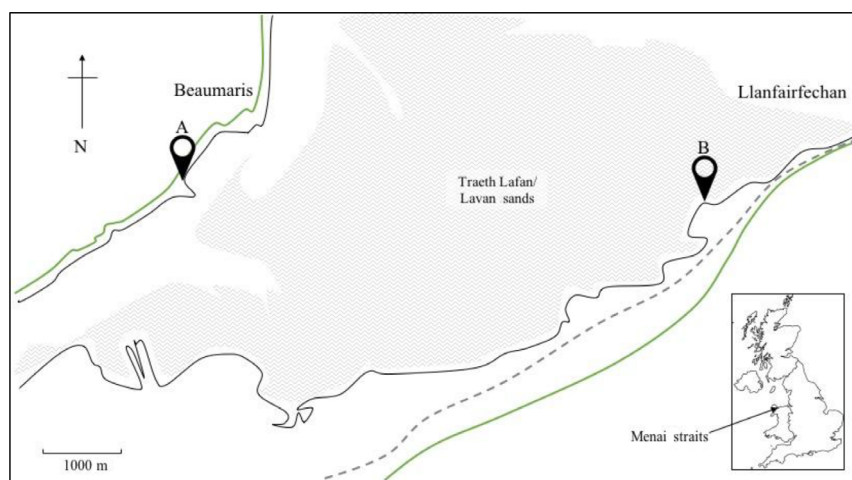

Figure 1 Map of the Menai Strait, UK showing the location of the two study locations. A is the Beaumaris study site and B is the Morfa Madryn reserve near Llanfairfechan. Lavan Sands is a protected area and is a prime location for many shore birds. Dashed line represents the train line and the green lines indicate main roads.

preening or alert) for 5 second or longer during an observation (see Video S1 clip of peeking and alert behaviour).

Disturbance from people, dog walkers and leisure craft/commercial vessels was recorded and the distance of anthropogenic disturbance to the focal bird was measured continuously using a compass and digital rangefinder (Nikon Aculon AL11), with the closest measurement being recorded in the dataset. As peeking birds generally show a preference for opening the eye facing a potential threat (Rattenborg *et al*., 1999) – it is important to consider the orientation of the animals relative to the observer and potential sources of disturbance. The line of sight from the observation point to the roost was approximately parallel to the coastline at both study sites, allowing us to reliably detect vigilance behaviour directed at both water-based and land-based disturbances (see Figs. S1 & S2). The time of focal observations and Julian day were also recorded.

The measurements of peeking (frequency, total duration and average duration) were extracted from video recordings, frame by frame, using the latest version of the behavioural software, Solomon coder Version Beta 17.03.22 (Peter, 2017). The behaviour was then transformed into rates or duration per minute to account for observations that did not reach three minutes in length (a minimum of 60 s observation was required for inclusion – with 75% of the dataset reaching the full three-minute period).

Data analysis

The three response variables (metrics of peeking behaviour) were analysed by constructing generalized linear models using the *lme4* package (Bates et al., 2005) in R (R Core Development Team 2019). The response variables included the peek frequency (1), total peek duration (2) and the average peek duration (3). Akaike's information criterion (AIC) was used for model selection (Burnham & Anderson, 2002). Poisson and Gaussian error structures were used for the peek frequency and the average peak duration, respectively. The total peak duration was analysed as a proportion of the total observation time using a success-failure binomial error structure – whereby 'successes' were measured as time spent peeking and 'failures' as total sleep duration. Collinearity was found between the disturbance categories and distance of the disturbance (with walkers and their dogs approaching more closely than leisure craft/commercial vessels or the observer); therefore, the latter was removed. Location was correlated with noise level and total sleep duration. As a result, noise level was removed from models containing the response variables peek frequency and the average peak duration, while location was then removed from models that included the total peak duration. The *leaps* function from the R package *leaps* (Lumley, 2013) was used to search for the best subsets of the variables for model selection. Variables with no or minimal effect on the models were removed prior to model selection. These were: presence/absence of crows and gulls, total daylight time, observation time from high tide and the observation time from sunrise.

