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Flight-initiation response reflects short- and long-term human visits to remote islets

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The increasing use of, and visits to, isolated territories by people (especially tourists) enables the investigation of how biodiversity reacts to evolutionarily novel pressures. We explored the behavioural reaction of a breeding seabird species, the Brown Noddy *Anous stolidus*, to our repeated visits at two study sites in the Chesterfield Islands, a newly classified reserve in the Coral Sea Natural Park. Repeated measures of flight-initiation distances (FIDs) at three sites and over time suggest that human visitations induced both a spatial phenotypical sorting or learning of individuals and a temporal habituation. In light of the novel 'Sit and Defend' mode of avian nest defence, the study finally provides the first dataset of FIDs for this species, and highlights management opportunities that could arise from the replication of such an approach to other breeding seabirds and therefore the conservation of remote island ecosystems.

Keywords: behaviour, disturbance, escape, learning, seabirds.

The remoteness of oceanic islands has allowed for the evolution and maintenance of rich and endemic biodiversity, isolated from many pressures including anthropogenic

ones (Tershy *et al.* 2015). The increasing use of, and visits to, these isolated territories by people (especially tourists) enables the investigation of how biodiversity reacts to evolutionarily novel pressures (Hall 2010). At the same time, development of integrated conservation strategies is required to prevent biodiversity changes and losses on islands associated with human presence (Tershy *et al.* 2015). A key challenge for environmental managers is to meet sometimes competing demands to balance human uses and natural values so they coexist (Saarinen 2016). Humans can impart a variety of changes to wildlife, such as introductions of invasive species, but they can also have an indirect effect associated with their mere presence (i.e. through disturbance, the disruption of normal behaviour or physiology; Weston *et al.* 2012). This disruption occurs when wildlife responds to people as if they are a threat associated with predators, i.e. animals escape to avoid being preyed upon (Frid & Dill 2002). The escape decision of animals facing approaching humans then depends on the animal's cost of escaping (body size, reproductive status) and on context (habitat openness, urbanization, resource availability) (Samia *et al.* 2015). The respective influences of cost, context and experience have still to be clarified.

Seabirds generally rely on isolated, 'low-disturbance' areas to reproduce. They are one of the most threatened animal groups at a global scale and their risk of extinction is increasing faster than any other group of birds (Xu *et al.* 2016). They are a priority for managers of protected oceanic and coastal areas, both as indicators of the quality of marine environments and as major targets of restoration, conservation and management programmes (Thibault *et al.* 2019). Human visitation to breeding sites constitutes one of the major pressures on seabird populations and managing these activities is a key challenge for their conservation (United Nations 2017).

Measuring the indirect effects of anthropogenic disturbances on animals' life history traits (weight, physiology) and demography (survival, reproductive success) appears to be the most common approach (Cianchetti-Benedetti *et al.* 2018). However, direct behavioural studies can provide a better measure of sensitivity of some species or groups of individuals to disturbance (Barros *et al.* 2016). Flight-initiation distance (FID) when approaching by walking, boat, or with a flying object can index the sensitivity of birds to disturbance (Weston *et al.* 2012). This method has the advantage of being non-invasive, minimizing the effects of different observers, and being inexpensive and easily transferable to conservation tools such as setbacks (Weston *et al.* 2012, Guay *et al.* 2013).

We explored the behavioural reaction of a breeding seabird species to repeated visits at a study site on remote islets in the Bampton-Chesterfield-Bellona archipelago, a newly classified reserve in the Coral Sea Natural Park. We studied Brown Noddies *Anous stolidus* which nest in low vegetation on the edges of islets. The

species is considered to be very sensitive to pressures from human visits, native predators and invasive species (Burger & Gochfeld 1988, Megyesi & Griffin 1996, Pandolfi & Bretagnolle 2002, Angel & Cooper 2006). We measured FID of nesting Brown Noddies at three sites during our first visits to account for a potential heterogeneity in the spatial distribution of escape behaviour that could be due to variation in the prevailing human environment. We then repeated these measures at the site most exposed to humans over 2 weeks to test whether a group of birds was capable of a behavioural habituation to our presence. Results are discussed considering the available knowledge of anti-predator behaviours in birds, and the ecology and management of the study species.

