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Regional drivers of clutch loss reveal important trade-offs for beach-nesting birds

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Coastal birds are critical ecosystem constituents on sandy shores, yet are threatened by depressed reproductive success resulting from direct and indirect anthropogenic and natural pressures. Few studies examine clutch fate across the wide range of environments experienced by birds; instead, most focus at the small site scale. We examine survival of model shorebird clutches as an index of true clutch survival at a regional scale (~ 200 km), encompassing a variety of geomorphologies, predator communities, and human use regimes in southeast Queensland, Australia. Of the 132 model nests deployed and monitored with cameras, 45 (34%) survived the experimental exposure period. Thirty-five (27%) were lost to flooding, 32 (24%) were depredated, 9 (7%) buried by sand, 7 (5%) destroyed by people, 3 (2%) failed by unknown causes, and 1 (0.1%) was destroyed by a dog. Clutch fate differed substantially among regions, particularly with respect to losses from flooding and predation. 'Topographic' exposure was the main driver of mortality of nests placed close to the drift line near the base of dunes, which were lost to waves (particularly during storms) and to a lesser extent depredation. Predators determined the fate of clutches not lost to waves, with the depredation probability largely influenced by region. Depredation probability declined as nests were backed by higher dunes and were placed closer to vegetation. This study emphasizes the scale at which clutch fate and survival varies within a regional context, the prominence of corvids as egg predators, the significant role of flooding as a source of nest loss, and the multiple trade-offs faced by beach-nesting birds and those that manage them.

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10 **Regional Drivers of Model Clutch Loss Reveal Important Trade-offs for Beach-nesting**
11 **Birds**

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33 **ABSTRACT** Coastal birds are critical ecosystem constituents on sandy shores, yet are
34 threatened by depressed reproductive success resulting from direct and indirect anthropogenic
35 and natural pressures. Few studies examine clutch fate across the wide range of environments
36 experienced by birds; instead, most focus at the small site scale. We examine survival of model
37 shorebird clutches as an index of true clutch survival at a regional scale (~ 200 km),
38 encompassing a variety of geomorphologies, predator communities, and human use regimes in
39 southeast Queensland, Australia. Of the 132 model nests deployed and monitored with cameras,
40 45 (34%) survived the experimental exposure period. Thirty-five (27%) were lost to flooding, 32
41 (24%) were depredated, 9 (7%) buried by sand, 7 (5%) destroyed by people, 3 (2%) failed by
42 unknown causes, and 1 (0.1%) was destroyed by a dog. Clutch fate differed substantially among
43 regions, particularly with respect to losses from flooding and predation. ‘Topographic’ exposure
44 was the main driver of mortality of nests placed close to the drift line near the base of dunes,
45 which were lost to waves (particularly during storms) and to a lesser extent depredation.
46 Predators determined the fate of clutches not lost to waves, with the depredation probability
47 largely influenced by region. Depredation probability declined as nests were backed by higher

48 dunes and were placed closer to vegetation. This study emphasizes the scale at which clutch fate
49 and survival varies within a regional context, the prominence of corvids as egg predators, the
50 significant role of flooding as a source of nest loss, and the multiple trade-offs faced by beach-
51 nesting birds and those that manage them.

52

53 Several iconic, threatened species of the world's coastlines nest on ocean-exposed sandy shores
54 (e.g., turtles, birds) and are thought to use nest-site selection to increase clutch success, hatchling
55 survival, and ultimately fitness (Refsnider & Janzen 2010; Spencer 2002). Sandy shores include
56 distinct habitat types (dunes, non-vegetated beach, surf-zone), each with variable attributes and
57 subject to a variety of pressures (e.g. predators, people, urban development) (Meager et al. 2012;
58 Schlacher et al. 2014). Heterogeneity of the sandy beach environment across space and time
59 implies that reproductive success for these species might depend on their flexibility in finding
60 suitable nest sites.

61 Coastal birds are important contributors to sandy beach and dune ecosystems, transferring
62 resources between marine and terrestrial systems (Huijbers et al. 2015), providing critical
63 nutrient inputs (Sekercioglu 2006), and sometimes filling the role of apex consumers (Brown et
64 al. 2015). They also act as surrogates for beach and dune conservation and may be prime
65 indicators of beach condition (Maslo et al. in press; Schlacher et al. 2014). Despite their
66 significant role in ecosystem function and management, persistence of many coastal bird
67 populations is severely threatened by direct and indirect anthropogenic impacts (e.g., Brinker et
68 al. 2007; Dowding & Murphy 2001; Van De Pol et al. 2010). Viability of resident coastal bird
69 populations is limited by failed nesting attempts (i.e. clutch failure) and high chick mortality

70 resulting from predation, flooding, and human disturbance (Erwin et al. 2006; Martín et al. 2015;
71 Tjørve & Underhill 2008).

72 For decades, researchers have examined potential factors influencing clutch survival of
73 coastal birds. They have identified a suite of egg and chick predators across several taxonomic
74 groups (Brooks et al. 2014; Ivan & Murphy 2005), evaluated links between direct and indirect
75 human interference and reproductive failure (Ruhlen et al. 2003; Weston & Elgar 2007), and
76 quantified the impact of high tides and storms on reproductive success (Brooks et al. 2013; Pol et
77 al. 2010). These studies were generally performed on small sections of coastline under relatively
78 uniform management and human use regimes (e.g., Dutton et al. 2005; Neuman et al. 2004), and
79 were assumed to experience similar conditions (e.g., Hardy & Colwell 2012; Morse et al. 2006).
80 Thus, we have a good understanding of threats coastal ground-nesting birds encounter at local
81 scales. For example, nests on beaches that are used heavily for human recreation may experience
82 higher direct mortality from trampling, crushing, and vandalism (Brooks et al. 2013; Pol et al.
83 2010); these areas might also support higher predator densities due to the provision of additional
84 food resources from garbage (Yasué & Dearden 2006). Nests on uninhabited beaches may
85 experience less chronic human disturbance, but be more vulnerable to severe acute human
86 impacts due to a lack of regulatory presence and enforcement (Brown et al. 2015; del Viejo et al.
87 2004). The suite of predators may also vary in response to variations in landscape connectivity,
88 habitat types and the presence of invasive species (Brown et al. 2015). While such studies are
89 important in understanding local threats and informing local management, it remains unclear
90 whether outcomes are more broadly applicable.

91 Conservation practitioners have at their disposal a portfolio of management options that
92 can be applied on a site-by-site basis (Maslo & Lockwood 2009; Neuman et al. 2004).

93 Management at a given site can improve reproductive success of a target species, although it can
94 be costly (e.g. Hecht & Melvin 2009). Further, managers must continuously monitor changing
95 site conditions to determine when and how to appropriately intervene (Cohen et al. 2016).
96 Mitigation of all threats places a heavy burden on beach-nesting bird managers, who are already
97 constrained for time and resources, and such efforts may be fruitless if nests are lost to flooding.
98 Importantly, even the most effective management at the local scale does not guarantee
99 population viability. Understanding the pressures reducing clutch success at a regional scale may
100 relieve some of the management burden by allowing managers to prioritize threat mitigation
101 within or across regions. Identifying the relative importance of the generalized predictors of
102 clutch failure across a regional scale may also increase population-level benefits of management.
103 Managers would increase both their confidence in deciding appropriately where and when to
104 apply specific interventions, as well as the efficiency with which management is implemented.

105 Determination of clutch fate of beach-nesting birds historically has been elusive (Ivan &
106 Murphy 2005; Mabee 1997), preventing the identification of generalized predictors of clutch
107 failure. Few studies investigate clutch survival over spatial scales that are large enough to
108 encompass different environmental conditions or gradients in anthropogenic pressures. To
109 address this gap, we examined beach-nesting bird clutch fate (using a model system of shorebird
110 nests and eggs) along 180 km of coastline selected to encompass a diversity of
111 geomorphological, anthropogenic, and predator environments. We identified the primary causes
112 of clutch loss among a suite of putative factors at a regional scale. By definitively assigning
113 clutch fate to a set of artificial nests distributed across varying beach habitats and examining an
114 exhaustive list of predictor variables hypothesized to influence clutch failure, we determined the

115 relative importance of predation, flooding, and human disturbance on the probability of clutch
116 loss.

117

118 **STUDY AREA**

119 We purposefully selected four study sites within the region of southeast Queensland, Australia
120 that differed in the types of likely mortality agents present, including two sand-barrier islands
121 (Bribie and Moreton Islands) and two mainland sections of the ocean-exposed coastline (Noosa
122 North Shore and Sunshine Coast; Fig. 1). Sites were separated between 12 and 27 km. The main
123 differences between sites were the presence of exotic and feral predators (red foxes, *Vulpes*
124 *vulpes*; dogs, *Canis familiaris*); the intensity of development and human use; and the types of
125 recreational activities (camping, fishing, off-road vehicles; Table 1). Basic habitat attributes were
126 similar between sites, all being ocean-exposed sandy beaches of intermediate morphodynamic
127 state, backed by generally low (typically 2 - 4 m) foredunes of 10 - 40 m width (Brown et al.
128 2015; Huijbers et al. 2015; Huijbers et al. 2013; Schlacher & Thompson 2012; Schlacher &
129 Thompson 2013; Schlacher & Thompson 2013; Schlacher et al. 2015a). Local geomorphology
130 varied, however, along these coasts (e.g. width and steepness of dunes and beaches), so the study
131 area also provided an opportunity to examine the influence of these variables on clutch survival.