Models were generated for each of the three response variables using the 10 explanatory variables associated with the three study hypotheses (outlined below). A total of 25 models

were constructed, one null model, one with only the disturbance parameter included, 18 additive models with disturbance and four without (see Appendix S1 and S2). Julian day was explored to see if the behavioural responses changed over the duration of the study, potentially as a result of habituation. The AIC values and weights where extracted using the *modavg* package (Mazerolle, 2016) for candidate models for each response variable. Model averaging was conducted across models accounting for ≥0.95 of the AICc weight to extract parameter β estimates and their 95% confidence intervals (CI). The significance of the results was assessed by whether the 95% CI overlapped zero.

Sociality

The *study site*, *position of the bird* within the roost, the *number of surrounding birds*, the *proportion of awake neighbours* and the *age* of the observed animal were used to explore the social drivers of vigilance while asleep, to compare with the well-established literature on vigilance behaviours while active (for review see Beauchamp, 2015). Vigilance was expected to be lower for individuals in the centre of the group and for those that were surrounded by increasing numbers of neighbours. However, vigilance was predicted to increase with the number of neighbours that were awake. Adult birds were expected to have lower levels of vigilance than lesser-experienced sub-adults – although younger animals needing more sleep could counter this.

Anthropogenic disturbance

Presence of *disturbance* (categorized as observer only, humans, humans & dogs, and vessels) and the level of *ambient noise* (dBA) were used to model how anthropogenic effects influenced vigilance measures. We predicted that the birds would be more vigilant and sleep less when exposed to higher noise levels and increased human activity – with people and dogs being the most threatening category of disturbance.

Environment

Ambient temperature and *wind speed* were used to model environmental effects. We predicted that vigilance would be reduced during colder weather as a result of the greater energetic costs of maintaining this behaviour. Whereas increasing wind speed was expected to result in elevated vigilance due to the challenge of flight in windy weather and the acoustical masking of approaching threats.

Results

Three models were generated for the frequency of peeking variable (Table 1). The top model accounted for 63% of the AIC weight, while the second and third contributed a further 34%, combined (Table 1). The largest effect was associated with a decline in peek frequency as the number of awake neighbours around the focal bird increased (Table 2). The second largest parameter effect was the exposure to leisure craft

or commercial vessels with the frequency of peeking increasing on average by one peek per minute (Fig. 2a). A location effect was found with Llanfairfechan having a higher frequency of peeking than Beaumaris (Table 2). An increase in ambient temperature resulted in greater frequency of peeking (Table 2), from 12 peeks/min at 5°C to 15 peeks/min at 14°C. The key parameter included in both top models was the number of awake neighbours (Table 2). There was a weak effect of increased peek frequency during stronger winds (Table 2).

Four models contributed 95% of the AIC weight for the total peek duration metric (Table 1), with the top model accounting for 41% of the AIC weight. The strongest variable effect across these models was associated with birds reducing their total duration of peeking in the presence of commercial vessels and leisure craft (Fig. 2b), while the second largest effect was the presence of people walking dogs, which resulted in greater total peek duration (Fig. 2b). Age was also a key parameter, with sub-adult birds having longer bouts of peeking than their adult counterparts (Table 2). An increase in ambient noise resulted in shorter total peek durations, while an increase in wind strength and number of birds surrounding was weakly related to a decrease of the total peek duration (Table 2).

Six models accounted for 95% of the AIC weight for the average peek duration, with the top model contributing for 31% of the AIC weight (Table 1). The largest parameter effect was the number of awake neighbours which led to an increase in the average peek duration (Table 2), while greater numbers of surrounding birds led to a decrease in the average duration of peeks from a mean of 3–1.5 s (Table 2; Fig 3). Higher wind speeds also resulted in a decrease in the average peek duration.

Discussion

Sleep is a crucial behaviour but it comes with the cost of greater vulnerability to a range of threats (e.g. predation and competition), with relatively few studies exploring the extent to which animals maintain and adjust their vigilance while asleep. We explored peeking behaviour in oystercatchers to determine how this was influenced by social context, human activity and environmental conditions.