METHODS

Study system

Fieldwork was conducted on two islets within the Chesterfield Islands, a V-shaped group of islets within the Bampton-Chesterfield-Bellona Archipelago. They lie in the middle of the Coral Sea (19°05′–21°50′S, 158°15′–159°35′E), more than 500 km west of the northern edge of New Caledonia's main island. Reefs and islets are distributed within an area of c. 24 000 km² and consist of two main plateaux which are classified as a natural reserve (IUCN Category 2). None of these islets is inhabited by either humans or mammalian predators but whaling and guano digging activities occurred there in the late 19th century (Borsa *et al.* 2010). We worked on two islets within the southern Chesterfield plateau: 'Loop' and 'Mouillage 1' (out of four), the latter being classified as an integral reserve since August 2018 (Gouvernement de la Nouvelle Calédonie 2018). Managers visit Loop on a regular basis (yearly or twice a year) to work at the meteorological station and conduct biodiversity monitoring, which could lead to a behavioural response. This is not the case on Mouillage 1. Moreover, there is one appropriate landing area along Loop's coast which favours visitations by boaters and fishermen, unlike for Mouillage 1. At the time of our study, the two islets hosted similar seabird communities: three species of Boobies, two of Noddies, two of Frigate-bird species, Wedge-tailed Shearwaters *Ardenna pacifica*, and about 100 breeding Sooty Terns *Onychoprion fuscatus*. Thereby, the soundscapes were similar across our sampling locations.

Brown Noddy is a widespread tropical seabird, present in the Pacific, Indian and Atlantic Oceans as well as in the Caribbean. It is abundant both globally (c. 180 000–1 100 000 individuals; IUCN 2019) and on the Chesterfield Islands (c. 4300 breeding pairs; DAM/SPE 2017). Population trends are considered to be stable

so that the species is considered of Least Concern (IUCN 2019). At our study sites, the species nests at the boundary between the beach sand and the herbaceous layer. The species is colonial, individuals practise shallow plunge diving, and some may mob predators (Wilson *et al.* 2010). Adults lay one egg either on a platform-shaped nest made of twigs or directly on the sand. Within the colony, birds nest close to each other with distance between nests varying from a dozen centimetres to a few metres.

Sampling

Six data replicates were collected on 'Loop' and two on 'Mouillage 1' between 10 and 22 April 2019. 'Loop' islet was divided into two parts according to the human regimen experienced by the birds. The 'high-use zone' is where the boat landing area is located. During the study period, it was visited daily by five people walking along the beach to access a colony of Wedge-tailed Shearwaters for a total of 19 visits. The 'low-use zone' of the islet was visited only twice for other reasons than the measurement of FIDs, five times in total.

FIDs were measured during three sessions only on the 'isolated' side of Loop islet, to reduce the disturbance of our visitations. Mouillage 1 was visited and sampled only twice. The number of breeding pairs was systematically censused at each site. FIDs were recorded from haphazardly selected individuals seated on nests, i.e. incubating eggs or pre-laying, to reduce a potential bias associated with the initial activity of individuals. We measured FID as the horizontal distance between the observer and the nest when the targeted individual flew away (Weston *et al.* 2012). We chose FIDs because: (1) alert distance (AD) is more dependent on the observer (Guay *et al.* 2013) and (2) AD and FID were close and difficult to separate in breeding Brown Noddies. A single observer initially walked along the swash zone to avoid disruption of focal birds. When an individual was selected, the observer walked perpendicular to this line to face the bird and minimize variation in starting distances (which strongly influences FID if not controlled; Weston *et al.* 2012) and the disruption of neighbouring individuals. As the geomorphology of the two islets was slightly different, Loop being very flat compared with Mouillage 1 with its central mound, we prioritized the sampling of individuals nesting at eye height relative to a standing human in the swash zone. Starting from the swash zone allowed for a consistent starting distance (≈ 12 m). When two nesting adults were very close (i.e. <10 cm), only one was sampled. All measurements were taken with a laser rangefinder (Makita LD060P). We recorded over 30 FIDs per sampling session and site to allow for statistical reliability while minimizing the risk of measuring the same individuals twice during a single session.

