Differential reactions to anthropogenic disturbance by two ground-nesting shorebirds [§]

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Many ground-nesting shorebirds experience a high level of anthropogenic disturbance, often to the detriment of their breeding success. This study investigated the responses of the Near-Threatened African Black Oystercatcher *Haematopus moquini* (ABO) and the Least Concern Kelp Gull *Larus dominicanus vetula* (KG) to anthropogenic disturbance during the pre-breeding and breeding season at three locations differing in levels of anthropogenic disturbance and colony size. Birds were directly approached from over 100 m away and markers were dropped at each behavioural reaction to the approach. Measuring back allowed a quantitative measure of the effects of disturbance. Stand response distances in breeding ABO were location sensitive, which related to disturbance level, showing that they stood up earlier in a highly disturbed location. Neither ambient conditions (wind speed and ambient temperature) nor nesting condition (egg age and clutch size) played a significant role in responses. Interestingly, breeding KG behaviour was affected by location, to a lesser extent by clutch size, but not by ambient conditions. Both ABO and KG significantly altered their behavioural responses to disturbance from pre-breeding to breeding. These results emphasise the need to have a buffer zone surrounding breeding areas excluding human presence to allow for the successful breeding of ABO.

Keywords: African Black Oystercatcher, buffer zone, Kelp Gull, manipulated disturbance, urbanisation

Introduction

A coastal ecosystem (beaches, dunes, wetlands, salt marshes and sea grasses) offers an important habitat for animals and plants (Abel et al. 2011). Currently, roughly three billion people live close to the coast globally and this number is expected to double by 2025 (Coverdale et al. 2013). In South Africa, coastal tourism is a major growing industry supported by increased coastal developments (Leseberg et al. 2000). Increasing tourism and expanding development puts pressure on the animals that live in this area (Abel et al. 2011).

We define anthropogenic disturbance as the behavioural and/or physiological response of an animal to human-based stimuli, such as the presence of people, dogs, and vehicles (Glover et al. 2011), and regard this as a primary biodiversity conservation concern (Gill 2007). Shorebirds are particularly vulnerable to anthropogenic disturbance, especially during periods leading up to and including the breeding season (Stillman and Goss-Custard 2002; Virzi 2010). Many shorebirds nest on the ground (Adams et al. 1999), and in South Africa their breeding season is throughout September to April, peaking between November and January (Hockey 2005). Breeding success can be negatively affected by natural events such as storms, windblown sand, and predation by birds and mammals, but also by high levels of anthropogenic disturbance (Leseberg et al. 2000; Calf and Underhill 2002). The peak breeding season coincides with the greatest influx of summer holidaymakers when stress placed on coastal ecosystems is highest (Leseberg et al. 2000).

Many aspects of the reproductive cycle can be negatively affected by anthropogenic disturbance, resulting in reduced breeding success, including selection of suboptimal, yet undisturbed, nest sites (Erwin 1980; Virzi 2010), desertion of breeding territories (Burger 1981; Hockey 2010), interruption of incubation bouts and decreased nest attendance (Burger 1981; Baudains and Lloyd 2007), increased predation, both natural (e.g. gull) and anthropogenic (e.g. canine) (Tjørve and Underhill 2008; Hockey 2010), increased thermal stress on both eggs and chicks (Hunt 1972; Leseberg et al. 2000), and disruption of foraging of both adults and fledglings (Verhulst et al. 2001; Thomas et al. 2003). Various seabird species react differentially to disturbance resulting in the aforementioned effects (Ikuta and Blumstein 2003).

The distance at which a human approaches before the bird moves away from the nest is termed the flight initiation distance (FID) (Ikuta and Blumstein 2003). There are

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[§] This paper is part of a special memorial issue commemorating the work of the late Philip Hockey

many factors that can influence FID: repeated exposure to humans decreases FID (Ikuta and Blumstein 2003), the presence of dogs greatly increases FID (Lord et al. 2001; Miller et al. 2001), and ambient temperature and clutch age can alter FID (Brown and Brown 2004). Furthermore, the time taken for a bird to return to incubating its clutch after the disturbance has passed has been shown to be dependent on time of day, modelled egg temperature, and clutch age (Yasué and Dearden 2006).

Anthropogenic disturbance has been and continues to be one of the main threats to African Black Oystercatcher *Haematopus moquini* populations (Jeffrey and Scott 2005). Currently, populations seem to be increasing after off-road vehicles were banned from use on the South African mainland coastline (as prescribed by the National Environmental Management Act [No. 107 of 1998]) (Hockey 2010), and following the spread of the invasive Mediterranean mussel *Mytilus galloprovincialis* (Hockey 2005). Conversely, Kelp Gulls *Larus dominicanus* are better adapted to people and to urbanisation (Washburn et al. 2013). Anthropogenic food sources, such as waste management facilities, discards from fish and cities waste (Washburn et al. 2013), have aided the range expansion and population increase of this species worldwide (Frixione et al. 2012), including the southern African race *L. d. vetula* (Crawford et al. 2009).

The breeding season of these two species peaks during December and January, coinciding with the period of highest number of holidaymakers in coastal areas. This results in increased levels of human disturbance and, although rarely practical, the development of buffer zones to exclude human access from breeding colonies may be beneficial. The aim of this study was to determine, and contrast, the responses to anthropogenic disturbance during the pre-breeding and breeding season of two ground-nesting shorebird species, the Near-Threatened African Black Oystercatcher (ABO; BirdLife International 2012a) and the urbanised, Least Concern Kelp Gull (KG; BirdLife International 2012b), through manipulated and unmanipulated disturbance trials.