Oystercatchers at both study sites demonstrated increased levels of peeking behaviour (vigilance) when exposed to human activity, including recreation and the presence of leisure craft or commercial vessels. However, the specific approach to monitoring threats (i.e. altering the frequency of surveillance and/or the duration) was dependent upon the source of disturbance. For example, when exposed to dog walkers, sleeping birds maintained the frequency of peeking events but increased the duration of time spent vigilant. Dogs are instinctively perceived as a source of danger by birds, more so than the presence of people (Lafferty, 2001). From observations, dog walkers generally kept to the permanent pathways when exercising their dogs, but the dogs often explored the area usually off-lead and swam in the water. Dogs are potential predators that can behave unpredictably, which may well be the reason that the birds increased the total time that they spent vigilant. Indeed, these findings concur with previous research, which demonstrates increase of vigilance, flee responses and changes in habitat use in a range of bird species when dogs are present (Lafferty, 2001; Banks & Bryant, 2007; Burger *et al*., 2007; Williams *et al*., 2009; Weston *et al*., 2012; Doherty *et al*., 2017).

Interestingly, the presence of leisure craft and commercial vessels elicited a different response from sleeping oystercatchers, which involved reducing the total duration of vigilance but increasing the peek frequency. Boats are likely to follow more predictable patterns and do not approach the birds directly, enabling the birds to spend less time being vigilant overall, while maintaining a higher rate of surveillance to monitor this source of disturbance. Research on mallards demonstrated that frequent scans of short duration are significantly more efficient

Table 1 Top models accounting for ≥0.95 of the AIC weight for peek frequency, total peek duration and average peek duration

	K	ΔAIC	AIC weight
Peek frequency			
Disturb + AwakeN + Age + Loc + Birds + Day + Temp + Wind + Time	12	0.00	0.63
Disturb + Temp + AwakeN + Age + Loc + Birds + Day + Pos + Wind + Time	13	1.61	0.28
Disturb + AwakeN + Birds + Wind	7	4.71	0.06
Total peek duration			
Disturb + Noise + Age + Birds + Day + Temp + Wind + Time	11	0.00	0.41
Disturb + Age + Noise + Birds + Day + Pos + Wind + Time	11	0.35	0.34
Disturb + AwakeN + Age + Noise + Birds + Day + Pos + Wind + Time	12	2.17	0.14
Disturb + AwakeN + Age + Noise + Birds + Day + Pos + Wind + Time + Temp	13	2.63	0.11
Average peek duration			
Disturb + AwakeN + Birds + Wind	8	0.00	0.31
Disturb + Temp + AwakeN + Age + Loc + Birds + Day + Pos + Wind + Time	14	0.57	0.23
Disturb + AwakeN + Age + Loc + Birds + Day + Temp + Wind + Time	13	1.13	0.18
Disturb + AwakeN + Age + Loc + Birds + Day + Pos + Wind + Time	13	2.08	0.11
Disturb + Birds + Day + Temp + Wind + Time	10	2.66	0.08
Disturb + Loc + Birds + Day + Temp + Wind + Time	11	4.66	0.03

K, number of parameters.

Table 2 The observed (β estimate ± 95% CI) relationship between the response variables and the model-averaged parameters from the top models