Analyses

To examine whether FIDs varied across a historical gradient of human useage, we tested for potential differences in mean FIDs during the first visit to each site using a one-way analysis of variance (ANOVA) and Tukey posthoc tests. To examine whether Noddies adjusted their FIDs to repeated exposure to humans, we focused on the part of Loop islet visited every day. We ran a generalized linear model (GLM) with a gamma distribution and inverse-link function, using the package 'lme4' v1.1.21 and checking graphically for the suitable error structures (Bates *et al.* 2014). We used FIDs as a response variable and the days since the start of the experiment as a discrete predictor. Bootstrapped confidence intervals were set at the 98% confidence level. Confidence intervals were calculated from 500 parametric bootstrap simulations, i.e. calculating the effect estimate from 500 resampled datasets to evaluate its uncertainty. Data were compiled and analysed using R v3.4.0 (R Core Team 2017). All results are presented as mean \pm standard deviation.

RESULTS

We counted 778 breeding pairs on Loop islet and 71 breeding pairs on Mouillage 1 (68 and 100%, respectively), with adults sitting on nests and brooding one egg. The remaining adults were pre-laying and no chicks were observed. Among the 455 measurements collected, 198 were collected on the 'disturbed' side of Loop islet, 159 on the 'isolated' side and 98 on Mouillage 1 Islet.

FIDs were slightly higher on Mouillage 1 than on Loop islet and within Loop islet slightly higher in the low-use zone than the high-use zone (Fig. 1a). However, these differences were not significant (mean difference = 1.08, adjusted $P = 0.082$). FIDs decreased with our repeated visitations to the high-use zone of Loop islet (Fig. 1b). The effect of time as a proxy of repeated visits on measured FID was significant (estimate: -5.64 ; 98% CI: -7.03 to -4.24). McFadden's *pseudo* R^2 for this model was 0.28.

DISCUSSION

This study reports two main results: (1) FIDs were generally short and (2) frequent human visits to a remote island affected the behaviour of breeding seabirds over a short timescale. The lower mean FIDs observed at Loop islet's high-use zone need to be confirmed.

We provide the first dataset on the FIDs of Brown Noddies approached by a single observer on a remote islet. Previous work conducted on Lancelin Island (Western Australia) estimated this distance to be 'within 2 m of target-breeding birds before flight initiation responses

were observed' (Barter 2004). Lancelin Island is popular for ecotourism and recreational activities. Located only 800 m from the mainland, it has been and still is frequently visited by people (Barter 2004). The FIDs of Brown Noddies on Lancelin Island broadly correspond to the FIDs we report at Loop's high-use zone after 6 days of daily visitations. The highest mean FID we measured (4.4 ± 1.8 m) was on the isolated Mouillage 1 islet, suggesting a relatively weak terrestrial predator avoidance strategy. Indeed, this FID is especially low given those known for other species of lighter (e.g. Common Tern *Sterna hirundo* 29.6 ± 5.9 m) or heavier body masses (e.g. Great Cormorant *Phalacrocorax carbo* 32.3 ± 20.6 m) and because open habitats such as those we studied are associated with longer FIDs (Blumstein 2003, 2006, Møller 2015, Samia *et al.* 2015). We acknowledge that the FIDs we report are of breeding birds and that FIDs of non-breeding birds may not be comparable (Weston 2019). The relatively short FIDs we report may at least partly be due to 'island tameness', the reduction of escape responsiveness with evolutionary isolation from predators (Blumstein & Daniel 2005). Short FIDs may also indicate that leaving the nest is costly. Air temperatures were high during sampling (27–28 °C) and absent birds risked their eggs overheating. Whatever the drivers of the short FIDs we describe, they are likely to accentuate the vulnerability of adult Brown Noddies to novel predators.

