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Communication

Avian Escape and Prevailing Light Levels

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Simple Summary

Birds must avoid predators and other threats by day and night, especially those living in urban areas. We measured the distance at which gulls moved away from an approaching person and measured light levels by day and night in Melbourne, Australia. We found a step-like change in escape distance, with longer distances in dull and darker conditions. This suggests that gulls can detect approaching people at least as well by night as by day but appear less tolerant of people when darker conditions occur.

Abstract

Anti-predator behaviour in birds is required by day and night but has barely been studied at night. For prey which detect predators visually, low light levels may diminish detection or monitoring of approaching threats. We conducted standardised approaches to Silver Gulls (*Chroicocephalus novaehollandiae*) by day and night along an urban foreshore in Melbourne, Australia, measuring light levels (Lux) experienced by the gull, Flight-initiation Distance (FID; the distance at which escape is initiated), and Starting Distance (the initial distance between the observer and the bird). We fitted models reflecting different conceptual possibilities for the relationship between Lux and FID. Support existed for a model with a stepwise effect of light on FID. Longer FIDs (i.e., earlier escape) in darker conditions suggest that gulls can detect an approaching threat in darkness at least as well as by day, but the tolerance of closer approaches may be diminished in dull and dark conditions, perhaps due to difficulty in monitoring an approaching threat and/or because nighttime represents a time of greater predator risk. Starting Distance was positively related to FID, a result commonly reported for many taxa by day.

Keywords: ALAN; gull; nighttime ecology; seabird

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1. Introduction

Urbanisation can impact wildlife behaviour, including those that are critical to their survival, such as predator escape behaviour [1]. The capacity of a species to adapt these behaviours is likely linked to its capacity to inhabit urban areas [2]. While several studies exist on these behavioural changes [3,4], nighttime behavioural ecology, especially that focused on predator escape behaviour, is sorely neglected even though escape behaviour for many taxa differs between day and night [5]. During the night, one of the significant changes wildlife experience with increasing urbanisation is an increased level of Artificial Light at Night (ALAN). Given vision is a common sensory cue used by prey species, sensory

efficiency and/or modalities used by prey to detect approaching predators may differ with prevailing light levels. Illumination at night varies greatly with location, moon phase, levels of ALAN, and cloud cover, among other factors [6]. However, explicit investigations of escape behaviour across measures of environmental illumination appear rare [1]. Here, we study a system featuring a single, functionally cathemeral and commensal species, which occupies the same open and accessible urban habitats by day and night, exhibits varying but relatively short response distances to humans in urban areas, and therefore enables comparison of escape behaviour across a wide range of light levels.

Silver Gulls, *Chroicocephalus novaehollandiae*, are a common, often commensal species in bayside Melbourne, Australia, where they roost and forage by day and night near or on human infrastructure and in parks [7]. Different bird species, with different ecologies and predator pressures, exhibit a variety of visual capabilities, including differing abilities to deal with low-light environments [8,9]. Like most gulls, it is assumed predator detection in the Silver Gull is mostly visual, at least by day [10,11], and therefore may be influenced by prevailing levels of illumination, as has been shown for other birds [12]. Specifically, low illumination might conceivably impair visual detectability of approaching threats in Silver Gulls (specific information on this is currently unavailable for Silver Gulls).

Here, we measure escape distances by measuring Flight-Initiation Distance (FID), the distance at which an animal flees from an approaching threat (in this case, a human) [13]. Starting Distance (Start_D; the initial distance between the focal bird and the observer [13]) is arguably the most common and important covariate for FID, so we measure that also. We propose several hypotheses regarding associations between light levels and FID in gulls (Figure 1) based on the following plausible mechanisms. Firstly, if the gulls primarily depend on their visual senses for predator detection, detection may be compromised and delayed in low light levels [8], resulting in shorter FIDs. Visual detectability of an approaching threat influences FID; for example, visual obstructions are associated with shorter FIDs in birds [14]. Alternatively or additionally, depending partly on the anatomy of the eye [11], very bright light shining directly into their eyes, such as the setting sun or the presence of a direct source of ALAN, might conceivably result in squinting or closure of eyes (*sensu* [15]), also delaying the detection of approaching threats and shortening of FIDs [12]. Conversely, detection of an approaching threat may not be diminished with lower light levels, but capacity to judge and monitor distance, or otherwise assess risk associated with an approaching threat, may be diminished in darker and/or very bright conditions, resulting in earlier escape (longer FIDs) (see [16]). These changes may be gradual, or show a step change indicating a threshold in the gull's visual capacity or risk assessment.