Behaviour	Parameter	β Estimate	95% CI
Peek frequency	Awake neighbours	**−0.30**	−0.47, −0.13
	Disturbance (vessels)	**0.13**	0.00, 0.26
	Location: Beaumaris	**−0.10**	−0.18, −0.01
	Temperature	**0.03**	0.01, 0.05
	Wind speed	**0.01**	0.00, 0.01
	Disturbance (people)	0.09	−0.08, 0.25
	Disturbance (people & dogs)	−0.07	−0.02, 0.07
	Position: Middle	−0.03	−0.11, 0.06
	Age Group: Adult	−0.02	−0.09, 0.05
	Surrounding birds	0.00	−0.00, 0.00
	Julian day	0.00	0.00, 0.00
	Time	0.00	0.00, 0.00
Total peek duration	Disturbance (vessels)	**−0.43**	−0.55, −0.31
	Disturbance (people & dogs)	**0.17**	0.06, 0.29
	Age Group: Adult	**−0.12**	−0.19, −0.06
	Ambient noise	**−0.02**	−0.02, −0.01
	Surrounding birds	**−0.02**	−0.03, −0.02
	Wind speed	**−0.01**	−0.02, −0.01
	Disturbance (people)	0.09	−0.05, 0.24
	Position: Middle	0.04	−0.03, 0.11
	Awake neighbours	−0.03	−0.17, 0.11
	Temperature	−0.01	−0.03, 0.01
	Julian Day	0.00	0.00, 0.00
	Time	0.00	0.00, 0.00
Average peek duration	Awake neighbours	**1.45**	0.19, 2.71
	Surrounding birds	**−0.05**	−0.08, −0.02
	Wind speed	**−0.05**	−0.08. −0.02
	Disturbance (vessels)	−0.77	−1.78, 0.24
	Position: Middle	0.47	−0.15, 1.09
	Age Group: Adult	−0.29	−0.82, 0.25
	Disturbance (people)	−0.24	−1.51, 1.03
	Location: Beaumaris	−0.19	−0.84, 0.47
	Disturbance (people & dogs)	−0.14	−1.15, 0.88
	Temperature	−0.12	−0.27, 0.02
	Julian day	0.00	−0.01, 0.00
	Time	0.00	0.00, 0.01

Bold text denotes β-estimates with 95% CI that do not overlap zero.

in terms of foraging efficiency compared with longer and less frequent scans (Fritz, Guillemain & Durant, 2002), while a recent theoretical study demonstrated that more frequent scans were associated with predators that could be detected from afar (Beauchamp & Ruxton, 2016). It is possible that this relationship could extend to sources of human disturbance, which can be detected at considerable distance (e.g. boat traffic). However, the trade-offs between the duration and frequency of vigilance in sleeping animals have rarely been investigated – a topic that would greatly benefit from future research effort.

The proportion of awake neighbours surrounding the observed animal was a key variable within the top models for peek frequency and average peek duration. The results suggest that individuals reduce the frequency of peeking if they have a higher proportion of awake neighbours, but substantially increase the average duration of peeking under these

conditions. Our findings support those of a study which focused on sleeping gulls, *Larus* sp. and their ability to copy the vigilant state of their neighbours (Beauchamp, 2009). The focal gulls were found to be more vigilant and slept less when neighbouring birds were awake and alert, indicating that vigilance monitoring was a key behaviour in this social species (Beauchamp, 2009). Similarly, oystercatchers form large social groups when foraging and sleeping, which enables them to share the task of predator detection, but also increases the intensity of competition, particularly during foraging (Goss-Custard, Cayford & Lea, 1999). These trade-offs may well be key in driving the greater levels of surveillance demonstrated by the focal animal when surrounded by awake neighbours. Whereas, being surrounded by a greater number of sleeping birds enabled them to reduce the average duration of peeking and depend on the vigilance of others, which conserves energy
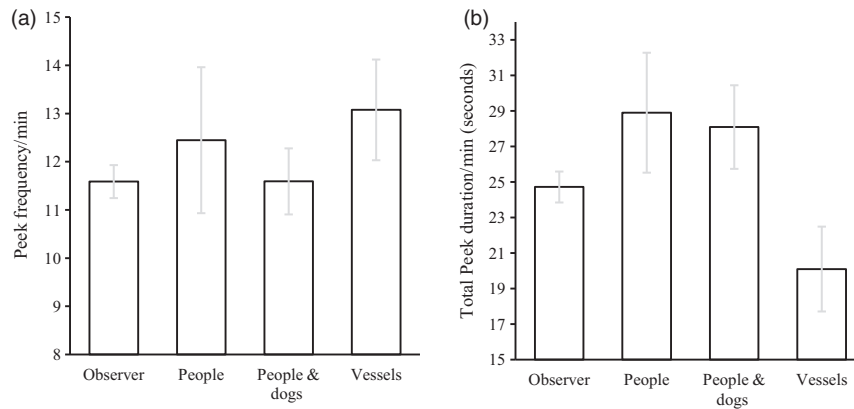
Figure 2 (a) The frequency of peeks per minute (mean ± SE) for the four disturbance categories and (b) the total peek duration per minute in seconds (mean ± SE) for the same disturbance categories.
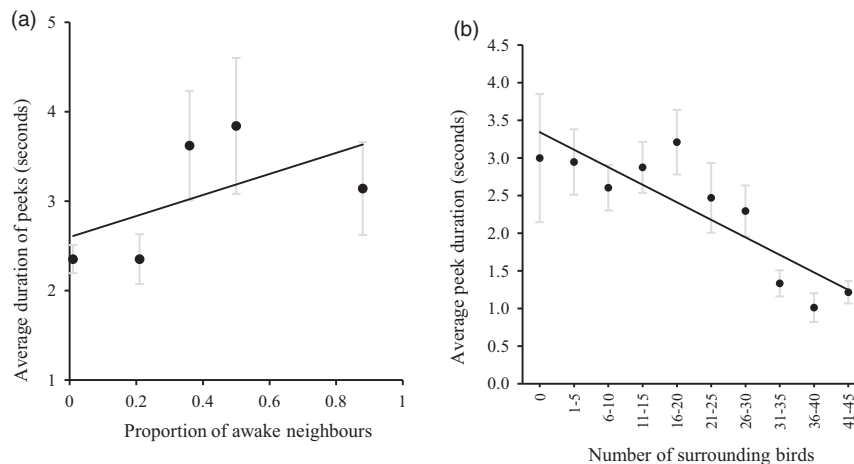