Materials and methods

Study sites

Three breeding colonies in Plettenberg Bay were chosen as study sites (Figure 1). Keurbooms Peninsula (34°02.4′ S, 23°23.1′ E) is a formally protected bird breeding colony (Keurbooms River Seagull Breeding Colony), part of the Keurbooms River Nature Reserve Complex, a 39 ha provincial nature reserve administered by CapeNature. This area disallows people and their pets access into the colony but the area is neither fenced nor often policed. It supports the second-largest breeding colony of ABO in Plettenberg Bay, and the largest mainland breeding colony of KG in South Africa (1 373 pairs; Whittington et al. in press). This site can be classified as a medium disturbance site. Lookout Beach (34°02.7′ S, 23°22.8′ E) is not a formally protected area and allows dogs restrained on leashes, but this regulation is rarely observed. Lookout Beach supports the largest breeding colony of ABO in Plettenberg Bay, the second-largest breeding colony of KG in Plettenberg Bay (50 pairs; Whittington et al. in press) and is classified as

a high disturbance site. Robberg Nature Reserve (RNR) supports the smallest breeding colony of KG (39 pairs; Whittington et al. in press) and ABO in Plettenberg Bay. The main breeding area is on Robberg Island (34°06.5′ S, 23°23.2′ E), which is connected to the mainland of RNR by a sandy beach. Dogs are not allowed into RNR and visitors are restricted to trails through the reserve and a boardwalk through sections of the breeding colony on Robberg Island, with this site being classified as a low disturbance site.

Data collection

All ABO nests at all three sites were monitored throughout the breeding season. A small selection of KG nests at each site were monitored. Nests were typically found during the scrape or early laying phase, and marked with wire rods and numbered tags placed within 3 m of each nest. Nest contents of all monitored nests were checked and recorded every 3–5 d.

Manipulated disturbance trials were done during the pre-breeding (September–October 2013) and breeding (October 2013–February 2014) season to quantitatively determine birds reactions to a controlled level of anthropogenic disturbance and whether ambient temperature, egg age and location affected reactions in pre-breeding and breeding birds. Individual roosting or incubating birds were approached in a straight line from more than 100 m away. A marker was dropped for every behaviour exhibited in reaction to the individual's approach. The bird's original location (roosting location or nest) was taken as the zero point and the markers distance from this point was measured to determine at which distance the
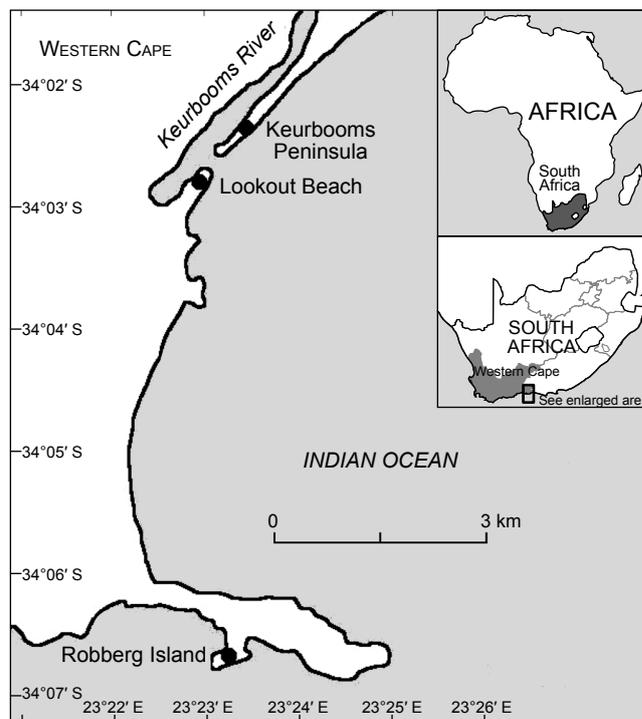

Figure 1: The location of the three study sites in Plettenberg Bay, Western Cape, South Africa

various behaviours were elicited. The behaviours that were measured include: observe, stand, walk, fly away, call and mobbing. Call was taken to be the ABO alarm call (*pic pic*), which is repeated more frequently the closer the predator gets to the nest (Hockey 2005), whereas it was taken as both the KG alarm call (*kwe-ah*, *kwe-ah*) or the attack call (*waaaaah*) (Crawford and Hockey 2005). These behaviours were not recorded systematically; the order in which they were recorded, and whether they were recorded at all, was bird-dependent. Ambient temperature and wind speed was recorded at 1 min intervals using a Kestrel 4000 Weather Meter. Once marker measurements were complete, the observer left the nest, starting a stopwatch that then measured the time taken for the incubating bird to return to the nest once the disturbance had been completed.

Observations of unmanipulated disturbance were conducted to investigate breeding birds' reactions to a variety of anthropogenic sources of disturbance generally experienced (beachgoers un/accompanied by dogs on/off the leash). Birds were observed through a telescope for a period of 30 min from a distance of more than 100 m from the nest. All movements and reactions on the part of both the human and bird were documented and the distance at which they occurred from the nest estimated using landmarks whose distance from the nest had been pre-measured. Time spent by the bird off the nest during the observation period was calculated and the time taken for the bird to return to the nest (if applicable) was recorded.