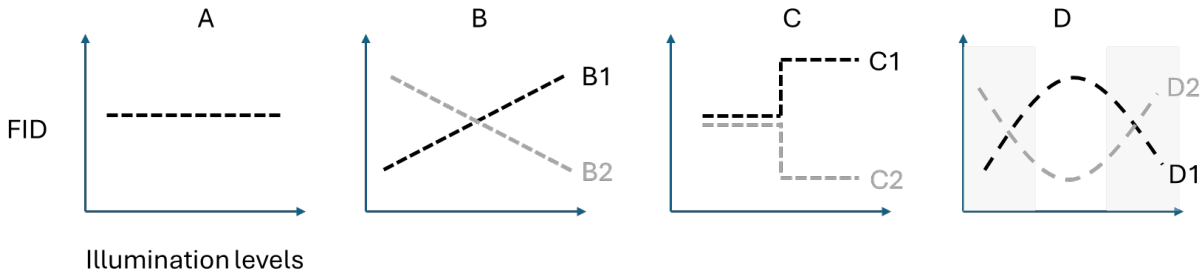


Figure 1. Conceptual models of possible relationships between illumination levels (Lux) and Flight-initiation Distance in Silver Gulls under two hypotheses: (1) that low light mediates the distance at which a threat can be detected, so FIDs are shorter when darker (black lines), or (2) the tolerance of an approaching threat is lower (i.e., longer FIDs) in darkness (grey lines). Possible responses involve (**A**) no association, perhaps due to non-visual sensory modalities being used, e.g., auditory cues; (**B**) a linear association between light and FID; (**C**) a step change associated with altered escape risk perception or sensory modalities with light; or (**D**) a parabolic association associated with limited visual detection or

tolerance/monitoring capacity when especially dark or especially bright (grey boxes). Note that if both processes occur simultaneously, then for (**B**–**D**) they could conceivably cancel one another out and result in (**A**).

2. Materials and Methods

Data were collected from Silver Gulls found along the Newport, Williamstown and Altona foreshores, Melbourne, Victoria, Australia (−37.8595° N, 144.9063° E). All study locations experienced heavy human usage, in general, and consisted of a walker/cycle trail approximately 10 m from the seawall, a roadway about 30–40 m inland of the seawall with street lighting and adjacent housing, mown grass with concrete paths, and abundant Silver Gulls on the ground by day and night.

We collected FID data using standard methods [5,13]. Briefly, once an undisturbed, unshaded, solitary gull was identified, a researcher (MAW in dull clothes) directly approached the bird at a slow walking pace. The approach ceased when the bird showed any escape behaviour (e.g., walking, flying). The distance between the researcher and the bird's original position (FID) was then estimated by pacing, with Starting Distance (Start_D) also estimated by pacing from the birds' initial location back to the position where the researcher initiated the approach. Pacing was used in preference to a laser rangefinder due to the short distances involved (i.e., often less than 10 m); previous studies found that the distance measured by pacing is comparable with other methods [17,18], and pacing has been used widely to estimate FIDs, e.g., [5,13,19]. All birds were on cut grass or adjacent concrete paths by day, dusk and night, and visible with the naked eye even on the darkest nights thanks to the strong contrast of white plumage against dark green grass or concrete and distant street lighting. No breeding occurred in the study area, so birds were non-breeding or off-duty breeders.

While we sampled multiple gulls at each location across several years (27 days across all seasons and in all months except for January; 1–17 samples per day; no more than one per 45 min; August 2019–March 2022). Most samples were collected around dusk, because illumination levels vary greatly then, but sampling spanned 10.5 h before dusk to 2 h after dusk. The likelihood of resampling the same individual was considered very low thanks to the abundant and mobile nature of the Silver Gull, and only a few approaches being made on any one day. A handful of approaches involved groups of gulls (not reflected in the above totals), and these were removed from the dataset as they were too few to include in analysis, and because group size can affect FID in birds [20]. Timing of sampling relative to light levels was haphazard and effectively random; opportunistic and unpredictable scheduling of field sessions occurred by day and night at all times of year.

Illumination was measured in Lux by moving to a bird's initial pre-escape position immediately following an approach, orienting the cosine collector of a light meter (Digitech QM1584, Cor_Tek, Busan, South Korea) slightly towards the direction of the observer's approach, and storing the value before any illumination was used. This was performed with the sensor at the height of a gull and indexed the ambient illumination available to the focal gull. All approached gulls were roosting, foraging or drinking (i.e., "starting behaviour", behaviours apparent at the commencement of an approach), and ambient light levels (Lux) did not differ between the three aforementioned starting behaviour categories (Kruskal-Wallace, $\chi^2_6 = 9.578$, $p = 0.1436$). Therefore, there was no confounding between ambient light levels and starting behaviour.