Figure 3 (a) The average peak duration in seconds (mean ± SE) as a function of the proportion of awake neighbours and (b) the average peek duration in seconds (mean ± SE) as a function of the number of surrounding birds.

and eventually maximizes their fitness (Beauchamp, 2003). Often studies fail to find a relationship between group size and vigilance as they rely on absolute flock sizes rather than the density of birds within a set radius, which is the method we used (see also Pöysä, 1994; Fernández-Juricic, Beauchamp & Bastain, 2007; Fernández-Juricic & Kowalski, 2011).

The results from our study also indicate that vigilance behaviour changes as a function of age with sub-adult birds being vigilant longer than their adult counterparts. Commonly, the opposite effect is documented, with a recent review of the literature by Beauchamp (2015) finding that more than two thirds of vigilance studies that considered age ($n = 51/75$) found that younger animals were less vigilant than adults, despite their often-greater risk of mortality. The two key mechanisms driving this pattern include the fact that juveniles tend to lack experience and have higher energy demands, which often causes them to rely on the vigilance of others (Griesser, 2003; Avilés & Bednekoff, 2007; Li *et al.*, 2012). Our results could be related to social rather than anti-predatory vigilance, as

oystercatchers are highly competitive and juvenile birds are more likely to be subordinate individuals and lose out on prime sleeping spots in the middle of the group (Marra, 2000). The yearly mortality of oystercatchers is dominated by sub-adults under the age of one because younger individuals are inexperienced, often out-competed for resources such as food and are unable to balance key trade-offs such as conserving energy and being vigilant (Davidson & Evans, 1982; Duriez *et al.*, 2012; Schwemmer *et al.*, 2014). Furthermore, the analysis of age discussed above focussed specifically on vigilance during foraging with insufficient evidence available to explore whether this holds for sleeping animals.