While human regimens are rarely quantified (Weston 2019), we observed slightly lower FIDs at one site that experiences greater exposure to humans. This difference was not significant and should thus be confirmed by further sampling, but it is consistent with the patterns expected as a result of learning (Blumstein 2016), phenotypic sorting of personalities (Møller 2017) or both. We also report a slight, but rapid decrease in FIDs with increasing exposure to humans over the timescale of days. This can probably be attributed to learning (Blumstein 2016, Møller 2017), as it is unlikely that individuals sampled in the same nests changed over our study period. In only 6 days, the mean FID measured on the same group of individuals dropped from 3.6 ± 1.3 to 1.8 ± 0.6 m (i.e. *c.* 50%), before stabilizing between 0.4 and 2.7 m afterward (1.9 ± 0.6 m). This would suggest a behavioural habituation to our repeated visits. Individuals could quickly learn from harmless visits and modify their escape behaviour to lower possible negative effects on their reproductive outputs (Møller 2015, Blumstein 2016). Of course, a behavioural habituation *stricto sensu* could only have been measured over time by repeatedly sampling the same known individuals. Banding was not possible in our study context and may have imparted a specific learning event on individuals; however, we tried repeatedly to target the same nests at each site and consider that our results at a group scale reflect a generalized behavioural shift among individuals. Examples of

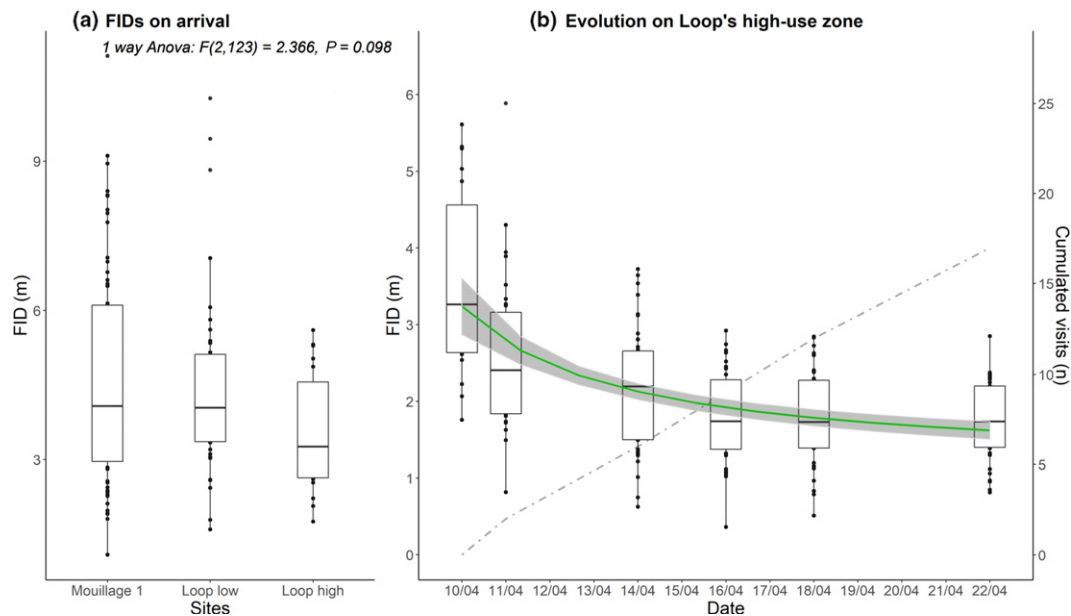


Figure 1. (a) Flight-initiation distances (FIDs) measured on Brown Noddies during the first visit at three sites. (b) Decrease in FIDs measured for breeding Brown Noddies over repeated approaches during a 2-week sampling session on Loop islet's high-use zone. The solid line represents the fitted generalized linear model with associated standard error. The dashed line represents the cumulative number of past human visits over time. [Colour figure can be viewed at wileyonlinelibrary.com]