132

133 **METHODS**

134 We experimentally mimicked nests of red-capped plovers, *Charadrius ruficapillus*, and
135 monitored with camera traps the fate of clutches (after Cardilini et al. 2013). Red-capped plovers
136 are widely distributed across Australia and breed in Queensland throughout the year, with a peak
137 in spring and summer (Marchant & Higgins 1993). Females typically lay two eggs of cryptic

138 colouration in a shallow scrape in the sand. For beach-nesting individuals, most nests are located
139 on the upper beach and in foredunes, either in the open, under vegetative cover, or next to
140 flotsam objects (Ekanayake et al. 2015a; Marchant & Higgins 1993).

141 To mimic plover clutches, we placed two European quail (*Coturnix japonica*) eggs in
142 shallow sand scrapes; quail eggs are approximately the same size, weight and colour as red-
143 capped plover eggs and have been used previously for these type of experiments (Maguire et al.
144 2010). We used survival of the model clutches as an index of real clutch survival, whilst
145 acknowledging that the presence and behaviour of an incubating adult may alter absolute clutch
146 loss rates (Smith et al. 2007). However, there is no a priori expectation that systematic bias
147 amongst regions would result from using experimental (modal) clutches. We obtained unwashed
148 quail eggs from a local hatchery 1 - 2 days prior to field deployment and handled them as little as
149 possible. The quail eggs used in this experiment were 32.5 ± 0.13 (SE) mm long and 24.8 ± 0.07
150 mm wide, and weighed 10.8 ± 0.10 g (real Red-capped Plover eggs are 30.42 ± 0.15 mm long
151 and 22.42 ± 0.07 mm wide; n = 73 Unpubl. Data).

152 **Model Clutch Survival Experiments**

153 We ran experiments during the late summer and early autumn of 2015 (Moreton Island: 31 Jan –
154 07 Feb; Noosa North Shore: 3 - 9 March; Bribie Island: 13 – 19 March; Sunshine Coast: 27 Apr
155 – 1 May). We placed nests approximately 800 m apart along the shore to minimize the
156 possibility of the same predator depredating more than one nest sequentially, whilst still
157 achieving adequate replication and dispersion within each region. We aimed for equal replication
158 levels at each site, but due to logistical constraints (travel times, access) the number of
159 experimental units varied between 27 and 38, with a total of 132 nests for the entire study (Table
160 2).

161 We positioned model nests to mimic natural plover nesting habitat (Lomas et al. 2014),
162 using the following criteria: i) position on the beach: on the upper part of the unvegetated beach
163 above the spring tide drift line near the base of the dunes (narrow strip of accumulated wrack
164 deposited by swash), in the fore-dune area (the dune slope above the lowest vegetation line up to
165 the first crest), or in the dune area (landward of the top of the fore-dune); ii) microhabitat
166 exposure: under vegetative cover, in the open next to flotsam, or in the open at least 2 m away
167 from flotsam; iii) microhabitat topography: in a hollow/swale/depression, or on a mound/ridge.
168 We randomly assigned nests to each nest locations category using a randomisation function in
169 Microsoft Excel, which was reapplied until we achieved 'reasonable' balance of nests between
170 factor levels to enable subsequent analysis. We determined the placement of the clutch
171 perpendicular to the water's edge by walking to the midpoint of the dune or fore-dune at
172 predetermined GPS coordinates and selecting the nearest location that met the randomly
173 allocated microhabitat criteria. For beach nests, we used the upper beach just below the fore-dune
174 to most closely mimic the location of real plover nests (Lomas et al. 2014; Maslo et al. 2011). To
175 allow equal chances for predation from both diurnal and nocturnal predators, we deployed half
176 the nests in the early morning and the other half just after sunset. There was no significant
177 difference ($p = 0.79$) in depredation between nests deployed near sunrise (24%) and those
178 deployed near sunset (26%).

179 We then monitored nests for a 5-day period with a digital passive infrared (PIR) motion
180 sensor camera (Scoutguard SG560Z-8M) concealed within 1 - 2 m of each nest, checking daily
181 for signs of predation. Camera operations followed protocols developed for beach scavengers
182 (Huijbers et al. 2015; Lomas et al. 2014). All work was conducted under Animal Ethics Permit
183 No. AN/A/14/84 issued by the University of the Sunshine Coast, and the Scientific Purposes

184 Permits WITK14608214 and WISP14609114 issued by the Queensland Government Department
185 of Environment and Heritage Protection.

186

187 **Environmental Variables**

188 We measured a suite of microhabitat attributes for each experimental nest. We recorded
189 vegetation characteristics as three complementary variables: i) small-scale (1-m² quadrat) plant
190 cover (%) centred at the scrape (digital photograph and Coral Point Count (CPCe) software); ii)
191 height and distance of vegetation nearest to nest (measuring tape); and iii) dune-wide vegetation
192 cover (line intercept along transects extending from the base of the foredune to the landward
193 edge of the feasible (potential) plover nesting habitat. We used a theodolite to measure four
194 complementary metrics that described the local geomorphology: i) distance and elevation of the
195 nest relative to the storm drift-line (visible as an accumulation of wrack on the upper beach near
196 the dunes); ii) distance and elevation relative to the seaward base of the foredune (defined as
197 distinct rise in the angle of the beach-face); iii) 'exposure' defined as the elevation of the nest
198 relative to the nearest two profile survey points along the beach-dune transect; and iv) dune
199 dimensions (max. dune ridge height, width of the dune field). We obtained distances of nests
200 from the nearest creek, rocky headland, and house using Google Earth. To index the type and
201 intensity of human activity, we counted (once every day during nest and camera checks) the
202 number of campsites, swimmers, fishers, and dog walkers during approximately 10 minutes
203 within 100 m of each experimental nest. Data collection occurred between 0700-1100 hours
204 consistently across all deployments. To account for potential differences in human use of shores
205 with respect to weekends, every site was sampled at least once during the weekend and four
206 times during the week.

207 We gathered wave data from wave-rider buoys operated by the Queensland Government
208 (<http://www.qld.gov.au/environment/coasts-waterways/beach/monitoring/>), using recordings
209 from the Brisbane buoy because it was close to the sites and contained the longest and most
210 complete time-series for the region. Wave heights differed significantly (ANOVA, $P < 0.005$)
211 among sites (Fig. 2).

212

213 **Data Analysis**

214 To identify the most important predictors of clutch fate, we first built a conditional inference tree
215 using the party package in the statistical programming environment R (Hothorn et al. 2006; R
216 Core Team 2014). This routine works by testing the hypothesis that the response variable clutch
217 fate, discrete with 5 levels: intact; flooded; depredated; disturbed by people; or other (covered by
218 sand, or unknown) is independent of the predictors. If this hypothesis is rejected, the routine
219 selects the predictor that has the strongest association with the response and splits the data in two
220 so as to best represent this association. The routine is then repeated recursively on each of the
221 resulting nodes, stopping in each case only when the null hypothesis of no association cannot be
222 rejected. The strength of this approach lies in the fact that because all predictors are reused at
223 each instance of binary partitioning, the routine can reveal not only important predictors, but also
224 statistical interactions and possible nonlinearity.

225 We supplemented the results of the conditional inference tree with conventional
226 generalized linear modeling (glm) for predated clutches. Clutches lost to flooding were almost
227 perfectly explained by the inference tree, while there were too few observations for disturbance
228 by people to support a more detailed analysis. Our glm employed a logit link function (binomial
229 family) and modeled clutch fate (depredated = 1; intact = 0) as a function of all available

230 unconfounded predictors. In this sense, we considered geographic coordinates, presence of
231 humans (including off-road vehicles and dogs), and both wave and tide metrics confounded with
232 region, because there was no within-region variation for any of these predictors. We used a
233 forward stepwise model-building approach based on the AIC corrected for finite sample sizes
234 (AICc), considering only main effects. This decision to omit interactions was based on initial
235 inspection of the data, which indicated a lack of replication and/or contrast in data across
236 potential interaction cells (especially those associated with site). Following the forward stepwise
237 selection process, we interrogated the final model by recalculating the AICc for all possible
238 combinations of variables used in model building (Quinn & Keough 2002) and used multi-model
239 inference to determine the relative importance of predictors based on their summed Akaike
240 weights (Burnham et al. 2011; Symonds & Moussalli 2011). Finally, we used standard log-
241 likelihood ratio tests to simplify the model by dropping predictors one at a time, starting with the
242 least important, until only significant terms ($\alpha = 0.05$) remained.

243

244 **RESULTS**

245 **Causes of Model Clutch Loss and Spatial Variability**

246 Flooding and depredation were the main causes of clutch failure, accounting for 27% and 25% of
247 all nests lost, respectively. Of the 132 nests deployed, 45 (34%) survived the full 5-day
248 experimental exposure period, 32 were depredated, 35 were lost due to flooding, and 7 were
249 destroyed by people (Table 3). Crows were the main predator, accounting for 75% of all
250 depredated clutches; red foxes accounted for 19% of depredated nests, whilst a single clutch each
251 was eaten by a ghost crab and a snake (Table 3). Red foxes visited a further eight nests at the
252 Noosa North Shore and Sunshine Coast, but they did not consume or detect the clutches in these

253 instances. A domestic dog trampled one clutch, and nine clutches were buried by wind-blown
254 sand.