Environmental conditions were also found to mediate the peeking responses of oystercatchers with stronger winds resulting in shorter average peek durations and increased peek frequency. Individuals compete for better positions to avoid exposure to higher winds causing increased interactions with others and thus higher social vigilance (Carr & Lima, 2010). Birds also could be adjusting their vigilance as their

manoeuvrability for fleeing predators in strong winds will be compromised (Quinn & Cresswell, 2004). Little is known about which sense oystercatchers utilize the most during predator detection, however, they are known for their very noisy 'peeping' calls. Therefore, it can be expected that stronger winds will reduce the effectiveness of auditory signals, as demonstrated in the American pika (*Ochotona princeps*) (Hayes & Huntly, 2005). It is possible that visual surveillance is increasing in frequency with stronger winds because auditory signalling is compromised, as shown in other species exposed to noisy environments (Rabin, Coss & Owings, 2006; Shannon *et al.*, 2014). During observations, mixed-species flocks were common at Llanfairfechan with red shanks, dunlin and knots being recorded frequently. Species which are more at risk of predation (i.e. species with smaller body mass) join other species to form mixed-species flocks (Sridhar, Beauchamp & Shanker, 2009). It is possible the oystercatchers are influenced by other species which are more responsive to potential threats. For example, red shanks are known to react to changes in the environmental conditions through increasing their false-alarm flights as attacks from aerial predators increase with stronger winds (Hilton, Ruxton & Cresswell, 1999). This could indirectly cause the oystercatchers to increase time spent monitoring the surroundings when they are in mixed-species flocks, but to the best of our knowledge, this is not an aspect of vigilance behaviour that has been formally studied.

Peek frequency increased with higher temperatures, which provides support for the thermoregulation hypothesis, where vigilance decreases with lower temperatures because of the higher thermoregulatory demands (Pravosudov & Grubb, 1995; Beauchamp, 2015; Ferretti *et al.*, 2019). This relationship is often not found when focusing on individuals that are foraging, as these birds can increase their energy intake by foraging for longer if resources are not limited (Boysen, Lima & Bakken, 2001). However, balancing thermoregulation is critical during the winter when food is less plentiful and temperatures often reach below freezing overnight. Oystercatchers are strongly affected by environmental changes and mortality increases sharply during harsh winters when birds have depleted lipid and protein reserves (Davidson & Evans, 1982; Duriez *et al.*, 2012; Schwemmer *et al.*, 2014). Maximizing food intake and conserving energy when there are no pressing activities is vital for winter survival of oystercatchers. Anthropogenic disturbance during cold winters could cause higher bird mortality as individuals fail to balance the demands of vigilance and thermoregulation.

Conclusion

Our study has highlighted that sleeping oystercatchers adjust their vigilance behaviour as a function of anthropogenic disturbance, but the specific approach (i.e. altering the rate of vigilance and/or the duration) is dependent upon the source of disturbance. Dogs present one of the most significant and unpredictable predatory threats associated with human activity, which resulted in significantly increased surveillance duration when they were present, whereas boat traffic was monitored with greater overall frequency of vigilance, but reduced overall duration. These findings highlight the different strategies that animals use to modulate and optimize their vigilance behaviour to different sources of potential threat, while also adding to the body of evidence demonstrating that the pattern of vigilance is as important as the amount of time invested (Sirot & Pays, 2011; Beauchamp & Ruxton, 2016). Social factors were also very important in shaping vigilance behaviour, with sleeping individuals reducing their vigilance when surrounded by a greater number of birds. However, this was mediated by the behaviour of these individuals – with elevated levels of vigilance exhibited among focal animals that had a greater number of awake neighbours surrounding them, demonstrating the importance of monitoring the vigilance behaviour of conspecifics. Oystercatchers demonstrate the ability to make fine-scale alterations to their vigilance while asleep, which enables them to very effectively detect potential threats such as predators, while maintaining a finely balanced energy budget. Increased human disturbance combined with ever-changing social and environmental conditions has the potential to greatly elevate the costs of vigilance and reduce sleep – particularly for younger less experienced individuals – which may ultimately have fitness costs for this species.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Map of the Beaumaris study site.
Figure S2. Map of the Llanfairfechan study site.
Appendix S1. The variable structure of the candidate models, which were used for the total peek duration. The baseline values for categorical variables were sub-adults for age, and edge for position.
Appendix S2. The variable structure of the candidate models, which were used for the frequency of peeks and average peek duration. The baseline values for categorical variables were Llanfairfechan for location, sub-adults for age, and edge for position.
Video S1. Peeking and alert behaviour of roosting oystercatchers at the Beaumaris study site.