Data analysis

We narrowed our analysis to three behavioural responses: the distance at which incubating adults stood up (eggs now exposed to ambient temperature), the distance at which birds began walking away from the nest (a measure of FID), and the time taken to return to incubate once the disturbance was past (a measure of time eggs were exposed to ambient temperature), hereafter return time (only measured during breeding). Egg age data was placed into the following categories to be used as categorical predictors: 1–10 d, 11–20 d, >20 d. The ABO incubation period is around 32 d (Hockey 2005), whereas the KG incubation period is around 26 d (Crawford and Hockey 2005). Clutch size data were placed into the following categories to be used as categorical predictors: one egg, two eggs, three eggs, one egg and one chick, two eggs and one chick, one chick, one egg and two chicks, and two chicks. Ambient temperature data were categorised as <20 °C, 20–25 °C and >25 °C, whereas wind speed data were categorised as 0.0–9.9 km h^{-1}, 10.0–19.9 km h^{-1} and ≥20.0 km h^{-1}.

All statistics were analysed using R version 3.1.2 (R Core Team 2014). Values are reported as mean ± SE. Generalised linear mixed models (GLMM) with a Gaussian distribution using a logarithmic link function were used to determine the effect of various explanatory variables on three response variables (stand, walk and return time), using individual nests as a random effect. Models were created using the lme function from the NLME package (Linear and Nonlinear Mixed Effects Models). All three response variables were log-transformed prior to analysis to approximate normality. A hierarchical approach was used to generate a set of *a priori* models.

First, the effect of species on each response variable was tested. Second, as responses were significantly different according to species (see below), the effect of breeding on stand and walk responses was tested separately for each species. Breeding was shown to have a significant effect on stand and walk responses (see below), thus a set of *a priori* models examining the effects of various explanatory variables on the three response variables were created separately for the breeding and non-breeding data of each species. There was insufficient data on known egg age for KG to test parental investment effects on responses to disturbance, so this was excluded from KG breeding models. Furthermore, stand response models for breeding KG were excluded due to an incomplete data set. Unfortunately, interactive effects were not included in any models as not all combinations of categorical variables were possible. Model averaging was used to select the most influential models along with AIC_c values (Akaike's information criterion corrected for a small sample size; Burnham and Anderson 2002). *T*-tests were used to investigate within variable significance. Hatching success was calculated as eggs hatched over eggs laid.

Results

A total of 90 disturbance trials were done on pre-breeding ABO, 99 trials were done on breeding ABO, 224 trials
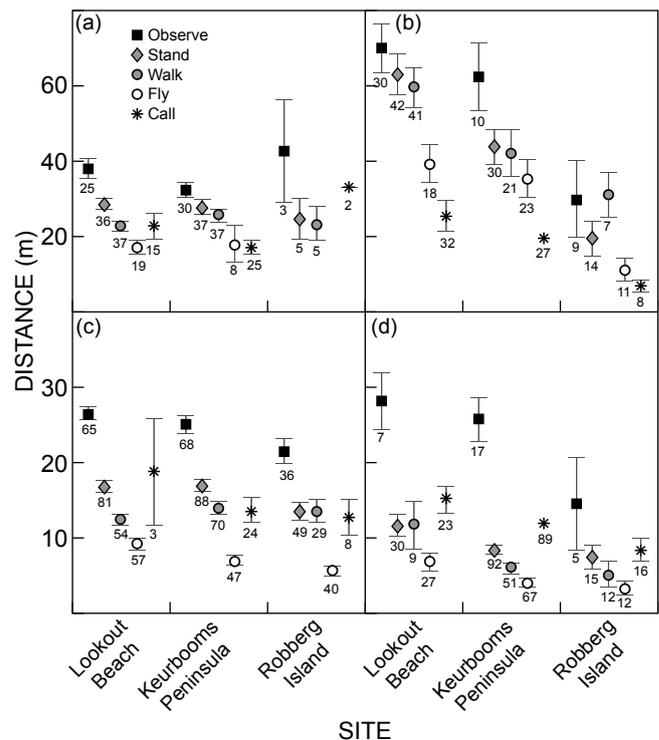

Figure 2: Behavioural responses (mean ± SE) of experimentally induced anthropogenic disturbance on (a) pre-breeding and (b) breeding African Black Oystercatchers, and (c) pre-breeding and (d) breeding Kelp Gulls at three sites in Plettenberg Bay, Western Cape, South Africa. Numbers beneath points indicate the sample size

were done on pre-breeding KG and 142 trials were done on breeding KG over the three sites. In general, ABO react sooner to disturbance when they are breeding than when pre-breeding, whereas the converse is evident for KG, which react later to disturbance when breeding than pre-breeding (Figure 2). Between the two species, ABO are more sensitive to disturbance than KG over both the pre-breeding and breeding season leaving the nest earlier (Figure 2), and returning to incubation much more slowly (Table 1).

For all three response variables tested statistically there were significant differences between species: stand ($F_{1,434} = 151.148$, $p < 0.001$), walk ($F_{1,319} = 143.416$, $p < 0.001$), and return time ($F_{1, 138} = 209.734$, $p < 0.001$) where ABO reacted much sooner to disturbance than KG (Figure 2). Breeding significantly influenced the stand and walk responses of each species. ABO stood ($F_{1,102} = 4.691$, $p < 0.05$) and walked away ($F_{1,101} = 41.271$, $p < 0.001$) from

the nest significantly earlier when breeding as compared to pre-breeding (Figure 2), whereas the opposite was observed in KG, which stood ($F_{1,330} = 103.178$, $p < 0.001$) and walked ($F_{1,216} = 80.198$, $p < 0.001$) significantly later during breeding, than pre-breeding (Figure 2).