255 Overall clutch survival differed significantly among sites (Mantel Cox test, Chi square =
256 20.26, df 3, $P \leq 0.001$; Fig. 3). Clutches placed on the Noosa North Shore survived longest and
257 in highest numbers compared with all other sites (Mantel - Cox min. $P = 0.039$; min. Hazard
258 Ratio - North Shore: Other Site = 0.40, 95% CI = 0.19 - 0.72). Survival patterns were
259 comparable for nests placed at Bribie Island and the Sunshine Coast (Mantel - Cox $P = 0.96$;
260 Hazard Ratio – Bribie Island: Sunshine Coast = 0.98, 95% CI = 0.53 - 1.81). Clutches on
261 Moreton Island had significantly lower survival rates than those on the Sunshine Coast ($P = 0.02$,
262 Hazard Ratio – Moreton: Sunshine Coast = 1.97; 95% CI = 1.12 - 3.45) but were comparable to
263 those on Bribie Island ($P = 0.27$; Hazard Ratio - Moreton: Bribie Island. = 1.37, 95% CI = 0.79 -
264 2.37).

265 The conditional inference tree (Fig. 4) strongly resolved distance from the drift line as a
266 significant ($P < 0.001$) predictor of flooding. Thirty-four of the 35 flooded nests in the study
267 were located on the upper beach above the spring. Site was a strong predictor of fate of the
268 remaining 97 clutches ($P = 0.011$). At mainland sites (Noosa North Shore and Sunshine Coast),
269 most of the 50 clutches not situated low on the shore remained intact ($n = 34$) for the duration of
270 the study, with the remainder depredated ($n = 9$), disturbed by people ($n = 6$), or lost to other
271 causes ($n = 1$). The group of nests from Bribie and Moreton Islands that was not lost to flooding
272 was further split on the basis of dune height ($P = 0.023$). Of the 31 nests located where dunes
273 were smaller than 2.49 m in height, more than half were destroyed by predators ($n = 17$). By
274 contrast, where dunes were taller than 4.5 m, only 3 of the 12 nests were lost to predators
275 (Fig. 4).

276 The forward stepwise binomial glm identified site, distance to nearest creek, dune height
277 and distance to nearest vegetation as the most important predictors (in order of addition to the
278 additive model) of depredation. Subsequent multi-model inference provided a slightly different
279 prioritization (relative importance of predictors based on their summed Akaike weights in
280 parentheses): site (1.00); dune height (0.77); distance to nearest vegetation (0.72); and distance to
281 nearest creek (0.69). Log-likelihood ratio tests indicated that removing distance to nearest creek
282 from the model did not cause a significant deterioration in model fit (Δ Deviance = 2.369, Δ DF =
283 1, $p = 0.124$), but that the subsequent removal of distance to nearest vegetation did cause the fit
284 to deteriorate significantly (Δ Deviance = 4.634, Δ DF = 1, $p = 0.031$). The final predictive model
285 therefore included main effects for region, dune height, and distance to nearest vegetation, and
286 explained 31.3% of the null deviation.

287 Coefficients from the final model indicate that at average values for dune height and
288 distance to nearest vegetation for each site, probability of depredation was significantly higher
289 than would be expected by chance at Bribie Island, significantly lower than would be expected
290 by chance at Noosa North Shore, but no different from null expectation at either Moreton Island
291 or the Sunshine Coast. The odds of depredation declined ($P = 0.010$) by a factor of 0.33 for every
292 metre of dune height and increased ($p = 0.036$) by a factor of 1.01 for every additional metre
293 away from the nearest vegetation (Table 3, Fig. 5).

294

295 **DISCUSSION**

296 Our broad-scale evaluation of the relative importance of multiple drivers of clutch loss on
297 beaches suggests that predation and flooding are important causes of clutch failure in a regional
298 context. Contrary to expectations that predation pressure is particularly strong on human-

299 dominated beaches (Seneviratne et al. 2012), predation across the entire study region was high,
300 even at sites with no or little human development. Specifically, corvids were responsible for the
301 majority of predated nests, complementing the suite of local-scale studies that increasingly
302 demonstrate corvids as the primary cause of clutch loss in beach- and ground-nesting birds
303 (Ekanayake et al. 2015b; Madden et al. 2015). As human commensals, corvids have rapidly
304 expanded their global population, with the highest densities occurring in areas of significant
305 urbanization (Hardy & Colwell 2012; Lauro & Tanacredi 2002; Rees et al. 2015b). Corvids are
306 highly mobile, moving readily between natural and highly urbanized areas (Whisson et al. 2015),
307 and their impact on reproductive success can be extreme (Burrell & Colwell 2012; Lima 2009).
308 While corvid densities are typically higher in urbanized areas (Marzluff et al. 2001; Rees et al.
309 2015a), the spillover effect of increased corvid recruitment has cascading effects on the avian
310 species in periurban environments (Marzluff et al. 2001). A troubling aspect of intense corvid
311 depredation is the limited and hitherto unconfirmed effectiveness of management responses
312 available. Very few studies examine the effects of corvid management on breeding bird
313 productivity, and they report small or equivocal effects (Forys et al. 2015; Neatherlin & Marzluff
314 2004; Velasco 2015).

315 Our results indicate that predation risk is higher for nests occurring in low-lying dunes
316 away from vegetation, and the biological explanation for this phenomenon remains unclear.
317 Corvids typically land within 1 m of the nest and approach on foot, or they discover nests while
318 walking around open substrate (Forys et al. 2015; Velasco 2015). Therefore, it is possible that
319 corvids, as visual predators (Ekanayake et al. 2015b), are less able to detect or access nests in
320 thicker vegetation (Rees et al. 2015b). Nest placement in shorebirds is partly about survival of
321 the clutch, but also about survival of the parents (Gillis et al. 2012; Tieleman et al. 2008); early

322 detection of incoming predators enables adults to survive to re-clutch multiple times within a
323 season and/or breed over several or many subsequent seasons (Dowling & Weston 1999; Lomas
324 et al. 2014). There may also be sublethal stress effects of incubating nests away from cover
325 (Amat & Masero 2004).

326 The sizeable proportion of clutches that failed due to flooding emphasized the severity of
327 flooding as a threat to coastal ground-nesting birds (Pol et al. 2010; Van De Pol et al. 2010).
328 Although many of the flooded nests in this study occurred during stormy weather on the
329 Sunshine Coast (53%) and Moreton Island (45%), we found little evidence that the type of large
330 wave occurrences that led to clutch losses in 2015 were atypical events. The number of days in
331 which maximum wave height exceeded the 90th percentile of historical records for the first five
332 months of each year ($n = 17$ days) was not significantly different from the mean of 14.6 days in
333 the previous 14 years, with only four years (2001, 2008, 2009, 2013) exceeding values recorded
334 in 2015 (Figure 2). Similarly, wave heights exceeded the top 1% of the historical record on only
335 a single day during the present study. The impact of storm or high tide events can be catastrophic
336 to bird reproduction, particularly if storms occur late in the incubation period when there is little
337 time for re-nesting. There exists considerable uncertainty about when storms will arise, where
338 they will be most severe, and for how long habitats will be impacted (Hemer et al. 2013; IPCC
339 2013; Schlacher et al. 2015b), suggesting that assessment of flood risk for beach-nesting birds is
340 imperfect (Lomas et al. 2014). Human-mediated flood risk abatement, if feasible, may be of
341 great importance to population viability.

342 Human disturbance accounted for the loss of ≤ 9 clutches at any site and only 11% across
343 the entire region, illustrating the relatively weak influence of this source of failure on beach-
344 nesting bird reproductive success. Human presence in the vicinity of a nest was not related to the

345 probability of clutch loss to direct human causes, as would be expected. In fact, we found no
346 significant effect of dogs, camping, off-road vehicles or proximity to development on the
347 probability of a nest being disturbed. These results suggest that passive management of human
348 disturbance (i.e. symbolic fencing, signage) is effective in reducing anthropogenic impacts to
349 beach-nesting birds in a regional context. Where human disturbance of nesting birds is severe in
350 a specific location, localized management can address the problem (del Viejo et al. 2004; Ruhlen
351 et al. 2003; Weston & Elgar 2007).

352

353 **CAVEATS**

354 The results described here result from the placement of model clutches within suitable plover
355 habitat. Model clutches are used extensively in research and when implemented carefully can
356 reveal important ecological patterns and processes (Berry & Lill 2003). We acknowledge beach-
357 nesting birds theoretically select nesting sites to reduce the risks of clutch loss, perhaps basing
358 their choice in part on previous nesting experiences. We also recognise that model clutches are
359 not associated with incubator behaviour, which either can be protective (i.e. defence) or may
360 render clutches more vulnerable to predation (e.g. visual and scent cues) (Ekanayake et al.
361 2015a). Indeed, model clutch studies are enlightening in terms of physical destruction of the eggs
362 (e.g. Buick and Paton 1983), but they shed no light on the impacts of disturbance (disruption of
363 incubation which may reduce egg viability), even though disturbance to breeding shorebirds is
364 considered a conservation threat (Maslo et al. 2012; Meager et al. 2012; Powell & Collier 2000;
365 Quinn et al. 1996; Schlacher et al. 2013; Weston et al. 2014). In a review of 80 studies, (Major &
366 Kendal 1996) report that artificial nests underestimate actual survival of real nests, while
367 cameras on nests either do not affect or slightly increase clutch survival (Richardson et al. 2009;

368 Sanders & Maloney 2002). Ekanayake et al. (2015a; 2015b) also used model clutches on a study
369 of red-capped plovers in southern Victoria and confirmed the comparability of natural and model
370 clutches in identifying egg predators.