behavioural habituation patterns of birds at such short timescales have apparently hitherto been undocumented.

In the context of remote islands free of mammalian predators, weak escape behaviour reflected by short FIDs could instead reflect strong defence behaviours (Megyesi & Griffin 1996). Although egg predators exist in our study system (e.g. Banded Rails *Gallinallus philippensis* feed on eggs of Brown Booby *Sula melanogaster*; M. Thibault unpubl. obs.) predators of adult Noddies may be absent or rare. This may have led to a 'Sit and Defend' strategy. In the absence of predators of adults, with high-density breeding, the greater risk for ground-nesting birds might be the loss of their breeding outputs. 'Boldness' (i.e. short FIDs) may effectively encourage depredation of nearby eggs defended by 'shyer' adults. The reaction toward novel encounters such as humans would then be guided by a trade-off between fear and protection of eggs/chicks. Such a strategy would also engender competition between nearby breeders in terms of their FIDs, possibly even selection, which may contribute to differences in FIDs between localities. A Sit and Defend strategy probably involves careful assessment of the risks to the adult associated with an approaching threat and predicts a rapid reduction in FID with exposure to a benign stimulus. We report results consistent with these ideas. In this study, humans were non-lethal agents, and birds exposed to people rapidly reduced their FIDs. Additionally, site-scale differences in FIDs were observed.

Management and research implications

Habituation of a group, as suggested by our results, is not universally benign (Baudains & Lloyd 2007). Such results call for a deeper understanding of the relationship between two habituation-like processes that could have different impacts on a disturbed population, namely learning and phenotypic sorting. Habituation should be tested in regard to different stimuli and at different intensities and time scales because it could help to explain the resilience of some species to human disturbance. Similarly, the phenotypic sorting potentially induced by frequent human visitations could underpin insidious processes influencing bird communities such as a decline in the local population of individuals that are more sensitive to disturbance (Martín *et al.* 2015). Here we were able to test the effect of a high frequency of visitations over a short period, suggesting that a habituation could be possible. However, tourism for example could also take the form of a low frequency of visitations but over longer periods. Past local studies have already suggested that long-term human visits on islands of the southern lagoon of New Caledonia could be associated with lower reproductive success in Brown Noddies (Pandolfi & Bretagnolle 2002).

Understanding the behavioural response of island fauna is critical in an era of increasing demand for nature-based tourism in remote places (Booth *et al.* 2011). Efforts to evaluate the vulnerability of island seabirds to indirect (human) and direct (habitat changes, invasive

species, pollution) pressures from frequent human visits will greatly assist management of these remote ecosystems. Recent calls were launched to warn scientists and environment managers against this forthcoming threat to remote tropical island ecosystems (Vidal *et al.* 2018). In these small and complex systems, uncontrolled changes occurring in the terrestrial compartments could have negative cascading effects on the surrounding marine environment (Lorrain *et al.* 2017, Graham *et al.* 2018). Thus, we believe that further studies should focus on: (1) multi-species assessments of the responses to human disturbances, (2) linking behavioural responses of individuals to fitness and demography, and (3) understanding the cascading effects on the island–reef continuum. Producing metrics such as FIDs for an ensemble of species and habitats could usefully assist managers in mitigating the impacts of ongoing changes in the use of these systems of very high conservation value (Weston *et al.* 2012).

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