Location was included in the best-fitting models for both walk and stand responses of pre-breeding ABO (Table 2), yet the effect was non-significant (Table 3). Wind significantly affected the stand response (Table 3), where birds stood up significantly earlier (34.7 ± 3.7 m) with wind gentle ($10.0–19.9$ km h^{-1}), than when it was light ($0.0–9.9$ km h^{-1}) (26.9 ± 1.2 m; $t = 2.04$, df = 16.99, $p < 0.05$) or moderate (≥ 20 km h^{-1}) wind (21.7 ± 5.0 m; $t = 2.1$, df = 10.8, $p < 0.05$). The stand response did not differ between light ($0.0–9.9$ km h^{-1}) and moderate (≥ 20 km h^{-1}) wind ($t = 1.0$, df = 5.58, $p = 0.355$). No variables significantly affected the walk response of pre-breeding ABO.

Location was included in the best-fitting models of the walk and stand response of breeding ABO (Table 4), and significantly affected both (Table 5). Breeding ABO stood significantly earlier on Lookout Beach (63.1 ± 5.3 m) than Keurbooms Peninsula (43.7 ± 4.7; $t = 2.57$, df = 66, $p < 0.05$) and Robberg (19.4 ± 0.5; $t = 5.19$, df = 30.5, $p < 0.001$), and significantly earlier on Keurbooms Peninsula than Robberg ($t = 3.04$, df = 24.4, $p < 0.01$). Similarly, breeding ABO walked away from the nest significantly earlier on Lookout Beach (59.8 ± 5.2 m) than Keurbooms Peninsula (42.1 ± 6.3; $t = 2.10$, df = 43.6, $p < 0.05$), and Robberg (31.1 ± 6.1; $t = 3.12$, df = 12.9,

Table 1: Time taken (seconds; mean $\pm$ SE, n in parentheses) for birds to return to incubate after experimentally induced anthropogenic disturbance has passed for breeding African Black Oystercatchers (ABO) and Kelp Gulls (KG)

| Species | Location | | |
	Lookout Beach	Keurbooms Peninsula	Robberg Island
ABO	411 ± 69 (43)	335 ± 57 (33)	353 ± 111 (12)
KG	59 ± 14 (27)	48 ± 7 (85)	38 ± 7 (16)

Table 2: Comparison of generalised linear mixed models explaining stand and walk responses of pre-breeding African Black Oystercatchers in Plettenberg Bay, Western Cape, South Africa. Only models with ∆AICc < 4 are displayed

Model	K^a	AICc	∆AICc	AICc weight	Log likelihood
Stand response					
Wind	5	68.72	0.00	0.63	−28.94
Location + Wind	7	70.95	2.23	0.21	−27.67
Walk response					
Null	3	68.29	0.00	0.65	−30.99
Location	5	71.49	3.20	0.13	−30.34
Temperature	5	72.21	3.92	0.09	−30.70

a Number of parameters

Table 3: The average of the best-fitting models weighted by AICc (∆AICc < 4), showing the effects of location, temperature, and wind on the stand and walk responses of pre-breeding African Black Oystercatchers in Plettenberg Bay, Western Cape, South Africa

Variable	Estimate	SE	Adjusted SE	z	Pr(>|z|)
Stand response					
Intercept	3.256	0.058	0.059	55.329	<0.001
Wind (10.0–19.9 km h^{-1})[a]	0.222	0.104	0.105	2.101	<0.05
Wind (>20.0 km h^{-1})[a]	−297	0.154	0.157	1.894	0.058
Location (Keurbooms)[b]	−0.090	0.084	0.085	1.048	0.295
Location (Robberg)[b]	−0.234	0.171	0.174	1.344	0.179
Walk response					
Intercept	3.106	0.055	0.056	55.263	<0.001
Location (Keurbooms)[b]	0.093	0.084	0.086	1.093	0.275
Location (Robberg)[b]	0.017	0.173	0.175	0.097	0.923
Temperature (>25.0 °C)[c]	0.019	0.165	0.168	0.113	0.910
Temperature (20.0–25.0 °C)[c]	0.073	0.103	0.105	0.693	0.488

a–c Categorical variables need to be compared to a baseline level. The baseline level for Wind was 0.0–9.9 km h^{-1}, for Location it was Lookout Beach and for Temperature it was <20.0 °C

$p < 0.01$), but values did not differ significantly between Keurbooms Peninsula and Robberg ($t = 0.97$, df = 15.4, $p = 0.348$). In addition to location, egg age significantly affected the walk response of breeding ABO (Table 5). Breeding ABO walked away from the nest significantly earlier (58.9 ± 6.4 m) when the eggs were old (>20 d) in comparison to when the eggs were young (1–10 d)

(41.7 ± 7.0 m; $t = -1.82$, df = 31, $p < 0.05$), but not when they were mid-developed (11–20 d) (50.3 ± 7.2 m; $t = -0.90$, df = 48.1, $p = 0.374$). There was no significant difference in the distance at which breeding ABO walked away from the nest when the eggs were young and mid-developed ($t = -0.86$, df = 32.2, $p = 0.398$). Interestingly, despite many variables being included in the

Table 4: Comparison of generalised linear mixed models explaining stand, walk, and return time responses of breeding African Black Oystercatchers in Plettenberg Bay, Western Cape, South Africa. Only models with ΔAICc < 4 are displayed