371 Model nests also permit otherwise infeasible studies to be performed. While common,
372 widespread nesting species may enable the study of real nests in some areas to address some
373 research questions (none were available on coasts in subtropical Australia). However, this would
374 represent a biased research effort because studies would be confined to species apparently coping
375 well with prevailing conditions; traditional yet abandoned habitats could not be assessed for
376 threats. Artificial nests permit an examination of egg predation risk in areas of suitable but often
377 unoccupied habitat, as we have done here. Calibration of this model egg study with real clutch
378 fate and survival (impossible here because no such data, which is strictly comparable, are
379 available) would not only be confirmatory, but would shed light on the utility of studies that use
380 model eggs to guide real nest management. We also note that survival estimates of real clutches
381 are often biased (e.g. Nichols *et al.* 1984).

382 **MANAGEMENT IMPLICATIONS**

383 As coastal bird populations continue to decline globally (e.g., Rodrigues et al. 2004), the
384 enhancement of reproductive success through active management plays an increasingly critical
385 role in species' persistence. Our analysis suggests that management of human disturbance
386 through symbolic fencing, signage, and regulatory measures across a region is likely enough to
387 effectively mitigate anthropogenic impacts. The significant influence of predation and flooding
388 on clutch loss at the regional scale demonstrates that actively addressing these threats will lead to
389 increased viability of beach-nesting bird populations. Predator management is typically
390 performed at the site scale and can be effective in the short-term, and targeted application may

391 increase clutch success (e.g., exclosures, electric fencing, removal; Maslo & Lockwood 2009;
392 Neuman et al. 2004). However, predator mortality may elicit a compensatory response (i.e.
393 increased reproduction) in affected populations and new individuals can quickly occupy open
394 niche space (Harding et al. 2001; Smith et al. 2010). Both corvids and foxes can disperse great
395 distances from their natal territories (Dekker et al. 2001; Marzluff et al. 2001), targeting source
396 populations within the region may have trickle-down benefits to beach-nesting birds. Predation
397 management, however, may be unnecessary and inefficient if nests are highly vulnerable to
398 flooding.

399 Managing flood risk of clutches is likely difficult to implement. Possibilities include
400 modifying habitats to maintain nesting areas at higher elevations, for example through dredge
401 spoil or ecologically sensitive beach nourishment. Identification of the sites within a region
402 where habitat modifications have the highest likelihood of providing benefits to the population
403 will be critical. At the location scale, moving nests or raising them before flood events can also
404 be attempted. In flood prone locations, a tractable strategy may to assess a clutch's vulnerability
405 to flooding (Haig et al. 2005; Sanders & Maloney 2002; Thomas et al. 2006) and then manage
406 failure risk for the subset of nests that are not flood prone (this also preserves any learnt,
407 adaptive, nest placement whereby birds learn to avoid flood prone habitats).

408 In short, conservation of coastal bird species in the presence of multiple threats and
409 measureable uncertainty requires practitioners to make hard choices about management
410 intervention. An understanding of the driving forces of clutch success at a regional scale offers
411 managers some confidence in developing strategies that promote the viability of coastal bird
412 populations (Meager et al. 2012) rather than mitigating impacts on a site-by-site or location-by-
413 location basis.

414

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416 We especially thank I. Franks for many hours help in the field and contributions by Prof.
417 Ischlberg. Nicholas Horrocks (and two anonymous reviewers) commented on the manuscript in a
418 most helpful and constructive manner.

419

420 **LITERATURE CITED**

- 421 Amat JA, and Masero JA. 2004. Predation risk on incubating adults constrains the choice of
422 thermally favourable nest sites in a plover. *Animal Behaviour* 67:293-300.
- 423 Berry L, and Lill A. 2003. Do predation rates on artificial nests accurately predict predation rates
424 on natural nests? The effects of nest type, egg type and nest-site characteristics. *Emu*
425 103:207-214.
- 426 Brinker DF, McCann JM, Williams B, and Watts BD. 2007. Colonial-nesting seabirds in the
427 Chesapeake Bay region: Where have we been and where are we going? *Waterbirds*
428 30:93-104.
- 429 Brooks GL, Sanders FJ, Gerard PD, and Jodice PG. 2013. Daily survival rate for nests and
430 chicks of least terns (*Sternula antillarum*) at natural nest sites in South Carolina.
431 *Waterbirds* 36:1-10.
- 432 Brooks GL, Sanders FJ, Gerard PD, and Jodice PG. 2014. Daily survival rate for nests of Black
433 Skimmers from a core breeding area of the southeastern USA. *The Wilson Journal of*
434 *Ornithology* 126:443-450.
- 435 Brown MB, Schlacher TA, Schoeman DS, Weston MA, Huijbers CM, Olds AD, and Connolly
436 RM. 2015. Invasive carnivores alter ecological function and enhance complementarity in
437 scavenger assemblages on ocean beaches. *Ecology* 96:2715–2725.
- 438 Burnham KP, Anderson DR, and Huyvaert KP. 2011. AIC model selection and multimodel
439 inference in behavioral ecology: some background, observations, and comparisons.
440 *Behavioral Ecology and Sociobiology*:1-13.
- 441 Burrell NS, and Colwell MA. 2012. Direct and indirect evidence that productivity of Snowy
442 Plovers *Charadrius nivosus* varies with occurrence of a nest predator. *Wildfowl* 62:204-
443 223.
- 444 Cardilini AP, Weston MA, Nimmo DG, Dann P, and Sherman CD. 2013. Surviving in sprawling
445 suburbs: suburban environments represent high quality breeding habitat for a widespread
446 shorebird. *Landscape and urban planning* 115:72-80.

- 447 Cohen JB, Hecht A, Robinson KF, Osnas EE, Tyre AJ, Brinker DF, Davis C, Hake M, Johnson
448 L, King E, Kocek A, Maslo B, and Melvin SM. 2016. Structured decision making for the
449 use of predator exclosures to recover a threatened species, the Atlantic Coast piping
450 plover. *Ecosphere*.
- 451 Dekker JJ, Stein A, and Heitkönig I. 2001. A spatial analysis of a population of red fox (*Vulpes*
452 *vulpes*) in the Dutch coastal dune area. *Journal of Zoology* 255:505-510.
- 453 del Viejo AM, Vega X, González M, and Sánchez J. 2004. Disturbance sources, human
454 predation and reproductive success of seabirds in tropical coastal ecosystems of Sinaloa
455 State, Mexico. *Bird Conservation International* 14:191-202.
- 456 Dowding JE, and Murphy EC. 2001. The impact of predation by introduced mammals on
457 endemic shorebirds in New Zealand: a conservation perspective. *Biological Conservation*
458 99:47-64.
- 459 Dowling B, and Weston MA. 1999. Managing a breeding population of the Hooded Plover
460 *Thinornis rubricollis* in a high-use recreational environment. *Bird Conservation*
461 *International* 9:255-270.
- 462 Dutton DL, Dutton PH, Chaloupka M, and Boulon RH. 2005. Increase of a Caribbean
463 leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest
464 protection. *Biological Conservation* 126:186-194.
- 465 Ekanayake KB, Weston MA, Nimmo DG, Maguire GS, Endler JA, and Küpper C. 2015a. The
466 bright incubate at night: sexual dichromatism and adaptive incubation division in an
467 open-nesting shorebird. *Proceedings of the Royal Society of London B: Biological*
468 *Sciences* 282:20143026.
- 469 Ekanayake KB, Whisson DA, Tan LXL, and Weston MA. 2015b. Intense predation of non-
470 colonial, ground-nesting bird eggs by corvid and mammalian predators. *Wildlife*
471 *Research* 42:518-528. <http://dx.doi.org/10.1071/WR15080>
- 472 Erwin RM, Sanders GM, Prosser DJ, and Cahoon DR. 2006. High tides and rising seas: potential
473 effects on estuarine waterbirds. *Studies in Avian Biology* 32:214.
- 474 Forsys EA, Hopkins D, Ingham P, Miller M, and Gluckman L. 2015. Do Effigies Deter Fish
475 Crows Hunting in a Black Skimmer Colony Mid-Season? *Southeastern Naturalist*
476 14:635-640.
- 477 Gillis H, Gauffre B, Huot R, and Bretagnolle V. 2012. Vegetation height and egg coloration
478 differentially affect predation rate and overheating risk: an experimental test mimicking a
479 ground-nesting bird. *Canadian Journal of Zoology* 90:694-703.
- 480 Haig SM, Ferland CL, Cuthbert FJ, Dingledine J, Goossen JP, Hecht A, and McPHILLIPS N.
481 2005. A complete species census and evidence for regional declines in Piping Plovers.
482 *Journal of Wildlife Management* 69:160-173.