FID was square-root transformed, while Start_D and Lux were $\log_e$ transformed and centred (i.e., scaled so the mean was zero). Initially, general linear mixed models (using the LME4 package in R [21]) modelled square-rooted FID against log Start_D and log Lux with four sections of comparable foreshore (each 100–200 m long and 50–100 m wide)

defined and incorporated as a random effect. However, singularity in models persisted even in more simplified random effects structures, so the random effect was dropped and linear models with only fixed effects were run (i.e., there was no location term). We fitted (1) a linear model (which tested all possibilities in Figure 1A,B), (2) a 'step model' with a threshold at a natural log Lux (centred) value (to assess the scenario in Figure 1C; see below for how the threshold was determined), and (3) two quadratic functions to assess the scenario in Figure 1D. The unconstrained quadratic featured a positive squared term (Figure 1, scenario D1), so we ran another quadratic model with a negative term (Figure 1D, scenario D2). Initially, we optimised the step model by running a set of models with 0.1 increments in the threshold value and selecting the model with the highest R^2 value (the optimal threshold was –0.2 log Lux centred, or *c.* 1650 Lux). We then compared all models using Akaike's Information Criteria adjusted for small sample sizes (AICc). Any model with ΔAICc > 2 was not considered further. All assumptions were checked using the DHARMa package in R [22].

3. Results

Ninety-nine approaches occurred (means ± SEs: Start_D, 12.7 ± 0.8 m; FID, 7.1 ± 0.4 m) across a large range of light conditions (11.7–92,400 Lux; median, 1652). All models featured a strong positive effect of Start_D (Table 1). Model selection identified one clearly best model which featured a step function (Table 1), such that longer FIDs occurred at light levels lower than the recorded threshold light levels, with the threshold occurring under conditions equivalent to an overcast, dull day (Figure 2).

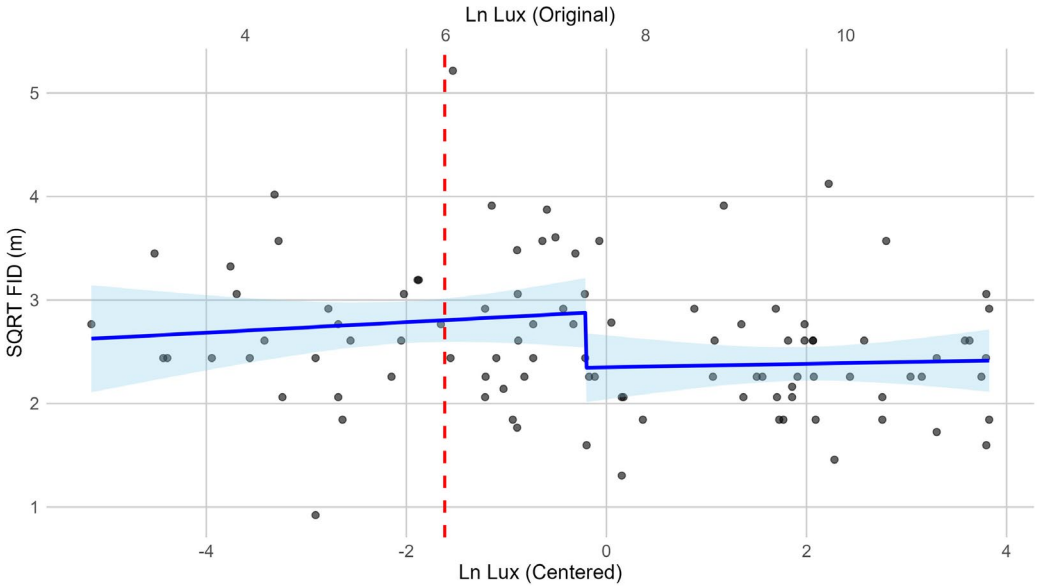


Figure 2. The relationship between Flight-initiation Distance and illumination (Log_e Lux) on centred (bottom axis) and original (top) scales (light blue shading = 95% CIs). For context only, the red dashed line indicates 400 Lux, i.e., the approximate illumination prevailing at dawn or dusk.

Table 1. Models and model selection showing coefficient estimates and standard errors (and *p*-values) AICc, ΔAICc and R^2. The top model is the clearly best model.