Model	K^a	AICc	ΔAICc	AICc weight	Log likelihood
Stand response					
Location	5	176.36	0.00	0.50	−82.77
Location + Age	7	178.90	2.55	0.14	−81.66
Location + Temperature	7	179.43	3.08	0.11	−81.93
Location + Wind	7	179.60	3.25	0.10	−82.01
Walk response					
Location + Age	7	125.88	0.00	0.35	−54.96
Location	5	126.44	0.56	0.27	−57.21
Age	5	128.52	2.64	0.09	−58.75
Null	3	129.28	3.40	0.06	−61.44
Return time response					
Null	3	208.03	0.00	0.26	−100.84
Clutch size	4	209.10	1.07	0.15	−100.26
Age	5	210.02	1.98	0.10	−99.57
Wind	5	210.04	2.01	0.09	−99.58
Temperature	5	211.04	3.00	0.06	−100.08
Clutch size + Age	6	211.32	3.29	0.05	−99.03
Age + Wind	7	211.36	3.33	0.05	−97.83
Clutch Size + Wind	6	211.52	3.49	0.05	−99.13

[a] Number of parameters

Table 5: The average of the best-fitting models weighted by AICc (ΔAICc < 4), showing the effects of explanatory variables on the stand, walk and return time responses of breeding African Black Oystercatchers in Plettenberg Bay, Western Cape, South Africa

Variable	Estimate	SE	Adjusted SE	z	Pr(>|z|)
Stand response					
Intercept	3.957	0.221	0.225	17.547	<0.001
Location (Keurbooms)[a]	−0.523	0.310	0.332	1.576	0.115
Location (Robberg)[a]	−1.655	0.425	0.454	3.644	<0.001
Age (11–20 d)[b]	0.123	0.181	0.185	0.664	0.507
Age (>20 d)[b]	0.254	0.179	0.183	0.393	0.164
Temperature (>25.0 °C)[c]	−0.264	0.285	0.272	0.904	0.366
Temperature (20.0–25.0 °C)[c]	0.016	0.207	0.212	0.074	0.941
Wind (10.0–19.9 km h⁻¹)[d]	−0.176	0.164	0.167	1.053	0.293
Wind (>20.0 km h⁻¹)[d]	−0.170	0.217	0.221	0.767	0.443
Walk response					
Intercept	3.762	0.219	0.222	16.911	<0.001
Location (Keurbooms)[a]	−0.443	0.216	0.232	1.909	0.056
Location (Robberg)[a]	−0.841	0.360	0.386	2.181	<0.05
Age (11–20 d)[b]	0.141	0.187	0.192	0.735	0.462
Age (>20 d)[b]	0.395	0.185	0.190	2.078	<0.05
Return time response					
Intercept	5.459	0.231	0.236	23.175	<0.001
Clutch size (2 eggs)[e]	0.274	0.253	0.259	1.059	0.290
Age (11–20 d)[b]	−0.109	0.278	0.285	0.381	0.703
Age (>20 d)[b]	0.276	0.269	0.276	1.001	0.317
Wind (10.0–19.9 km h⁻¹)[d]	−0.371	0.237	0.242	1.531	0.126
Wind (>20.0 km h⁻¹)[d]	−0.031	0.337	0.345	0.090	0.928
Temperature (>25.0 °C)[c]	−0.565	0.430	0.440	1.284	0.199
Temperature (20.0–25.0 °C)[c]	−0.185	0.292	0.300	0.618	0.537

[a–e] Categorical variables need to be compared to a baseline level. The baseline level for Location was Lookout Beach, for Age it was 1–10 d, for Temperature it was <20.0 °C, for Wind it was 0.0–9.9 km h⁻¹ and for Clutch Size it was 1 egg

best-fitting models (Table 4), none significantly affected the time taken for breeding ABO to return to incubate (Table 5).

Location and temperature were the most common variables in the best-fitting models for the stand and walk responses of pre-breeding KG (Table 6). Both location and temperature significantly affected the stand response, whereas the walk response was significantly affected by temperature only (Table 7). Pre-breeding KG stood up significantly later at Robberg (13.7 ± 1.2 m) than at Keurbooms Peninsula (17.1 ± 0.8 m; t = 2.3, df = 91.6, p < 0.05) and Lookout Beach (16.9 ± 0.8 m; t = 2.2, df = 90.3, p < 0.05), but the stand response did not differ significantly between Lookout Beach and Keurbooms Peninsula (t = −0.1, df = 166.8, p = 0.894). Furthermore, pre-breeding KG stood up significantly later when the temperature was >25 °C (12.3 ± 2.2 m) than when the temperature was <20 °C (17.0 ± 0.8 m; t = 2.02, df = 14.1, p < 0.05), but not when the temperature was 20.0–25.0 °C (16.1 ± 0.7 m; t = −1.65, df = 13.7, p = 0.122), nor did the stand response differ significantly between <20 °C and 20.0–25.0 °C (t = 0.81, df = 195.3, p = 0.417). Pre-breeding KG walked away from approaching disturbance significantly later when the temperature was >25.0 °C (9.3 ± 1.8 m) than when the temperature was <20 °C (14.5 ± 0.9 m; t = 2.53, df = 12.1, p < 0.05), but not when the temperature was 20.0–25.0 °C (13.1 ± 0.8 m; t = −1.90, df = 11.2, p = 0.084),

nor did the stand response differ significantly between <20 °C and 20.0–25.0 °C (t = 1.14, df = 134.3, p = 0.258).