- 483 Harding EK, Doak DF, and Albertson JD. 2001. Evaluating the Effectiveness of Predator
484 Control: the Non-Native Red Fox as a Case Study. *Conservation Biology* 15:1114-1122.
- 485 Hardy MA, and Colwell MA. 2012. Factors influencing Snowy Plover nest survival on ocean-
486 fronting beaches in coastal northern California. *Waterbirds* 35:503-656.
- 487 Hecht A, and Melvin SM. 2009. Expenditures and effort associated with recovery of breeding
488 Atlantic Coast Piping Plovers. *The Journal of wildlife management* 73:1099-1107.
- 489 Hemer MA, Fan Y, Mori N, Semedo A, and Wang XL. 2013. Projected changes in wave climate
490 from a multi-model ensemble. *Nature climate change* 3:471-476.
- 491 Hothorn T, Hornik K, and Zeileis A. 2006. Unbiased recursive partitioning: A conditional
492 inference framework. *Journal of Computational and Graphical Statistics* 15:651-674.
- 493 Huijbers CM, Schlacher TA, Schoeman DS, Olds AD, Weston MA, and Connolly RM. 2015.
494 Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the
495 loss of raptors from urbanized sandy beaches. *Diversity and Distributions* 21:55-63. DOI:
496 10.1111/ddi.12282
- 497 Huijbers CM, Schlacher TA, Schoeman DS, Weston MA, and Connolly RM. 2013. Urbanisation
498 alters processing of marine carrion on sandy beaches. *Landscape and Urban Planning*
499 119:1– 8.
- 500 IPCC. 2013. Climate change 2013: the physical science basis. Contribution of Working Group I
501 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. *Long-*
502 *term Climate Change: Projections, Commitments and Irreversibility*, Cambridge Univ
503 *Press, Cambridge, UK, and New York.*
- 504 Ivan JS, and Murphy RK. 2005. What preys on piping plover eggs and chicks? *Wildlife Society*
505 *Bulletin* 33:113-119.
- 506 Lauro B, and Tanacredi J. 2002. An examination of predatory pressures on Piping Plovers
507 nesting at Breezy Point, New York. *Waterbirds* 25:401-409.
- 508 Lima SL. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under
509 the risk of predation. *Biological reviews* 84:485-513.
- 510 Lomas SC, Whisson DA, Maguire GS, Tan LX, Guay P-J, and Weston MA. 2014. The influence
511 of cover on nesting red-capped plovers: a trade-off between thermoregulation and
512 predation risk?
- 513 Mabee TJ. 1997. Using eggshell evidence to determine nest fate of shorebirds. *The Wilson*
514 *Bulletin*:307-313.
- 515 Madden CF, Arroyo B, and Amar A. 2015. A review of the impacts of corvids on bird
516 productivity and abundance. *Ibis* 157:1-16.

- 517 Maguire GS, Stojanovic D, and Weston MA. 2010. Conditioned taste aversion reduces fox
518 depredation on model eggs on beaches. *Wildlife Research* 36:702-708.
- 519 Major RE, and Kendal CE. 1996. The contribution of artificial nest experiments to understanding
520 avian reproductive success: a review of methods and conclusions. *Ibis* 138:298-307.
- 521 Marchant S, and Higgins PJ. 1993. *Handbook of Australian, New Zealand and Antarctic Birds,*
522 *Volume 2 (Raptors to Lapwings)*. Melbourne: Oxford University Press.
- 523 Martín B, Delgado S, Cruz Adl, Tirado S, and Ferrer M. 2015. Effects of human presence on the
524 long-term trends of migrant and resident shorebirds: evidence of local population
525 declines. *Animal Conservation* 18:73-81.
- 526 Marzluff JM, McGowan KJ, Donnelly R, and Knight RL. 2001. Causes and consequences of
527 expanding American Crow populations. *Avian ecology and conservation in an*
528 *urbanizing world*: Springer, 331-363.
- 529 Maslo B, Burger J, and Handel SN. 2012. Modeling foraging behavior of piping plovers to
530 evaluate habitat restoration success. *The Journal of wildlife management* 76:181-188.
- 531 Maslo B, Handel SN, and Pover T. 2011. Restoring Beaches for Atlantic Coast Piping Plovers
532 (Charadrius melodus): A Classification and Regression Tree Analysis of Nest-Site
533 Selection. *Restoration Ecology* 19:194-203.
- 534 Maslo B, Leu K, Faillace C, Weston MA, Pover T, and Schlacher TA. in press. Selecting
535 umbrella species for conservation: A test of habitat models and niche overlap for beach-
536 nesting birds. *Biological Conservation*.
- 537 Maslo B, and Lockwood JL. 2009. Evidence-based decisions on the use of predator exclosures in
538 shorebird conservation. *Biological Conservation* 142:3213-3218.
- 539 Meager JJ, Schlacher TA, and Nielsen T. 2012. Humans alter habitat selection of birds on ocean-
540 exposed sandy beaches. *Diversity & Distributions* 18:294-306. DOI: 10.1111/j.1472-
541 4642.2011.00873.x
- 542 Morse JA, Powell AN, and Tetreau MD. 2006. Productivity of Black Oystercatchers: Effects of
543 recreational disturbance in a national park. *The Condor* 108:623-633.
- 544 Neatherlin EA, and Marzluff JM. 2004. Responses of American crow populations to
545 campgrounds in remote native forest landscapes. *Journal of Wildlife Management*
546 68:708-718.
- 547 Neuman KK, Page GW, Stenzel LE, Warriner JC, and Warriner JS. 2004. Effect of mammalian
548 predator management on Snowy Plover breeding success. *Waterbirds* 27:257-263.
- 549 Pol Mvd, Vindenes Y, Sæther B-E, Engen S, Ens BJ, Oosterbeek K, and Tinbergen JM. 2010.
550 Effects of climate change and variability on population dynamics in a long-lived
551 shorebird. *Ecology* 91:1192-1204.

- 552 Powell AN, and Collier CL. 2000. Habitat use and reproductive success of Western Snowy
553 Plovers at new nesting areas created for California Least Terns. *The Journal of wildlife*
554 *management*:24-33.
- 555 Quinn GP, and Keough MJ. 2002. *Experimental design and data analysis for biologists*. New
556 York: Cambridge University Press.
- 557 Quinn J, Morris R, Blokpoel H, Weseloh D, and Ewins P. 1996. Design and management of bird
558 nesting habitat: tactics for conserving colonial waterbird biodiversity on artificial islands
559 in Hamilton Harbour, Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*
560 53:45-57.
- 561 R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for
562 Statistical Computing, Vienna, Austria. . <http://www.R-project.org/>
- 563 Rees J, Webb J, Crowther M, and Letnic M. 2015a. Carrion subsidies provided by fishermen
564 increase predation of beach-nesting bird nests by facultative scavengers. *Animal*
565 *Conservation* 18:44-49.
- 566 Rees JD, Webb JK, Crowther MS, and Letnic M. 2015b. Ravens are a key threat to beach-
567 nesting birds.
- 568 Refsnider JM, and Janzen FJ. 2010. Putting eggs in one basket: ecological and evolutionary
569 hypotheses for variation in oviposition-site choice. *Annual Review of Ecology, Evolution,*
570 *and Systematics* 41:39-57.
- 571 Richardson T, Gardali T, and Jenkins SH. 2009. Review and meta-analysis of camera effects on
572 avian nest success. *The Journal of wildlife management* 73:287-293.
- 573 Rodrigues AS, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LD, da
574 Fonseca GA, Gaston KJ, and Hoffmann M. 2004. Effectiveness of the global protected
575 area network in representing species diversity. *Nature* 428:640-643.
- 576 Ruhlen TD, Abbott S, Stenzel LE, and Page GW. 2003. Evidence that human disturbance
577 reduces Snowy Plover chick survival. *Journal of Field Ornithology* 74:300-304.
- 578 Sanders MD, and Maloney RF. 2002. Causes of mortality at nests of ground-nesting birds in the
579 Upper Waitaki Basin, South Island, New Zealand: a 5-year video study. *Biological*
580 *Conservation* 106:225-236. [http://dx.doi.org/10.1016/S0006-3207\(01\)00248-8](http://dx.doi.org/10.1016/S0006-3207(01)00248-8)
- 581 Schlacher TA, Meager JJ, and Nielsen T. 2014. Habitat selection in birds feeding on ocean
582 shores: landscape effects are important in the choice of foraging sites by oystercatchers.
583 *Marine Ecology* 35:67-76.
- 584 Schlacher TA, Nielsen T, and Weston MA. 2013. Human recreation alters behaviour profiles of
585 non-breeding birds on open-coast sandy shores. *Estuarine, Coastal and Shelf Science*
586 118:31-42.