Model	Intercept	Log_e(Lux)	Log_e(Start_D)	$Log_e(Lux)^2$	AICc	ΔAICc	R^2 (Adj.)
Step	2.7235 ± 0.0547 $p < 0.0001$	−0.3941 ± 0.0788 $p < 0.0001$	0.8638 ± 0.0889 $p < 0.0001$	NA	135.1364	0.0000	0.5259
Linear	2.5826 ± 0.0486 $p < 0.0001$	−0.0860 ± 0.0209 $p = 0.0001$	0.8653 ± 0.0922 $p < 0.0001$	NA	141.9304	6.7940	0.4923

Table 1. *Cont.*

Model	Intercept	Log_e(Lux)	Log_e(Start_D)	$Log_e(Lux)^2$	AICc	ΔAICc	R^2 (Adj.)
Quadratic Forced (Inverted "U"; Concave Down)	2.6052 ± 0.0682 $p < 0.0001$	−0.0873 ± 0.0211 $p = 0.0001$	0.8641 ± 0.0926 $p < 0.0001$	−0.0041 ± 0.0087 $p = 0.6366$	143.6965	8.5601	0.4881
Unconstrained Quadratic ("U"; Concave Up)	2.6052 ± 0.0682 $p < 0.0001$	−0.0873 ± 0.0211 $p = 0.0001$	0.8641 ± 0.0926 $p < 0.0001$	0.0041 ± 0.0087 $p = 0.6366$	143.6965	8.5601	0.4881

4. Discussion

Our results support an effect of prevailing light on FID of the Silver Gull, specifically scenario C2 (Figure 1), with a small threshold/step in FIDs such that they were slightly longer in dull and dark conditions (≤1650 Lux, the threshold we describe, and an illumination which might be found on an overcast dull day). Rendall et al. [5] also reported that nighttime FIDs of Silver Gulls were longer than those by day (although they did not measure light levels, used a binary day/night variable, and excluded twilight samples). These results suggest two main outcomes. Firstly, the approaching threat was detected at distances exceeding FIDs exhibited in lighter conditions. For at least some bird eyes, the capacity to adapt to low light is substantial, but limits exist [8,23]. Such constraints might conceivably explain the step-like nature of the function we fitted, although this is unlikely because (1) the step occurred in relatively bright illuminations and (2) the longer FIDs exhibited in darker conditions suggest the capacity to detect approaching humans persisted even in the darkest conditions we sampled. Secondly, FIDs were longer in the darkest conditions, suggesting greater perceived risk or diminished capacity to judge risk [13] in darker conditions. Dullness and darkness might act as environmental cues signalling greater probability of encounters with crepuscular or nocturnal predators *sensu* [24], thereby evoking longer FIDs. The modality of anti-predator behaviour in birds can differ between day and night [25], and nocturnal escape involving flying may be especially risky [26], so the costs of escape may also differ between day and night and influence FID [27].

Some gulls use auditory cues to assess predator risk, at least by day [28], and it is conceivable that different sensory modalities are used to detect predators at different illuminations [5]. We did not index the acoustic cues associated with our approaches to gulls, but these would likely have been equivalent by day and night (same observer, substrates, etc.), as would have been the prevailing acoustic environment (e.g., traffic noise). Future studies would ideally simultaneously measure acoustic and visual cues associated with approaching threats to birds at night.

Starting Distance is almost always positively and significantly associated with Flight-Initiation Distance across a wide variety of avian and non-avian vertebrate taxa [5,13]. This effect may be functional (e.g., focal animals may judge risk based on persistence of approach), or artefactual (e.g., longer approaches may risk misinterpreting random movements of the focal animal as escape) [29]. Recently, the positive association between Starting and Flight Initiation Distance has been documented for birds and mammals by night as well as by day [5], and here we show the effect exists for Silver Gulls across a wide variety of ambient illumination levels, including darkness (i.e., it featured in all fitted models). Examining the relationship between Starting and Flight Initiation Distance in extremely dark conditions (for taxa which detect predators visually) may offer insights as to the functional significance, if any, between Starting and Flight Initiation Distances. If an approaching stimulus is undetectable, then any positive relationship between Starting and Flight Initiation Distance would evidently be artefactual.

Urban gulls evidently exhibit suitable escape behaviour from humans by night as well as by day, potentially facilitating their use of urban coastlines by night and day. We did not

experience especially dark conditions, which is typical of urban areas under skyglow. Dark conditions (through removal of sources of ALAN) in urban areas may alter escape distances and even influence gull usage of urban areas by night. Exploring their escape behaviour in darker conditions than we sampled by using thermal technologies [5] would further the understanding of their escape ecology. We suggest urban gulls offer an especially useful study system to explore antipredator behaviour and impacts of prevailing light in urban environments.

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Data Availability Statement: We will provide this data upon reasonable request.

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Abbreviations

The following abbreviations are used in this manuscript:

FID	Flight Initiation Distance
Start_D	Starting Distance

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