Location and temperature both feature in the best-fitting models explaining the behavioural responses of breeding KG (Table 8), yet temperature did not have a significant effect while location and clutch size did significantly affect the distance at which breeding KG stand in response to disturbance (Table 9). Breeding KG stood up significantly earlier at Lookout Beach (11.7 ± 1.5 m) than Keurbooms Peninsula (8.4 ± 0.6 m; t = 1.97, df = 39.4, p < 0.05) and Robberg Island (7.5 ± 1.7 m; t = 1.85, df = 35.21, p < 0.05). The stand responses at Keurbooms Peninsula and Robberg Island were not significantly different (t = 0.52, df =18.2, p = 0.606). Clutch size also affected stand response distance where birds incubating a clutch consisting of two eggs and one chick stood significantly later (4.5 ± 1.4 m) than those incubating a one-egg clutch (11.0 ± 1.1 m; t = 3.62, df = 7.7, p < 0.01), and a one-egg, one-chick clutch (10.0 ± 1.1 m; t = 3.06, df = 6.2, p < 0.05). The stand response of birds incubating other clutch sizes were similar. As with ABO, none of the explanatory variables tested significantly affected the return time of breeding KG (Table 9).

Unfortunately, due to the small sample size of unmanipulated disturbance trials, no statistical analyses could be done. Dogs off the leash elicited the earliest reaction from the ABO yet surprisingly not the KG (Table 4). The

Table 6: Comparison of generalised linear mixed models explaining stand and walk responses of pre-breeding Kelp Gulls in Plettenberg Bay, Western Cape, South Africa. Only models with ΔAICc < 4 are displayed

Model	K[a]	AICc	ΔAICc	AICc weight[b]	Log likelihood[c]
Stand response					
Location + Temperature	7	333.06	0.00	0.70	−159.27
Location	5	335.91	2.85	0.17	−162.82
Walk response					
Temperature	5	284.41	0.00	0.45	−137.00
Null	3	285.52	1.11	0.26	−139.68
Location + Temperature	7	287.30	2.89	0.11	−139.27
Temperature + Wind	7	288.37	3.96	0.06	−136.80

[a] Number of parameters

Table 7: The average of the best-fitting models weighted by AICc (ΔAICc < 4), showing the effect of location, temperature, and wind on the stand and walk responses of pre-breeding Kelp Gulls in Plettenberg Bay, Western Cape, South Africa

Variable	Estimate	SE	Adjusted SE	z	Pr(>|z|)
Stand response					
Intercept	2.791	0.069	0.069	40.381	<0.001
Location (Keurbooms)[a]	0.015	0.082	0.082	0.177	0.859
Location (Robberg)[a]	−0.337	0.092	0.093	3.627	<0.001
Temperature (>25.0 °C)[b]	−0.408	0.158	0.159	2.562	<0.05
Temperature (20.0–25.0 °C)[b]	−0.099	0.074	0.074	1.345	0.179
Walk response					
Intercept	2.502	0.085	0.085	29.404	<0.001
Temperature (>25.0 °C)[b]	−0.480	0.214	0.216	2.225	<0.05
Temperature (20.0–25.0 °C)[b]	−0.118	0.102	0.102	1.15	0.247
Location (Keurbooms)[a]	0.082	0.110	0.111	0.739	0.460
Location (Robberg)[a]	−0.071	0.138	0.139	0.509	0.611
Wind (10.0–19.9 km h⁻¹)[c]	−0.057	0.104	0.105	0.541	0.588
Wind (>20.0 km h⁻¹)[c]	−0.137	0.360	0.363	0.379	0.705

[a–c] Categorical variables need to be compared to a baseline level. The baseline level for Location was Lookout Beach, for Temperature it was < 20.0 °C, and for Wind it was 0.0–9.9 km h⁻¹

presence of a stationary picnicker extended the return time of the ABO, with a person walking along the beach allowed the fastest return time (Table 4). KG stood at the disturbance but did not feel threatened enough to leave the nest bowl regardless of the disturbance factor (Table 4).

A total of nine ABO pairs making 14 nesting attempts were monitored on Lookout Beach, eight pairs making nine nesting attempts on Keurbooms Peninsula, and five pairs making seven nesting attempts on Robberg. Hatching success on Lookout Beach was 59% (22 eggs laid), 54% on Keurbooms Peninsula (13 eggs laid) and 33% on Robberg (12 eggs laid). Hatching success of KG breeding on Lookout Beach was 41%, 46% on Keurbooms Peninsula and 2% on Robberg Island (MW unpublished data).

Discussion

Both African Black Oystercatchers and Kelp Gulls reacted to manipulated anthropogenic disturbance, and sites with more disturbance showed higher levels of reactions. Species reactions to manipulated disturbance were not influenced uniformly by the categorical predictors tested. ABO are known to be sensitive to anthropogenic disturbance (Leseberg et al. 2000), yet only breeding, not pre-breeding, responses were significantly affected by location (and by proxy levels of natural anthropogenic disturbance). Breeding ABO stand response distance was affected by location, regardless of egg age, clutch size, ambient temperature or wind speed. This suggests that

Table 8: Comparison of generalised linear mixed models explaining stand and return time responses of breeding Kelp Gulls in Plettenberg Bay, Western Cape, South Africa. Only models with ΔAICc < 4 are displayed