- 587 Schlacher TA, and Thompson L. 2012. Beach recreation impacts benthic invertebrates on ocean-
588 exposed sandy shores. *Biological Conservation* 147:123–132.
- 589 Schlacher TA, and Thompson L. 2013. Environmental control of community organisation on
590 ocean-exposed sandy beaches. *Marine and Freshwater Research* 64:119-129. DOI
591 10.1071/MF12172
- 592 Schlacher TA, and Thompson L. 2013. Spatial structure on ocean-exposed sandy beaches:
593 faunal zonation metrics and their variability. *Marine Ecology Progress Series* 478:43–55.
594 Doi: 10.3354/meps10205
- 595 Schlacher TA, Weston MA, Lynn D, Schoeman DS, Huijbers CM, Olds AD, Masters S, and
596 Connolly RM. 2015a. Conservation gone to the dogs: when canids rule the beach in small
597 coastal reserves. *Biodiversity and Conservation* 24:493-509. doi: 10.1007/s10531-014-
598 0830-3
- 599 Schlacher TA, Weston MA, Schoeman DS, Olds AD, Huijbers CM, and Connolly RM. 2015b.
600 Golden opportunities: A horizon scan to expand sandy beach ecology. *Estuarine, Coastal
601 and Shelf Science* 157:1-6.
- 602 Sekercioglu CH. 2006. Increasing awareness of avian ecological function. *Trends Ecol Evol*
603 21:464-471.
- 604 Seneviratne SI, Nicholls N, Easterling D, Goodess CM, Kanae S, Kossin J, Luo Y, Marengo J,
605 McInnes K, and Rahimi M. 2012. Changes in climate extremes and their impacts on the
606 natural physical environment. *Managing the risks of extreme events and disasters to
607 advance climate change adaptation*:109-230.
- 608 Smith PA, Gilchrist H, and Smith JN. 2007. Effects of nest habitat, food, and parental behavior
609 on shorebird nest success. *The Condor* 109:15-31.
- 610 Smith RK, Pullin AS, Stewart GB, and Sutherland WJ. 2010. Effectiveness of predator removal
611 for enhancing bird populations. *Conservation Biology* 24:820-829.
- 612 Spencer R-J. 2002. Experimentally testing nest site selection: fitness trade-offs and predation risk
613 in turtles. *Ecology* 83:2136-2144.
- 614 Symonds MRE, and Moussalli A. 2011. A brief guide to model selection, multimodel inference
615 and model averaging in behavioural ecology using Akaike's information criterion.
616 *Behavioral Ecology and Sociobiology*:1-9.
- 617 Thomas G, Lanctot R, and Székely T. 2006. Can intrinsic factors explain population declines in
618 North American breeding shorebirds? A comparative analysis. *Animal Conservation*
619 9:252-258.
- 620 Tieleman BI, Van Noordwijk HJ, and Williams JB. 2008. Nest site selection in a hot desert:
621 trade-off between microclimate and predation risk. *The Condor* 110:116-124.

- 622 Tjørve KMC, and Underhill L. 2008. Influence of disturbance and predation on breeding success
623 of the African Black Oystercatcher, *Haematopus moquini*, on Robben Island, South
624 Africa. *Waterbirds* 31:83-96.
- 625 Van De Pol M, Ens BJ, Heg D, Brouwer L, Krol J, Maier M, Exo KM, Oosterbeek K, Lok T,
626 and Eising CM. 2010. Do changes in the frequency, magnitude and timing of extreme
627 climatic events threaten the population viability of coastal birds? *Journal of Applied*
628 *Ecology* 47:720-730.
- 629 Velasco VN. 2015. Investigation of Non-Lethal Electric Shock on American Crows as a Predator
630 Aversion Treatment for Reducing Depredation on California Least Tern Eggs.
- 631 Weston MA, and Elgar MA. 2007. Responses of incubating hooded plovers (*Thinornis*
632 *rubricollis*) to disturbance. *Journal of Coastal Research*:569-576.
- 633 Weston MA, Schlacher TA, and Lynn D. 2014. Pro-environmental beach driving is uncommon
634 and ineffective in reducing disturbance to beach-dwelling birds. *Environmental*
635 *Management* 53:999-1004.
- 636 Whisson DA, Weston MA, and Shannon K. 2015. Home range, habitat use and movements by
637 the little raven (*Corvus mellori*) in a coastal peri-urban landscape. *Wildlife Research*
638 42:500-508. <http://dx.doi.org/10.1071/WR15039>
- 639 Yasué M, and Dearden P. 2006. The potential impact of tourism development on habitat
640 availability and productivity of Malaysian plovers *Charadrius peronii*. *Journal of Applied*
641 *Ecology* 43:978-989.
- 642
- 643

644 Table 1. Comparison of study regions within SE-Queensland, Australia with respect to likely
645 causes of clutch mortality associated with shore- and dune-nesting birds. Assessments are based
646 on five years of field studies at these locations by TAS and MW.

Region	Foxes, Dogs, Cats	Off-road vehicles	Dune camping	Urban Development
Moreton Island	no	yes	yes	none
Bribie Island	yes	yes	limited	moderate
Noosa North Shore	yes	yes	yes	sparse
Sunshine Coast	yes	no	no	intense

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651 Table 2. Summary of fates after five days of experimental clutches on ocean-exposed beaches

652 and dunes at four study sites in southeast Queensland, Australia, during Jan.-May 2015.

Fate of Nest	Moreton Island	Noosa North Shore	Bribie Island	Sunshine Coast	Total
Carnivores					
Ghost crab		1 (3%)			1 (1%)
Torresian crow	10 (27%)	1 (3%)	12 (44%)	1 (3%)	24 (18%)
Red fox		2 (5%)		4 (13%)	6 (5%)
Snake		1 (3%)			1 (1%)
Carnivores all species	10 (27%)	5 (13%)	12 (44%)	5 (17%)	32 (24%)
Domestic dog				1 (3%)	1 (1%)
Flooded	17 (46%)	1 (3%)	1 (4%)	16 (53%)	35 (27%)
Intact	7 (19%)	27 (71%)	4 (15%)	7 (23%)	45 (34%)
People		5 (13%)	2 (7%)		7 (5%)
Sand burial	2 (5%)		7 (26%)		9 (7%)
Unknown	1 (3%)		1 (4%)	1 (3%)	3 (2%)
	37	38	27	30	132

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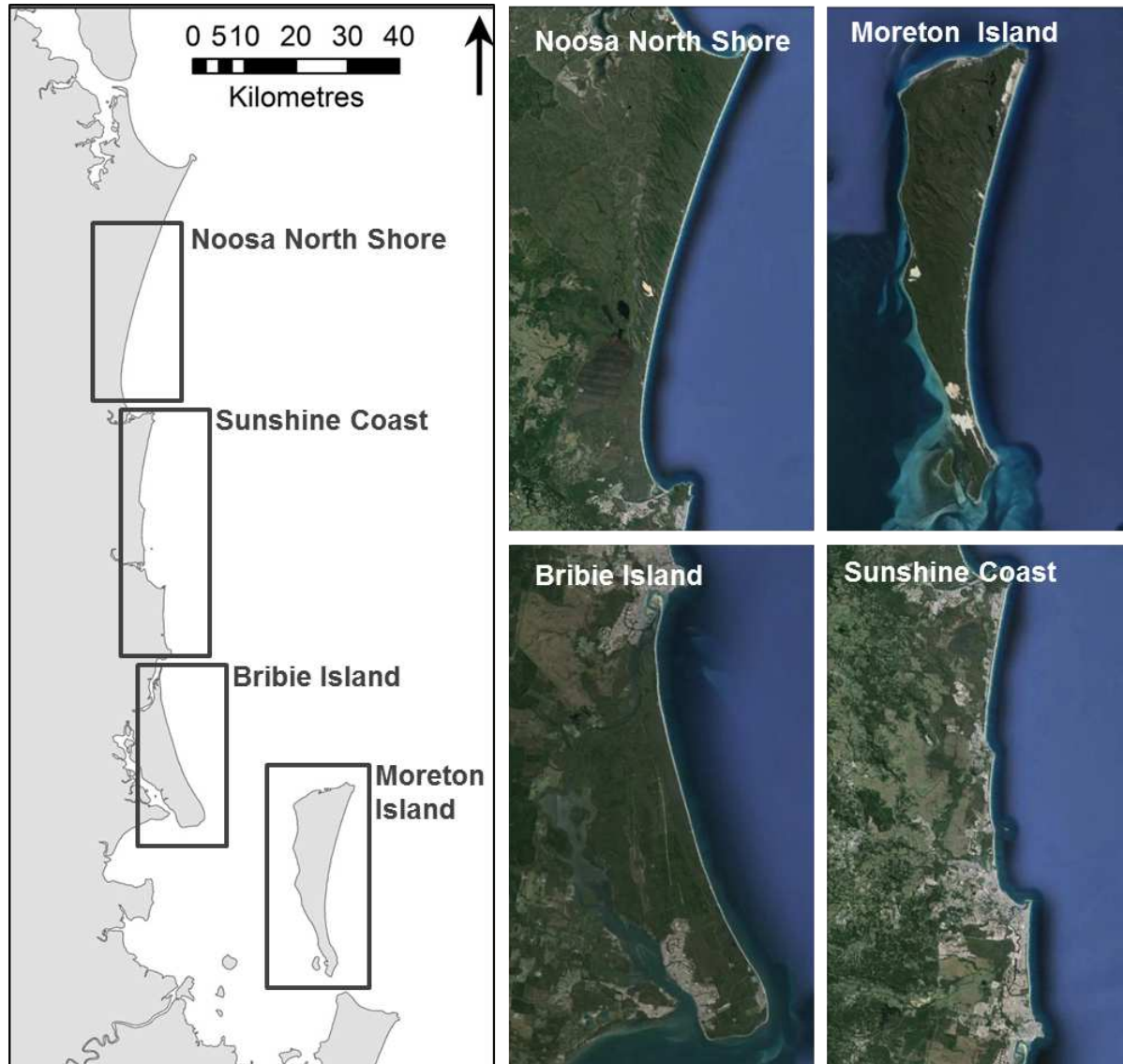
655 Table 3. Summary of final binomial generalized linear model used to predict the probability of
656 depredation for experimental nests placed in the four study regions within SE-Queensland,
657 Australia, 2015. Estimates for model coefficients refer to log-odds ratios and are additive on the
658 model intercept, which represents the log-odds of depredation at Bribie Island.
659

	Estimate	Std Err	z	p-value
(Intercept)	2.964	1.018	2.912	0.0036
Region Moreton Island	0.078	0.9738	0.081	0.9358
Region Noosa North Shore	-3.660	0.906	-4.041	5.33×10^{-05}
Region Sunshine Coast	-0.604	0.976	-0.619	0.5360
Dune Height (m)	-1.106	0.432	-2.561	0.0104
Dist. to Vegetation (m)	0.011	0.005	2.095	0.0362

Null deviance: 99.099 on 73 degrees of freedom
Residual deviance: 68.765 on 68 degrees of freedom
AIC: 80.765

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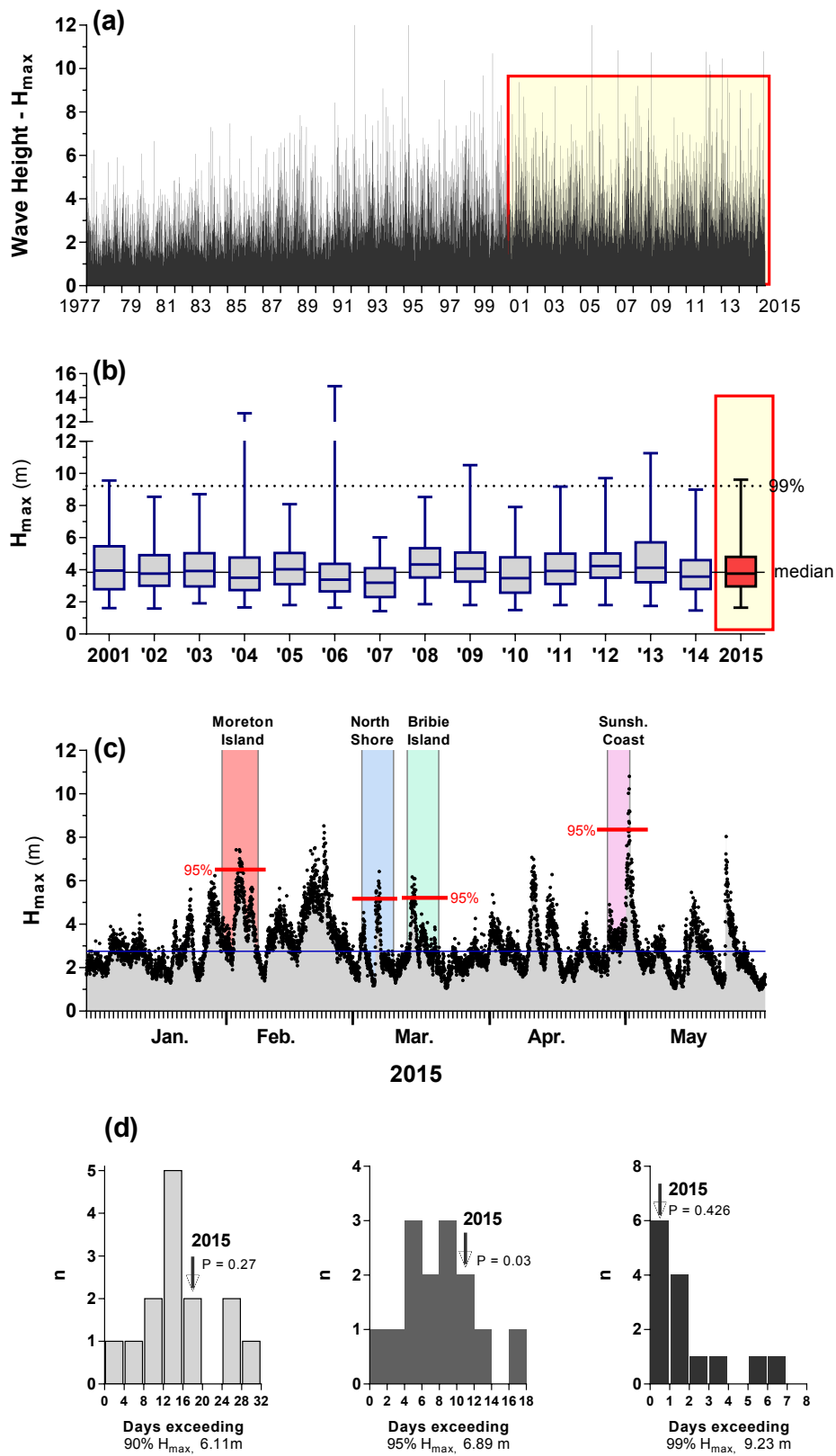
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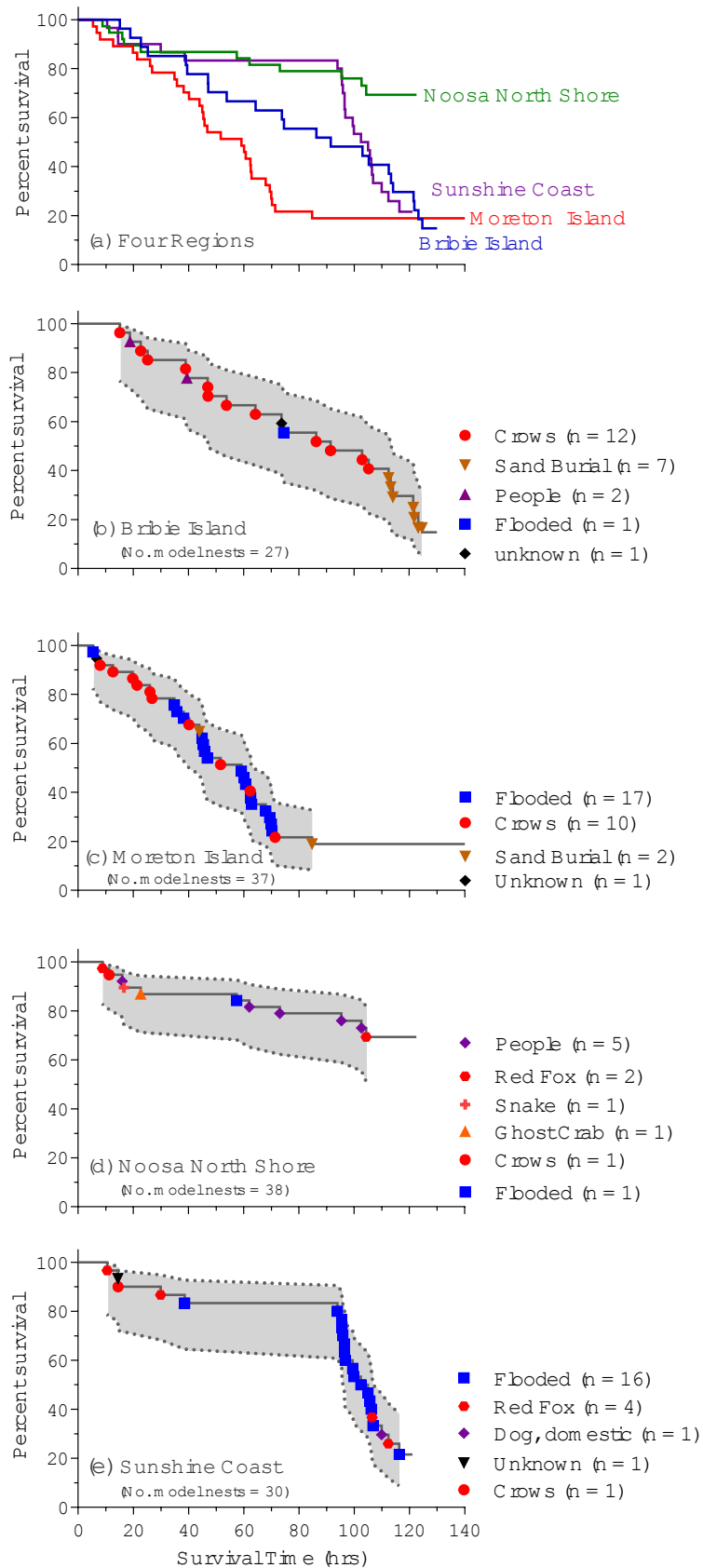
662

663 Figure 1. Location of study regions in southeast Queensland in Eastern Australia where we
664 monitored experimental nests on beaches and dunes on Moreton Island (n = 38), Bribie Island
665 (n = 27), the Noosa North Shore (n = 38), and the Sunshine Coast (n = 30) in early 2015. Image:
666 Google, 2015 Digital Globe.