Model	K^a	AICc	ΔAICc	AICc weight[b]	Log likelihood[c]
Stand response					
Location + Clutch size	11	334.43	0.00	0.23	−155.16
Clutch size + Temperature	11	335.85	1.42	0.11	−155.87
Location + Clutch size + Wind	13	336.04	1.60	0.10	−153.54
Location + Clutch size + Temperature	13	336.21	1.78	0.09	−153.63
Clutch size + Temperature + Wind	13	336.34	1.90	0.09	−153.69
Clutch size	9	336.46	2.02	0.08	−158.52
Clutch size + Wind	11	336.64	2.21	0.08	−156.26
Temperature	5	337.48	3.05	0.05	−163.51
Location + Clutch size + Temperature + Wind	15	337.99	3.56	0.04	−152.01
Temperature + Temperature	7	338.37	3.94	0.03	−161.75
Return time response					
Temperature	5	305.98	0.00	0.49	−147.73
Null	3	307.89	1.91	0.19	−150.85
Location + Temperature	7	308.63	2.66	0.13	−146.83
Location	5	309.83	3.85	0.07	−149.66

[a] Number of parameters

Table 9: The average of the best-fitting models weighted by AICc (ΔAICc < 4), showing the effects of explanatory variables on the stand and return time responses of breeding Kelp Gulls in Plettenberg Bay, Western Cape, South Africa

Variable	Estimate	SE	Adjusted SE	z	Pr(>$\mid z \mid$)
Stand response					
Intercept	2.460	0.300	0.302	8.154	<0.001
Location (Keurbooms)[a]	−0.319	0.208	0.211	1.517	0.129
Location (Robberg)[a]	−0.632	0.289	0.292	2.164	<0.05
Clutch size (1 chick)[b]	−0.170	0.379	0.411	0.414	0.679
Clutch size (1 egg + 1 chick)[b]	0.417	0.349	0.378	1.103	0.270
Clutch size (2 chicks)[b]	−0.072	0.403	0.437	0.165	0.869
Clutch size (2 eggs)[b]	−0.268	0.163	0.177	1.517	0.129
Clutch size (2 eggs + 1 chick)[b]	−0.988	0.409	0.444	2.227	<0.05
Clutch size (3 eggs)[b]	−0.680	0.213	0.231	2.945	<0.01
Temperature (>25.0 °C)[c]	−0.684	0.346	0.373	1.834	0.067
Temperature (20.0–25.0 °C)[c]	−0.437	0.300	0.324	1.349	0.177
Wind (10.0–19.9 km h⁻¹)[d]	0.285	0.148	0.162	1.759	0.078
Wind (>20.0 km h⁻¹)[d]	0.052	0.271	0.297	0.174	0.862
Return time response					
Intercept	3.925	0.350	0.352	11.155	<0.001
Temperature (>25.0 °C)[c]	−0.284	0.355	0.380	0.749	0.454
Temperature (20.0–25.0 °C)[c]	−0.614	0.306	0.328	1.872	0.061
Location (Keurbooms)[a]	−0.281	0.203	0.206	1.367	0.172
Location (Robberg)[a]	−0.221	0.282	0.286	0.773	0.440

[a–d] Categorical variables need to be compared to a baseline level. The baseline level for Location was Lookout Beach, for Clutch size it was 1 egg, for Temperature it was < 20.0 °C, and for Wind it was 0.0–9.9 km h⁻¹

these birds are most sensitive to the level of disturbance they experience regardless of other factors. Surprisingly, location also significantly affected the stand response of both pre-breeding and breeding KG, which are not thought to be a species particularly sensitive to disturbance. Lookout Beach is a popular beach for summer holidaymakers, especially families with active children and unleashed dogs. The highly variable and unpredictable movements make the ABO more alert, and readily inclined to walk away from the nest to hide its location; they do not appear to become habituated to a regular high level of disturbance, but rather spend a longer time off the nest than at other locations with lower disturbance levels (Table 1). Access to Keurbooms Peninsula is mostly restricted to water transport or a long walk from the Keurbooms side and as a result is not as heavily populated as Lookout Beach. Movements of the beachgoers are highly constrained due to the aggressive nature of the large KG breeding colony, which provides umbrella protection of the ABO nesting here such that they allow a closer approach than at Lookout Beach before standing and walking away from the nest. Visitors to Robberg Nature Reserve are required to remain on paths and walkways and so their movements are, for the most part, predictable. A combination of predictable movements and nests with good views of the surrounding area allows for reduced reactions to disturbance (Figure 2). Data from this study show that nest location can affect the response to disturbance by ABO and KG. The age of the clutch also affects the walk response of breeding ABO, where birds walk away from the nest earlier with older eggs in an attempt to better camouflage the location of the nest. Egg age did not affect responses of breeding KG, but clutch size influenced their stand response. None of the variables tested significantly affected return time in KG. The aggressive nature of this species' nest defence appears to preclude the effects of other factors.

Surprisingly, return time of breeding ABO was also not significantly affected by any of the variables tested. It was expected that ambient temperature would be the most important factor, as unattended eggs run the risk of overheating (Brown and Downs 2003), as well as being predated. Indeed, embryos of ground-nesting birds are known to die within exposure time of between 2 min (Grant 1982) and 15 min (Maclean 1967). The return to nest time of ABOs varied on average from 5 min 35 s (Keurbooms Peninsula; Table 1) to 6 min 51 s (Robberg Island; Table 1), after experimental disturbance, and spent between 9 min 15 s (picnicker; Table 10) and 14 min 40 s (dog off leash;

Table 10) off the nest during natural disturbance events, suggesting a high threat of lethal exposure to eggs.

Temperature has also been seen to play an important role in other studies: Crowned Lapwings showed constrained nest defence at higher temperatures allowing for maximum incubation to keep eggs cool (Brown and Brown 2004), and a study on Malaysian Plovers showed faster return times to the nest at a higher modelled egg temperature, relating to ambient temperature (Yasué and Dearden 2006). Unexpectedly, egg age resulted in no change in behaviour nor in return time unlike other studies (Brown and Brown 2004; Yasué and Dearden 2006). Similarly, clutch size did not affect stand response distance nor return time and has been shown to not affect nest defence intensity in Black-tailed Gulls (Kazama et al. 2010). These surprising results provide evidence that anthropogenic disturbance is an over-riding concern for sensitive species such as ABO experiencing high levels of anthropomorphic disturbance, and that this should be seen as a primary concern in terms of managing populations of such species where disturbance regularly occurs.

Breeding ABO and KG reacted differentially, both in rapidity and order of behaviours, to standardised experimental anthropogenic disturbance, in this case the direct approach of one the authors (which the birds presumably treat as an approaching predator; Frid and Dill 2002; Beale and Monaghan 2004). ABO are more sensitive to human disturbance than KG and for every behavioural reaction documented during manipulated trials they reacted earlier (i.e. at a further distance from the nest) (Figure 2). Not only were species response distances different but the order in which the behavioural reactions were elicited also differed. During the breeding season the order of ABO behavioural reactions to disturbance were as follows: observe – stand – walk – fly – call; the order of KG behavioural reactions were: observe – call – stand – walk – fly – mob (Figure 2). The combination of reaction distances and reaction order shows contrasting nest defence strategies by these two species. ABO primary nest defence mechanism is camouflage: leaving the nest while the predator is still a distance away enables the location of the nest (and eggs) to remain hidden; furthermore, by calling only once far away from the nest the bird distracts the predator from the true location of the nest. Conversely, KG primary nest defence mechanism is aggression: maintaining optimal egg or chick microhabitat and preventing predation by conspecifics appears to be prioritised as KG do not move from incubation duties until the threat is relatively close, preferring to call a warning before moving from the nest

Table 10: The behavioural responses (mean ± SE, *n* in parentheses) during unmanipulated disturbance trials on breeding African Black Oystercatchers (ABO) and Kelp Gulls (KG) while incubating eggs

Disturbance	Species	Stand (m)	Time off the nest (s)	Return to incubation (s)
Picnicker	ABO	10 ± 2 (4)	555 ± 222 (4)	240 ± 88 (4)
	KG	5 (1)	0 (1)	0 (1)
Walker	ABO	38 ± 8 (16)	836 ± 170 (16)	218 ± 76 (16)
	KG	25 ± 5 (5)	0 (5)	0 (5)
Dog off the leash	ABO	45 ± 15 (3)	880 ± 465 (3)	160 ± 87 (3)
	KG	20 (1)	0 (1)	0 (1)

and viciously attacking (mobbing) the predator. Mobbing can be done individually, yet is more often communal with parents from surrounding nests joining in the attack of the predator, which is intimidating enough to drive dogs and people from the breeding colony (SVdV and MW pers. obs.). These contrasting nest defence strategies are further supported by pre-breeding and breeding comparisons of stand and walk response distance. ABO allow for a closer approach in the pre-breeding season (Figure 2) as they do not need to hide the location of a nest, whereas KG move from their roosting location sooner in the pre-breeding than breeding season (Figure 2) as they do not need to protect the nest.

Observations from unmanipulated disturbance trials showed that ABO regarded dogs as the greatest threat compared to walkers or picnickers. This has also been shown to be the case with New Zealand Dotterels (Lord et al. 2001). Curiously, KG do not conform to this tendency, most likely due to their aggressive nature and nest defence strategy.

This study shows that even highly urbanised species such as KG show differential responses to disturbance in areas where disturbance rates are higher, suggesting that even adaptable species are negatively influenced by anthropogenic disturbance. Of concern, the presence of dogs near a breeding colony is highly disruptive to breeding ABO and existing legislature should be implemented and strictly monitored during the breeding season. Furthermore, by developing zones surrounding breeding colonies where human presence and/or activities are restricted, the breeding success of various species may be improved. By defining a restricted area around these breeding colonies based on the distance at which ABO stand and expose eggs to ambient temperature, other species such as KG, as well as others that breed in the area, will by default experience reduced anthropogenic disturbance during the breeding season. ABO are currently classified as Near Threatened (BirdLife International 2012a) and have a low hatching success in Plettenberg Bay (Lookout Beach 59%, Keurbooms Peninsula 54% and Robberg Island 33%; this study), and although the overall population is increasing (BirdLife International 2012a), this should not reduce conservation efforts. Reducing the number of people, and increasing the minimum distance to which they can approach breeding birds, has a positive effect on breeding populations and allows them to react as they would in an entirely natural, undisturbed area (Ikuta and Blumstein 2002). This is especially important during the breeding season where ABO reactions are intensified, leaving the nest earlier than they would a roosting place in the pre-breeding season.

Due to the rapidly expanding urban environment, and popularity of coastal areas for summer holidays, which coincide with the breeding season of many shorebirds, it becomes important to understand the extent of the effect of the disturbance on these birds. From this appropriate management plans can be put into place for the conservation of undisturbed breeding areas for the birds. Further research on the effects of anthropogenic disturbance on breeding shorebirds should include more detailed observations of unmanipulated anthropogenic disturbance, studies of the effects of disturbance on time–energy budgets and individual hatching success, surveys of beach-goer opinions, and investigating the effects of environmental education and awareness campaigns.

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