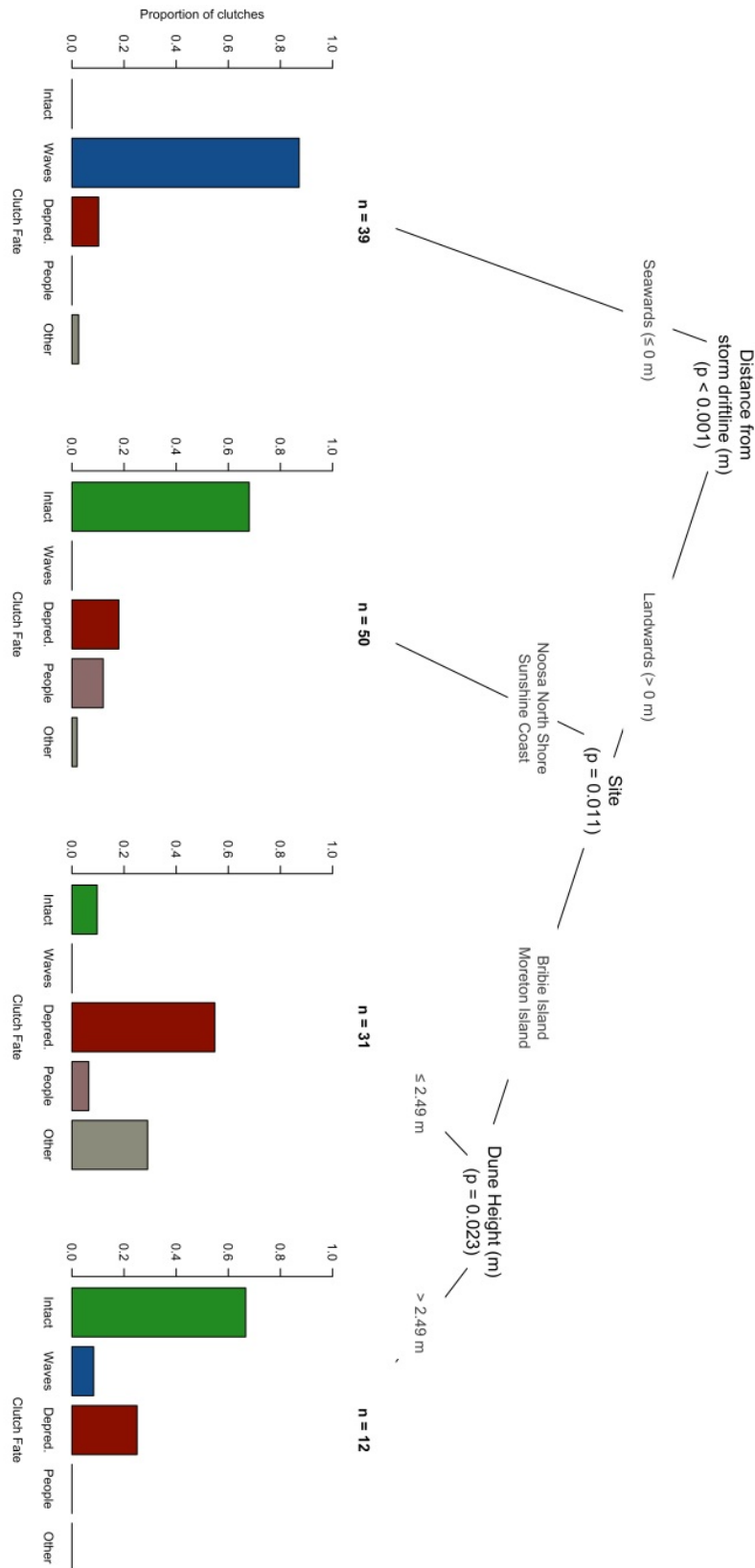
667



669 Figure 2. Wave height data recorded offshore (ca. 10 km) from the beaches on which
670 experiments in nest survival of shore- and dune-nesting plovers were conducted in early 2015
671 (cf. Fig. 1 for region locations), SE-Queensland, Australia. a) – longer-term record of maximum
672 wave height from 1977 to 2015. b) – Summary of maximum wave height for the first five
673 months of each year from 2001 to 2015 for which data at comparable recording frequency (30
674 min) were available; c) – maximum wave height during the study; d) – comparison of the
675 frequency of large wave events between 2015 and the period 2001 to 2014. Large wave events
676 are defined as days on which maximum wave height exceeded the 90th (left panel), 95th (centre
677 panel) or 99th (right panel) percentile of the historical record; p values refer to t-tests contrasting
678 the 2015 value with the mean of the preceding 14 years.
679



682 Figure 3.
 684 curves for: a)
 685 (Moreton
 688 Island, Noosa
 689 and the
 692 Coast,
 694 Australia)
 695 individual
 698 identified
 700 loss over the
 702 the
 704 in each
 705 (numbers in
 708 are the actual
 709 experimental
 712 attributed to a
 714 cause; shaded
 716 95%
 718 intervals of
 719
 720
 721
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Survival
 all sites
 Island, Bribie
 North Shore,
 Sunshine
 Queensland,
 and b - e)
 sites showing
 causes of nest
 time span of
 experiments
 region
 parentheses
 number of
 clutches lost
 specific
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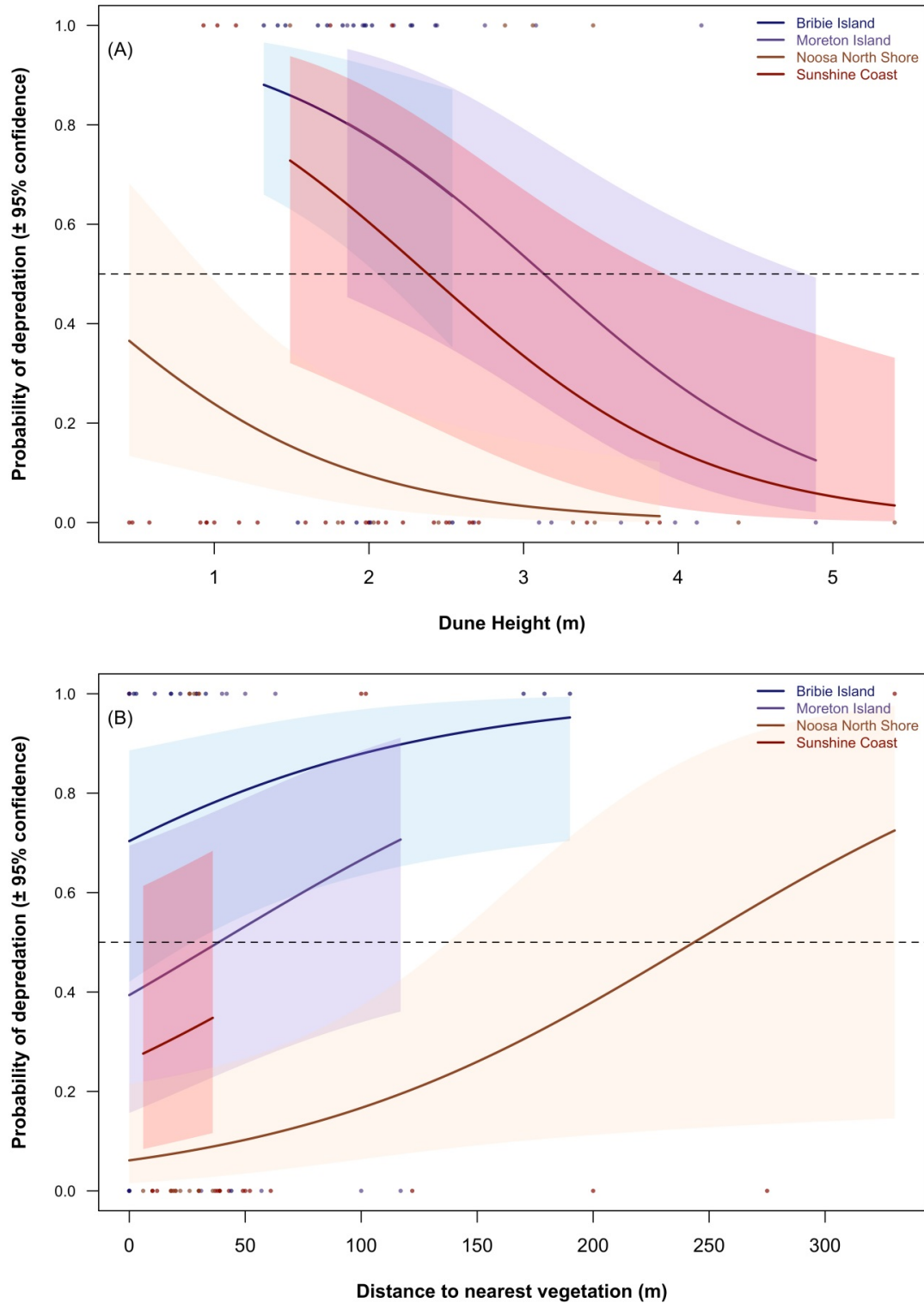
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745 Figure 4. Conditional inference tree indicating the primary predictors of each clutch fate category
746 for all experimental nests placed with the study region of SE-Queensland, Australia, 2015: intact,
747 flooded, depredated, disturbed by people, and other (buried by sand, unknown). Variables are
748 ranked based upon the strength of their association with specific clutch fates and their
749 quantitative values are split to best represent the relevant association.

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753 Figure 5. Influence of dune height and distance to nearest vegetation on the probability of
754 experimental clutch depredation across all study sites within SE-Queensland, Australia, 2015.
755 Shaded regions indicate 95% confidence intervals.